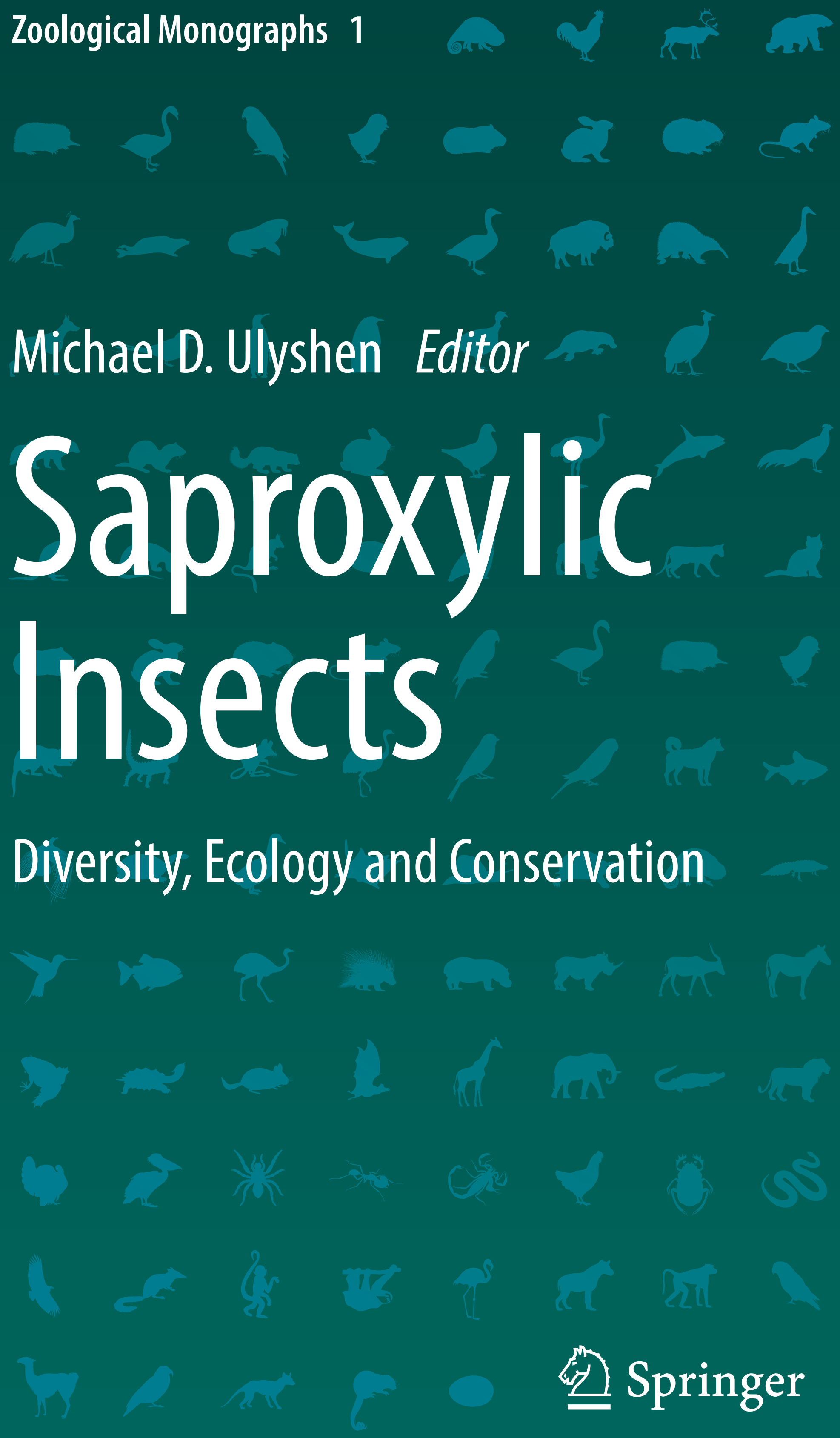

Zoological Monographs 1

Michael D. Ulyshen *Editor*

Saproxylic Insects

Diversity, Ecology and Conservation

Springer

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Volume 1

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Preface and Acknowledgments

About 6 years have passed since Stokland et al. published their excellent book on the "Biodiversity in Dead Wood," a review of saproxylic life from the European perspective. With contributions from 84 authors and reviewers from 21 countries, this volume strives to expand and build upon the foundation established by that work. The 25 chapters included here are in-depth considerations of prioritized topics but are united by several broad objectives that were communicated and agreed upon at the outset. These objectives include (1) incorporating information from tropical and subtropical forests, (2) recognizing the key roles social insects play in saproxylic assemblages, (3) highlighting some of the less commonly studied taxa, and (4) addressing the value of highly decomposed wood. If successful, this collective effort should result in a more global and holistic understanding of saproxylic insects including their diversity, ecology, and vulnerability to ongoing and emerging threats.

I am deeply grateful to Heike Feldhaar for inviting me to edit this book and to the many researchers who either wrote or cowrote chapters, served as reviewers, or provided images used in the preparation of figures. Reviews of individual chapters were provided by the following individuals, in alphabetical order: Keith Alexander (UK), Manfred Asche (Museum für Naturkunde, Germany), Susan Baker (University of Tasmania, Australia), Matthew Bertone (North Carolina State University, USA), Meredith Blackwell (Louisiana State University and University of South Carolina, USA), James Cane (USDA Agricultural Research Service, USA), Kevin Chase (University of Minnesota, USA), Natalie Clay (Louisiana Tech University, USA), Savel Daniels (Stellenbosch University, South Africa), Francesca Della Rocca (University of Pavia, Italy), Gary Dodson (Ball State University, USA), Brian Forschler (University of Georgia, USA), Reinhard Gaedike (Bonn, Germany, c/o Senckenberg Deutsches Entomologisches Institut, Germany), Alejandra García-López (University of Alicante, Spain), Simon Grove (Tasmanian Museum and Art Gallery, Australia), James Hammond (Canadian Forest Service, Canada), Ernst Heiss (Tiroler Landesmuseum, Innsbruck, Austria), Rob Higgins (Thompson Rivers University, Canada), Scott Horn (USDA Forest Service, USA), Jen-Pan Huang

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Finally, I would like to thank my family for their patience on nights and weekends when this project distracted me from them.

Athens, GA Michael D. Ulyshen

Contents

Part I Diversity

Part II Ecology

Part III Conservation

Part IV Methodological Advancements

Chapter 1
An Introduction to the Diversity, Ecology, and Conservation of Saproxylic Insects

Michael D. Ulyshen and Jan Šobotník

> *Thousands upon thousands of lives would cease and their races become extinct were it not for the occasional death of such a jungle giant as this.*
>
> Beebe (1925)

Abstract Much like flowering plants set the stage for an explosion of herbivore and pollinator diversity, the origin of dead wood in early Devonian forests (~400 mya) was followed by an incredible diversification of life, giving rise to some of the most successful morphological adaptations and symbioses on Earth. Approximately one third of all forest insect species worldwide depend directly or indirectly on dying or dead wood (i.e., saproxylic), with major functional groups including wood feeders, fungus feeders, saprophages, and predators. Although beetles and flies dominate saproxylic insect communities worldwide, other orders are represented by a wide variety of species as well, and the composition of these assemblages varies biogeographically. Most notably, termites (Blattodea) and the subsocial beetle family Passalidae are both largely restricted to the tropics where they play a major role in the decomposition process. The large body of European research linking declines of saproxylic insect diversity to reductions in the amount of dead wood and old trees across the landscape serves as a cautionary tale for researchers and land managers working in other parts of the world. The conservation of saproxylic insects everywhere can be promoted by efforts to provide an adequate amount and variety of dead wood and old trees across space and time. The preservation of old-growth forests is also critically important as they support relict populations of the most sensitive species. There is a strong need for research outside the boreal and temperate

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zones to develop a more global appreciation for the diversity and ecology of saproxylic insects and to inform management strategies for conserving these organisms in subtropical and tropical forests.

Although William Beebe made his observations of “the little people of bark and wood” in a South American rainforest, he could have reached this same conclusion from studying a recently fallen tree in any of the world’s forests. Indeed, approximately one third of all forest insect species are saproxylic, meaning they depend, either directly or indirectly, on dying or dead wood. Directly dependent species are those that consume parts of woody stems (i.e., bark, phloem, or wood) for food, whereas indirectly dependent species include those that feed on other wood-dependent species (e.g., wood-rotting fungi or other saproxylic organisms), require dead wood for nesting purposes, etc. In addition to the strictly dependent saproxylic species, a very large number of other invertebrates are known to benefit from the presence of dead wood in forests but do not require it. Such taxa include a wide variety of litter-dwelling invertebrates that concentrate near logs, hibernating insects that overwinter within the shelter provided by dead wood, soil feeders that encounter richer food sources underneath fallen wood, and predators that respond opportunistically to an abundance of prey in and around woody debris. While dying and dead wood represent some of the most critical resources to life in forests worldwide, only in the past few decades have researchers turned their attention to the importance of dead wood to biodiversity, with most work taking place in boreal or temperate forests. Moreover, although saproxylic insects are thought to provide some key ecosystem services, research on the value of these organisms to the resiliency and productivity of forests is only just beginning.

Early research on saproxylic insects focused primarily on the small fraction of saproxylic insects that pose a threat to forest health and reduce the marketability of timber products or are pests of wooden structures. In temperate zones, wood-boring beetles have received the most attention (Hickin 1963), whereas termites have long been the focus of study in the tropics. This difference in focus among regions reflects the uneven distribution of social insects, especially termites and ants, which generally become more abundant and diverse toward equator (King et al. 2013). Whereas termites are absent from boreal forests and are represented by just a handful of species in temperate forests, the number of species present at tropical forest locations ranges from several dozen to well over a hundred (Krishna et al. 2013). As a consequence of these patterns, the literature on the diversity and ecology of saproxylic insects is largely fragmented along taxonomic and geographic lines. Efforts to unite these bodies of knowledge are needed to achieve a more holistic understanding of saproxylic insects including how their diversity and functions may vary geographically.

This book represents an effort by researchers around the world to summarize the current state of knowledge about the diversity, ecology, and conservation of insect life in dying and dead wood. Because a comprehensive coverage of this vast topic is not possible within the covers of a single book, our main aims here include (1) uniting bodies of literature on social and nonsocial saproxylic insects that have, until now, existed in relative isolation from one another; (2) addressing a number of neglected topics including some less-studied orders or families of saproxylic insects, insects associated with highly decomposed woody substrates, and the diversity and ecology of wood-dwelling insect assemblages in tropical forests; and (3) providing the most up-to-date coverage of topics of particular ecological importance or interest to those making forest management decisions. Before further introducing the chapters that follow, it is worth taking a moment to consider the history of insect life in dead wood. Below we briefly discuss the origins and properties of woody plants, the origins and diversification of wood-dwelling insects, and a timeline of research on saproxylic insects.

1.1 Origins and Properties of Wood

1.1.1 Origins

Fossils of a small shrub-like plant similar to the genus *Psilophyton* from the early Devonian (~407 mya) represent the earliest known records of wood (Gerrienne et al. 2011). Although the evolution of wood is thought to have initially been driven by hydraulic constraints (Gerrienne et al. 2011), wood also proved to be an effective solution to the challenge of maintaining an upright growth form arising from competition for sunlight among plants (Cichan and Taylor 1990). The earliest known arborescent plants appeared in the middle Devonian, approximately 380 million years ago (Willis and McElwain 2002). By the late Devonian and Carboniferous, much of the Earth's land surface was covered in dense forests. These early forests consisted of a mixture of spore-producing and early seed-producing tree species (Stein et al. 2007; Willis and McElwain 2002). The spore producers included lycopsids (lycopods), sphenopsids (giant horsetails), filicopsids (ferns), cladoxylopsids, and progymnosperms (extinct), whereas the early seed producers included pteridosperms (seed ferns, extinct) and *Cordaites* (extinct). Pteridosperms would later give rise to the gymnosperms (cycads, ginkgos, and conifers) and angiosperms (flowering plants) that dominate modern forests (Frohlich and Chase 2007).

Vascular cambium arose multiple times in the evolution of plants (Cichan and Taylor 1990), and the tree lineages listed above differed in how wood was arranged within their stems. Many of these early trees possessed unifacial vascular cambium and only produced small amounts of secondary xylem. One highly successful but now-extinct genus of trees from the period, for instance, was *Lepidodendron*, a lycopod that grew up to 35 m tall and over a meter in trunk diameter (Scheckler 2001; Willis and McElwain 2002). Because the stems of *Lepidodendron* possessed unifacial cambium and produced little wood, most of their support came from an extremely thickened cylinder of bark. In contrast, other early trees, like most forest

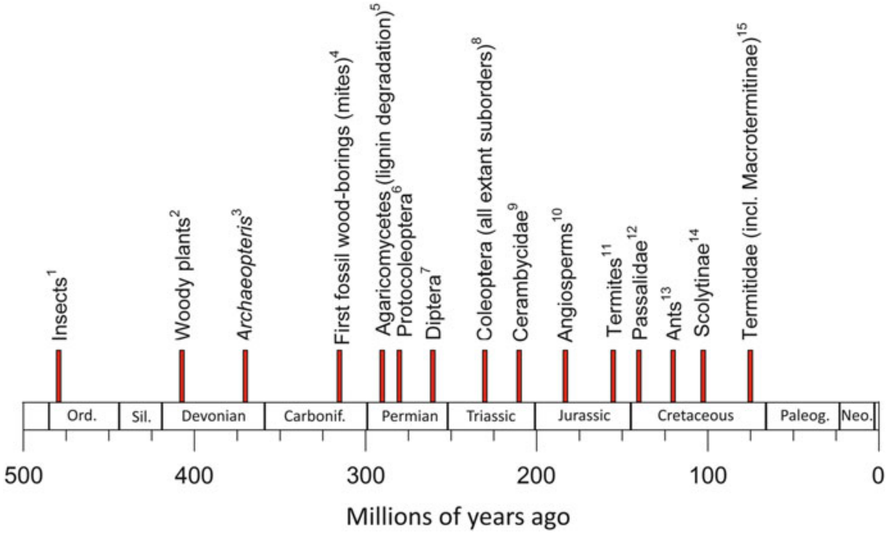

Fig. 1.1 Timeline showing major events in the history of saproxylic life (many of the dates given here represent median values from ranges reported in the literature). Superscripts refer to the following references: 1: Misof et al. (2014), 2: Gerrienne et al. (2011), 3: Willis and McElwain (2002), 4: Cichan and Taylor (1982), 5: Floudas et al. (2012), 6, 8, 11, 13, 15: Grimaldi and Engel (2005), 7: Bertone and Wiegmann (2009), 9: Wang et al. (2014), 10: Bell et al. (2010), 12: Scholtz and Chown (1995), 14: Hulcr et al. (2015)

trees living today, possessed bifacial cambium which produces secondary phloem in addition to secondary xylem. Although easily taken for granted in modern forests, the appearance of trees possessing bifacial vascular cambium was a major step in the evolution of plants (Spicer and Groover 2010) as well for arthropods and other organisms. The first such trees were progymnosperms such as *Archaeopteris*. These trees grew 10–30 m in height and produced thick woody stems similar in morphology to those of modern conifers (Meyer-Berthaud et al. 1999; Scheckler 2001). Perhaps due to their perennial lateral branches, deep-rooting structures, and megaphyllous leaves, *Archaeopteris*-dominated forests of the carboniferous and their fossils can be found worldwide (Willis and McElwain 2002). Thus a plausible approximate beginning of dead wood as an abundant and widespread resource was the appearance and rapid spread of *Archaeopteris* in the late Devonian 370 million years ago (Fig. 1.1).

1.1.2 Modern Wood Producers

Trees, woody shrubs, and lianas are the principle wood-producing plants in modern ecosystems. All extant species can be categorized as gymnosperms or angiosperms (flowering plants) depending on whether their seeds are "naked" or enclosed within ovaries. Gymnosperms are much older and consist of many fewer species than angiosperms. Tree forms include approximately 310 species of cycads, 1 ginkgo, and roughly 615 species of conifers. Although conifers such as pine, spruce, and fir still dominate forests in many regions and represent some of our most valuable timber trees, they have been largely displaced by angiosperms throughout much of the world. Angiosperms include many thousands of species and can be distinguished between monocots or dicots depending on whether their seeds contain one embryonic leaf (i.e., cotyledon) or two. Although some monocots such as palms, bamboo, and banana trees are arborescent, their stems lack vascular cambium and do not produce wood. Other nonwoody arborescent plants such as "tree ferns" also lack vascular cambium and are therefore not considered true trees (Thomas 2000).

1.1.3 Basic Growth Patterns and Products of Woody Stems

All modern wood-producing plants exhibit both primary (length) and secondary (girth) growth arising from the division of undifferentiated cells in special meristematic tissues. Primary growth occurs in apical meristems located at the tips of shoots and roots, whereas secondary growth occurs in the vascular cambium, a lateral meristem, between the bark and the wood. As mentioned previously, the vascular cambium in modern plants is bifacial, producing secondary phloem to the outside (i.e., the inner bark) and secondary xylem (wood) to the inside. A third type of meristem called the cork cambium contributes to the outermost layers of bark. The cork cambium first arises from parenchyma cells in the cortex (i.e., the outer layer of the stem) and later from parenchyma cells in older, nonfunctional layers of phloem (Wilson and White 1986). The walls of cells produced by this meristem become impregnated with wax and suberin, their protoplasts die, and their lumina become air-filled (Wilson and White 1986). These resulting layers of outer bark function to prevent water loss and protect underlying tissues from various external threats such as fire.

Though essential to the life of a plant, the phloem layer is so thin as to be easily overlooked when viewed in cross section (Fig. 1.2). The youngest innermost layers, often only 0.2–0.3 mm in width (Wilson and White 1986), are responsible for distributing organic substances produced in leaves throughout the rest of the plant and are particularly rich in sugars. Not surprisingly, therefore, a wide variety of organisms target these tissues in dying or recently dead trees (see Sect. 1.2.3.1). Phloem remains active in the transport of photosynthates for just a few years in most species. Older tissues become blocked by callose or crushed by the forces of continued cambial activity (Wilson and White 1986). Old layers of phloem gradually become incorporated into the outer bark.

Wood provides support for the plant and is responsible for conducting water and minerals upward from the roots. Successive layers of secondary xylem are often visible in cross section as distinct annual rings. These reflect changes in growth rate

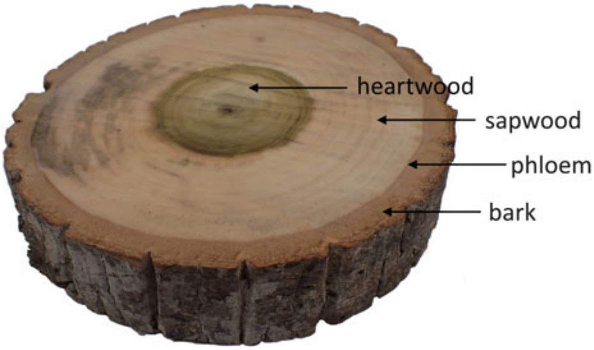

Fig. 1.2 Cross section of a woody stem (*Liriodendron tulipifera* L.)

and are most obvious in regions experiencing strong seasonality with respect to precipitation or temperature. In temperate regions, for instance, fast-growing wood produced early in the year (i.e., "early wood") is typically less dense (consisting of wider cells with thinner cell walls) and usually lighter in color than slow-growing "late wood" (Panshin and de Zeeuw 1970). By contrast, in relatively stable tropical regions where conditions change little over the course of the year, it is not uncommon for trees to lack clearly visible growth rings.

Many tree species produce heartwood which is often visible in cross section as a central core of darkened wood surrounded by younger sapwood (Fig. 1.2). Heartwood differs greatly from sapwood in several physical and chemical properties. Most notably, heartwood contains greater concentrations of "extractives," a variety of extraneous compounds including waxes, fatty acids, alcohols, steroids, higher carbon compounds, and resins which give it its dark color and have an inhibitory effect on decay (Rayner and Boddy 1988; Panshin and de Zeeuw 1970). These compounds are de novo synthesized (from materials stored in parenchyma cells) in a narrow transition zone in which ethylene levels are high and metabolic levels are increased (Rayner and Boddy 1988). In addition, tyloses often form in the heartwood of many hardwood tree species, thereby partially or completely blocking vessels. This reduces permeability (Panshin and de Zeeuw 1970) and causes heartwood to be drier and harder than sapwood and also more resistant to all kinds of decay (Cornwell et al. 2009 and references therein; Thomas 2000). Furthermore, nitrogen, phosphorus, and potassium concentrations are generally lower in the heartwood than in sapwood, although the concentrations of magnesium and calcium sometimes exhibit the opposite pattern (Meerts 2002). Although heartwood is much richer in defensive secondary metabolites compared to sapwood and its extracts have a clear inhibitory effect on most organisms (Noll et al. 2016), certain species of fungi, the "heart-rot fungi," specialize on heartwood and can play a central role in the creation of tree cavities (Thomas 2000; Rayner and Boddy 1988).

1.1.4 The Structure and Composition of Wood

Cells produced by the vascular cambium are either oriented parallel (i.e., “axial elements”) or perpendicular (i.e., “radial elements”) to the stem or root (Shigo 1984). The axial elements include vessels, tracheids, fibers, parenchyma, and resin ducts (Shigo 1984). As soon as the cellular contents of vessels and tracheids die, they become functional in water transport. Fibers have heavily lignified cell walls and provide a supportive function to the stem. They too are usually, but not always, dead at maturity. Parenchyma cells remain alive in functional wood (the wood becomes heartwood once they die) and store starch along with other compounds. Some of the substances stored by parenchyma cells are converted to defensive compounds that have an inhibitory effect on decay fungi and bacteria (Shigo 1984). The radial elements of wood include ray cells (primarily parenchyma) and resin ducts. The ray cells are arranged in vertical bands that divide the stem into sections. These divisions are not complete, however, as the bands of cells are not continuous throughout the length or across the width of the stem. These cells perform an important function in the radial transfer of nutrients from the outer bark to the inner parts of the wood. They also play a key role in tylose formation.

Wood (i.e., the walls of xylem cells) mostly consists of cellulose, hemicelluloses, and lignins although a wide variety of other less common compounds are present as well. The most common organic compound on Earth is cellulose, a polysaccharide consisting of a linear chain of approximately 500–14,000 β-glucose units that accounts for 40–45% of wood weight (Wilson and White 1986; Sjostrom 1993; Leschine 1995). Cellulose is an exceptionally strong molecule and plays an important role in cell wall structure. As discussed in later sections, very few organisms are capable of breaking the bonds between the β-glucose subunits, and this has given rise to numerous symbiotic relationships between saproxylic insects and microbes. Hemicelluloses are also polysaccharides, comprised of various *D*-pentose sugars forming branched polymers of up to 3000 units (Sjostrom 1993), and account for 20–40% of wood weight (Wilson and White 1986). Lignin, making up 20–35% of wood weight, is a heterogeneous biopolymer lacking a well-defined structure but consisting in general of phenylpropanoid units (*p*-hydroxyphenyl, guiacyl, syringyl, sinapyl, and others), all being aromatic cores with hydroxylated side chains linked together by C–C or ether bonds (Wilson and White 1986; Freudenberg and Nash 1968). Lignin plays a fundamental role in protecting cellulose and hemicelluloses from enzymatic attack. The large lignin molecules fill spaces between cellulose and hemicelluloses in cell walls, bonding predominantly with the latter (Jeffries 1987). Unlike cellulose and hemicellulose, lignin is hydrophobic which aids in water conduction (Wilson and White 1986). Together, cellulose, hemicelluloses, and lignin form a complex matrix generally referred to as lignocellulose.

The digestion of lignocellulose requires specialized enzymes: cellulases, hemicellulases, and ligninases. Three basic types of cellulases are needed to cleave the polymer into glucose units, and these are endo-β-glucanase (cleaving the internal bonds of cellulose), cellobiohydrolase (breaking usually two glucose units from the chain end), and β-glucosidases (splitting the glucose oligomers into monomers) (Lo et al. 2011). These cellulases can be organized into supramolecular complexes allowing cellulose to be fully digested (Bayer et al. 1998; Brune and Ohkuma 2011). Hemicellulases are digested by a wider range of less-specialized enzymes, due to their heterogeneous chemical nature and branched molecular pattern (Jeffries 1987). Ligninases include many diverse enzymes, peroxidases, phenoloxidases, and laccases, produced by many fungi, and also some bacteria and actinomycetes (Singh and Chen 2008; Sigoillot et al. 2012). Among microorganisms, fungi are the most important and conspicuous (i.e., often forming macroscopic structures like mycelia and fruiting bodies) organisms capable of digesting lignocellulose. Filamentous fungi are particularly effective at decomposing wood as they can quickly extend deep within the wood and can translocate water and nutrients between locations through their mycelia (Jeffries 1987). Three main wood-rotting fungal types, as summarized by Rayner and Boddy (1988), are as follows: (1) white rot fungi, which cause degradation of all basic units of wood (cellulose, hemicellulose, and lignin), are common in hardwoods and have a more tropical distribution; (2) brown (or red) rot fungi, which are incapable of degrading lignin, are primarily associated with conifers and have more of a northern distribution; and (3) soft rot fungi degrade cellulose and hemicellulose but cause less extensive degradation than brown rot and give the wood a more spongy consistency. Soft rot is largely confined to situations where white rot and brown rot are inhibited, such as wood saturated with water. Bacteria also play significant role in the process of wood degradation (Kim and Singh 2000) but, due to their small size and limited mobility, are typically more active in situations where mycelial fungi are less abundant (Rayner and Boddy 1988; Kim and Singh 2000). Examples of situations favoring bacterial activity include aquatic environments, tree wounds and sap flows, highly decomposed wood, and wood comminuted or egested by insects (Kim and Singh 2000; Ausmus 1977). Three recognized forms of bacterial decay, as summarized by Kim and Singh (2000), are as follows: (1) tunneling by bacteria that penetrate cell walls and appear to be capable of metabolizing lignin in addition to cellulose and hemicellulose; (2) erosion by bacteria present in wood cells that create troughs in the cell walls; and (3) cavitation by bacteria that is less well-known and apparently restricted to certain situations but involves forming cavities within the cell walls. Interestingly, fungi can digest wood in aerobic conditions, while other wood-digesting microorganisms are more often anaerobic, due to the need of protecting their extracellular enzymes from damage by oxidation (Leschine 1995). While fungi and bacteria are the primary decomposers in all ecosystems, other organisms known to produce the enzymes necessary to break down one or more compounds comprising the lignocellulose matrix include protozoa (e.g., ciliates or metamonads; Breznak 1982; Ohkuma et al. 2005; Leschine 1995) and examples from a few groups of Metazoa including Mollusca (e.g., *Haliotis*, *Mytilus*, or *Bankia*; Suzuki et al. 2003; Xu et al. 2001; Dean 1978), Nematoda (Smant et al. 1998), crayfish (Byrne et al. 1999), termites and other cockroaches (Lo et al. 2000; Watanabe et al. 1998), beetles (Girard and Jouanin 1999), and even certain sea squirts (Dehal et al. 2002).

In addition to being so recalcitrant, and despite being rich in energy content, wood is not a very nutritious resource compared to other plant tissues (e.g., leaves, flowers, seeds, etc.) and especially compared to animal tissues (Woodwell et al. 1975; Käärik 1974). The nitrogen content of wood, for instance, is only 0.03–0.1% by dry weight compared to 1–5% for living herbaceous tissues (Käärik 1974, and reference therein). Of the three major constituents of woody stems, phloem tends to be the most rich in sugars and nutrients followed by sapwood and heartwood (Woodwell et al. 1975). Readers interested in a much more detailed description of wood anatomy are referred to major textbooks on the subject such as Panshin and de Zeeuw (1970) or Wilson and White (1986).

1.1.5 Differences Between Gymnosperms and Angiosperms

It is worth briefly reviewing some important differences in the structure and composition of wood produced by gymnosperms and angiosperms. Gymnosperm wood is generally more uniform and consistent in structure among taxa than that of angiosperms (Wilson and White 1986). This is because the wood of gymnosperms consists almost entirely of tracheids, narrow, and elongated axial elements (commonly 100 times longer than wide) with highly lignified and thickened cell walls. These cells are responsible for providing structural support in addition to the conduction of water. Some gymnosperm genera (e.g., *Pinus*, *Picea*, *Larix*, and *Psedotsuga*) also possess resin canals which produce and carry resin for use in defense and wound response. Angiosperm wood, by contrast, contains a much more varied array of axial elements. These include tracheids, parenchyma, vessel elements, fiber tracheids, and fibers. In addition, these cell types appear in different proportions and in different arrangements among tree species (Wilson and White 1986). Unique to angiosperms, vessel elements are shorter and generally wider than tracheids. They are arranged end-to-end longitudinally to form water-conducting vessels. Vessels can be distributed uniformly within each growth ring (diffuse-porous trees), concentrated at the beginning of each tree ring (ring-porous trees) or some variation of this. Unlike the tracheids of gymnosperms, the tracheids and vessels of angiosperms provide little structural support. This function is instead performed by fibers, long needle-like cells with thick and heavily lignified walls. The mechanical strength of angiosperm wood is a function of its density which, in turn, is related to the proportion of fibers (Wilson and White 1986). Angiosperms produce a wide range of wood densities but on average produce denser wood than gymnosperms. The two categories of trees are therefore often referred to as "hardwoods" and "softwoods," respectively. It is also relevant to mention that gymnosperm wood tends to contain more lignin than angiosperm wood (Weedon et al. 2009) and generally has lower mineral nutrient concentrations including, most notably, nitrogen, potassium, and magnesium (Meerts 2002). Such differences have important implications for relative decay rates with the wood of gymnosperms decaying more slowly than that of angiosperms (Weedon et al. 2009).

1.1.6 Variety of Wood

Dead wood is a highly variable resource depending on a wide variety of intrinsic and extrinsic factors, and this in large part explains why it supports so many species of insects and other organisms. The diversification of woody plants over the past 400 million years has resulted in tens of thousands of species distributed unevenly around the world. There are more than 60,000 tree species in the world (Beech et al. 2017) as well as many other woody shrubs and lianas. Tropical forests contain the highest diversity of woody plants, with as many as 283 species per hectare in Peru alone (Phillips et al. 1994), whereas many temperate or boreal forests are dominated by just one or several species. There are important physical and chemical differences in the dead wood produced by these various species. The most obvious differences concern stem diameter which exhibits a wide range of interspecific variation as well as intraspecific variation (i.e., depending on tree age) and of course decreases with distance from the ground within individual trees. In addition, the structure of wood varies considerably among species, with major differences between the wood of gymnosperms and angiosperms (see Sect. 1.1.5).

In addition to these intrinsic differences in wood properties, extrinsic factors also play a vital role in increasing the variety of dead wood in forests. The degree of sun exposure experienced by a woody substrate, for example, can result in major differences in wood temperature and moisture content (Graham 1925). Moreover, the posture (standing or fallen) and vertical position of wood relative to the forest floor also has important implications for wood conditions (Fig. 1.3). The wood of standing dead trees (i.e., snags) or of dead branches attached to living trees is typically drier and decomposes more slowly than wood lying on the forest floor or dead roots belowground. It is not uncommon for a large proportion of dead wood volume to be standing or suspended. In old-growth forests in southern Finland, for instance, Siitonen et al. (2000) found that about 63% of dead wood volume consisted of logs, with the rest consisting of intact or broken snags. Similar results were obtained in managed stands (after excluding man-made dead wood), with only about 56% of the dead wood volume consisting of logs on the forest floor (Siitonen et al. 2000). Furthermore, a considerable amount of aboveground dead wood exists within the stems of aging trees. The decomposing cores of living trees often result in the formation of hollows which form a special habitat for many organisms when they become open to the outside (Micó 2018; see Chap. 21). One of the most distinguishing features of old-growth forests is the presence of very old large-diameter “veteran” trees (Siitonen et al. 2000; Spies et al. 1988; Franklin et al. 1981). These living but declining trees are of immense ecological value due to the tree cavities they provide as well as the many dead branches they contain within their crowns.

Another process contributing to dead wood variety concerns the chemical and physical changes wood experiences as it decomposes. Although a number of decay classification systems have been developed, three are of particular relevance with respect to the succession of insects (see Sect. 1.2.4). The first and shortest of these is

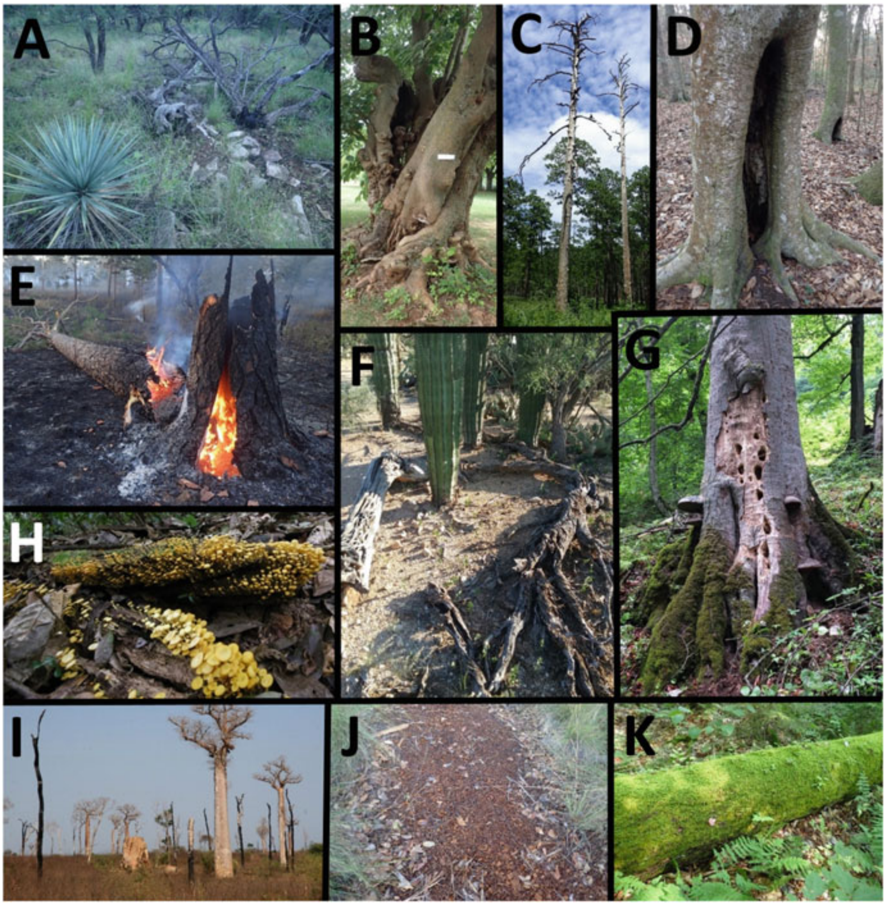

Fig. 1.3 Examples of dead wood variety. (**a**) Montane pine-juniper forest, Arizona; (**b**) veteran *Broussonetia papyrifera* (L.) L'Hér. Ex Vent. (a nonnative species) at Monticello, the historic home of Thomas Jefferson, Virginia; (**c**) dead *Pinus palustris* Mill. snags in old-growth longleaf pine forest, Georgia; (**d**) hollow-bearing *Magnolia grandiflora* L. in old-growth Beech-Magnolia forest, Florida; (**e**) *Pinus taeda* L. following a prescribed burn, Florida; (**f**) dead acacia (right) and the wood-like ribs of a saguaro cactus (left) in the Sonoran desert, Arizona; (**g**) dead *Fagus orientalis* Lipsky with fungal fruiting bodies in old-growth Caspian Hyrcanian forest, Iran; (**h**) highly decomposed wood with fungal fruiting bodies, Thailand; (**i**) charred wood in burned Baobab forest, western Madagascar; (**j**) thin layer of highly decomposed pine, Arizona; (**k**) moss-covered log in the Adirondacks, New York (Images (**a**–**f**), (**j**), and (**k**) by Michael Ulyshen, image (**h**) by Jan Šobotník, and images (**g**) and (**i**) by Martin Gossner)

the phloem phase which lasts until the nutritious phloem layer beneath the bark gets entirely degraded by insects and fungi. The second phase is the subcortical-space phase which begins as soon as the phloem layer becomes partly degraded and continues until the bark has completely fallen away from the wood. The final rot phase is the longest and does not end until the wood has become completely humified and incorporated into the soil. At the time of death, it is common for a tree to contain a wide variety of rot holes and pockets of decay. The process of falling to the ground often results in considerable fragmentation and breakage, and these damaged areas decay more rapidly than intact portions. Moreover, portions of the tree in contact with the soil decay more quickly than elevated portions due to differences in moisture levels. Different parts of the tree are colonized by different wood-decaying fungi, which results in diverse kinds of rot, and attacks by wood-feeding arthropods or scavenging vertebrates are similarly patchy. Sapwood usually decays more rapidly than heartwood, and early wood decays more quickly than late wood. It is clear from these and other influences that wood decay is not a homogeneous process, even within the same piece of wood. Although various classification schemes have been developed for assigning a piece of wood to a particular decay class, such designations overlook the inherent variability of wood decay in nature. Because it is not uncommon for a single log to contain wood at widely varying stages of decomposition, Pyle and Brown (1999) proposed that decomposing woody substrates are best thought of as falling along a continuum of decay class variability.

1.2 Origins and Diversity of Life in Dead Wood

Much like flowering plants set the stage for an explosion of pollinator and herbivore diversity (Grimaldi and Engel 2005), the appearance of dead wood in early Devonian forests was followed by a diversification of saproxylic insect life, giving rise to some of the most successful morphological adaptations (e.g., the elytra of beetles) and symbiotic relationships on Earth. Because wood provides relatively moist conditions during times of drought, relatively warm conditions during periods of cold, protection from many kinds of irradiation, and insulation from fire (Blackman and Stage 1924; Holmquist 1926, 1928, 1931; Jabin et al. 2004; Seibold et al. 2016a), the first invertebrates to utilize dead wood in early forests likely consisted primarily of refuge seekers and opportunists that only later became specialists of this new substrate.

1.2.1 Origins

It is clear from the fossil record and phylogenetics that life was slow to utilize woody debris in early forests. For example, fungi with the ability to degrade lignin (i.e., white rot) are thought to have originated roughly 120 million years after progymnosperms like *Archaeopteris* became major components of early forests (Fig. 1.1). This lag may explain the high rate of organic carbon accumulation during the intervening Carboniferous period (Floudas et al. 2012) and underscores the recalcitrance of lignocellulose as well as the low nutritional quality of wood. The borings of insects and other arthropods provide the earliest and best fossil evidence for animal life in dead wood. Frass-filled oribatid mite burrows in petrified *Cordaites* wood from the Lower-Middle Pennsylvanian (Carboniferous) represent the earliest records of wood-boring arthropods (Cichan and Taylor 1982). Indeed, oribatid mites appear to have been the pioneering wood-boring arthropods for millions of years until major wood-boring insect groups arose in the Permian (Kellogg and Taylor 2004; Labandeira et al. 1997). Larger diameter frass-filled galleries in petrified glossopterid wood from the Permian (Zavada and Mentis 1992) may represent the earliest fossil evidence of insect activity in dead wood, possibly attributable to beetles (Labandeira et al. 2001). The earliest beetle-like insects are thought to have originated soon after the *Agaricomycetes* [but see Toussaint et al. (2017)] and were likely wood feeders, much like modern Archostemata (e.g., Cupedidae and Micromalthidae) which belong to the basal-most suborder of extant beetles (Grimaldi and Engel 2005; Yan et al. 2017). Borings within conifer-like wood from the Middle Permian represent the first evidence of wood-boring beetles, tentatively attributed to Permocupedidae, an extinct family of beetles ancestral to Archostemata (Naugolnykh and Ponomarenko 2010). Late Permian fossil beetle galleries analogous to those of modern bark beetles, but preceding scolytines by well over 100 million years, were recently discovered in China (Feng et al. 2017). They were presumably made by an extinct early lineage of Polyphaga and represent the earliest known evidence of subsocial behavior in saproxylic insects. The first eusocial animals on Earth were termites which also originated as wood feeders in the late Jurassic (Bourguignon et al. 2015). By the time termites and ants appeared on the scene, the diversity of beetles we know today was largely in place (Grimaldi and Engel 2005). There can be little doubt that the arrival of these social insects resulted in profound changes to saproxylic food webs, however, especially in tropical forests where the highest diversity and abundance of termites and ants are found.

1.2.2 Insect Diversity

The total number of saproxylic insect species worldwide remains far from known (Stokland et al. 2012), and this is also true for most regions of the world. Progress continues to be limited by a shortage of taxonomic knowledge although molecular tools can be expected to resolve many current problem areas including the existence of cryptic species (Garrick and Bouget 2018; see Chap. 25). Estimates from the best-studied forests in developed areas (e.g., northern Europe) suggest approximately 20–30% of all forest insects are saproxylic. Recognition of this in Britain led Elton (1966) to suggest that dying and dead wood represent one of the two or three most important resources for animal life in forests. The most diverse and well-studied order of insects found in dead wood throughout the world is Coleoptera. The earliest beetle, as mentioned above, was most likely saproxylic, and 122 of all 187 extant beetle families (65%) contain saproxylic members (Gimmel and Ferro 2018; see Chap. 2). Saproxylic beetles range more widely in size (<1 mm for families like

Fig. 1.4 *Orthognathotermes gibberorum* Mathews (Termitidae: Termitinae), a wood-soil interface feeder, French Guiana (Jan Šobotník)

Ptiliidae and Ciidae to >150 mm for certain Scarabaeidae and Cerambycidae) and functional group than other orders. They also include a number of economically important groups like bark and ambrosia beetles (Curculionidae: Scolytinae, Platypodinae) and wood-boring beetles (Cerambycidae, Lymexylidae, Bostrichidae, etc.) that can be major forest pests.

Blattodea is perhaps the second most studied group of wood-dependent insects, due to the inclusion of termites into this order (Bignell 2018; see Chap. 11). Termites are primarily found in tropical and subtropical regions (Fig. 1.4) where they are by far the most dominant wood-feeding insects and also include some serious pests of wooden structures. Hymenoptera is another order which contains many saproxylic members, including parasitoids of other saproxylics that provide an important ecosystem service (Hilszczański 2018; see Chap. 6). Diptera has received surprisingly little attention from researchers considering about half of all families contain saproxylic members, and they rival beetles as the most diverse order of saproxylic insects (Ulyshen 2018b; see Chap. 5). The orders Hemiptera (Gossner and Damken 2018; see Chap. 9) and Lepidoptera (Jaworski 2018; see Chap. 10) contain relatively few saproxylic species, but those species tend to be highly specialized for life in dead wood and are sometimes sensitive to forest management activities. The fact that the term saproxylic includes species indirectly dependent on dying and dead wood, like many fungus-feeding and predatory taxa, also adds greatly to the proportion of species assigned to this category. Major functional groups of saproxylic insects are discussed briefly below.

1.2.3 Functional Groups

Saproxylic insects can be assigned to any number of functional groups, and various classification systems have been proposed (Bouget et al. 2005; Stokland et al. 2012; Krivosheina 2006; Hövemeyer and Schauermann 2003). For the purpose of this introduction, we limit our discussion here to four broad groupings: phloem feeders, wood feeders, fungus feeders, and predators. While these are all functions performed by saproxylic insects, such designations are often somewhat arbitrary at the species level as it is not uncommon for a species, even at a single developmental stage, to qualify for multiple categories. Many wood-boring beetles, for instance, begin life feeding on phloem before tunneling into the wood. Within the wood the larvae often obtain some of their nutrients from microbial biomass that is ingested along with the wood, and it is not uncommon for them to prey upon other insects they happen to encounter in their tunnels. At later stages of decomposition, the wood ingested by wood feeders consists mostly of fungal biomass and other microbes, and these species are commonly considered saprophagous. These four groupings also fail to capture the entire diversity of saproxylic insects. Species that feed on sap flows, for instance, are considered by many to be saproxylic (Alexander 2008) and can be assigned to their own functional group. The same is true for cavity-nesting bees and wasps (Bogusch and Horák 2018; see Chap. 7) as well as aquatic insects confined to water-filled tree holes. Although incomplete, sometimes arbitrary, and overlapping, these four broad groupings, briefly introduced below, provide a simple and useful framework for categorizing the major functions performed by saproxylic insects.

1.2.3.1 Phloem Feeders

The soft, sugary, and protein-rich layer of secondary phloem located just beneath the bark is a particularly desirable resource and ultimately gave rise to a diverse assemblage of phloem feeders (e.g., bark beetles, cerambycids, buprestids, etc.) and their predators. Host-specific defensive compounds present in these tissues are largely responsible for the high degree of host specialization observed within these groups today (Wende et al. 2017). As proposed by Graham (1925), insects that feed on phloem fall into two main groups. One consists of species, like many bark beetles, that never leave the zone between the bark and the wood, while the other group consists of species that begin feeding on the phloem but later bore into the wood. This latter group includes many species of wood-boring beetles (e.g., cerambycids, buprestids, etc.) that attack dying or recently dead trees but are not capable of colonizing wood that lacks phloem. Some beetle species are considered secondary phloem feeders. The endangered beetle *Pytho kolwensis* Sahlberg (Pythidae), for instance, colonizes large trunks of Norway spruce in the boreal regions of Europe and Russia after bark beetles and other primary phloem feeders have left (Siitonen and Saaristo 2000). Even after the phloem layer has been completely consumed, a large diversity of invertebrates can be found living or sheltering within the subcortical space between the bark and wood. The same is true for damp-wood termites, which primarily colonize the subcortical space of freshly fallen trunks, where numerous colonies fiercely compete until most are eliminated or fused with stronger neighbors (Thorne et al. 2003).

1.2.3.2 Wood Feeders

Despite being hard to chew, difficult to digest, and characterized by very low nutrient concentrations, wood represents a very rich substrate in terms of energy content and is therefore consumed by a wide variety of wood-feeding insect taxa. These include various groups of Blattodea (*Cryptocercus* wood roaches and termites from all families except for Hodotermitidae), as well as numerous Coleoptera (Anobiidae, Bostrichidae, Brentidae, Buprestidae, Cerambycidae, Lymexylidae, Zopheridae, and many others that feed on decomposing wood), Diptera (Pantophthalmidae, Tipulidae: *Ctenophora*), Lepidoptera (Cossidae, Hepialidae, Sesiidae), and Hymenoptera (Siricidae, Xiphydriidae). Surviving on a diet of wood is largely made possible for these organisms by interactions with fungi, prokaryotes, and other microbes. Although cellulases belong to the ancestral biochemical machinery of protostomes and deuterostomes (Lo et al. 2003), they have been lost in many insect taxa. Even modern wood-feeding groups usually produce just some of the cellulases needed for cellulose digestion, most frequently β-glucosidases and sometimes also endo-β-glucanases (Lo et al. 2011). These insect cellulases are thus called incomplete, as cellulose digestion must necessarily be aided by symbiotic microorganisms (predominantly bacteria including actinomycetes and fungi including yeasts and, to a lesser extent, protists) (Breznak 1982; Dillon and Dillon 2004; Lo et al. 2011). Complete cellulases are known only from some bacteria and fungi (Tomme et al. 1995). As a consequence, virtually all wood-feeding insects benefit from endo- or ecto-symbioses with microbes capable of degrading lignocellulose (Birkemoe et al. 2018; see Chap. 12). Symbioses between insects and microbes are in some cases so specialized that insects obtain nutrition from wood without ingesting it. Thompson et al. (2014) showed that *Sirex noctilio* F. larvae extract and consume liquids from wood shavings rather than consume the wood itself. The liquid contains compounds liberated by the enzymatic activities of the insect's fungal symbiont.

In addition to the important role fungal symbionts play in digesting wood, a large proportion of the nitrogen requirements of many wood-feeding insects comes from nitrogen-fixing prokaryotic endosymbionts within their guts (Ulyshen 2015). Nitrogen fixation is an energy-demanding process and is typically only seen in insects feeding on N-poor substrates. Consistent with this pattern, rates of nitrogen fixation in termites decrease along the humification gradient, typically being higher in species that feed on sound wood compared to species feeding on more highly decomposed wood and being mostly absent from soil-feeding or fungus-growing taxa (Breznak et al. 1973; Yamada et al. 2007; Tayasu et al. 1997).

1.2.3.3 Fungus Feeders

Dead wood is quickly colonized by a variety of wood-digesting fungi, bacteria, and other microbes which collectively account for a large proportion of total biomass of rotting wood as decomposition proceeds (Jones and Worrall 1995; Noll et al. 2016). It is thus inevitable for these organisms to be consumed, whether intentionally or not, by wood-feeding insects. Fungal biomass is more nutritious than wood and therefore acts to enrich the food of many insects in addition to providing the enzymes necessary to digest the wood itself (Kukor and Martin 1986). Various termite taxa, for example, have been shown to feed preferentially on wood decayed by fungi, with documented benefits to colony size and health (Becker 1965; Smythe et al. 1971; Hendee 1935; Cornelius et al. 2002). The distinction between wood feeding and fungus feeding is unclear for many saproxylic insect species, especially within highly decayed wood. Fungi are thought to be the main source of nutrition for certain "wood-feeding" passalid (Mishima et al. 2016) and lucanid (Tanahashi et al. 2009) beetles, for example. The consumption of wood by many insects may therefore be consistent with the peanut butter and cracker analogy developed by Cummins (1974) for decomposers of coarse particulate organic matter in stream ecosystems. That is, wood consumption may represent just a strategy utilized by some saproxylic insects to obtain the more nutritious microbial biomass. Fungi also play an important role in translocating nutrients into wood from external sources, thus further reducing the nutritional limitations imposed by wood on wood-feeding insects (Filipiak 2018; see Chap. 13).

Many other insects are obligate fungus feeders. Some, such as the Hemipteran family Aradidae, feed on fungal hyphae under bark (Gossner and Damken 2018; see Chap. 9). Many others, including a large diversity of beetles and flies, feed on fungal fruiting bodies (Jonsell et al. 2001; Epps and Arnold 2010; Graf-Peters et al. 2011). Perennial fruiting bodies that provide a relatively stable resource often support a highly specialized fauna (Jonsell et al. 2001), with approximately half of the species being monophagous (Jonsell and Nordlander 2004). One of the most specialized groups of obligate fungus feeders are species that feed on symbiotic fungi they cultivate within their galleries or nests (Birkemoe et al. 2018; see Chap. 12). There are two major examples of this among saproxylic insects. The first concerns ambrosia beetles of the families Curculionidae [Scolytinae and Platypodinae, including the eusocial Australian platypodine *Austroplatypus incompertus* (Schedl)] and Lymexylidae. These insects cultivate their symbiotic fungi on the walls of their tunnels, and adults carry the symbionts within special structures on their bodies called mycangia.

The other major group of insects that cultivate symbiotic fungi is Macrotermitinae, the most basal subfamily of the crown termite family Termitidae (Fig. 1.5). Macrotermitinae are commonly referred to as the "fungus-growing termites" due to their association with ectosymbiotic fungi (Basidiomycetes: Agaricales: *Termitomyces*) (Poulsen et al. 2014; Bignell 2016). The fungus represents the principal food source for the colony, providing protein-rich asexual spores

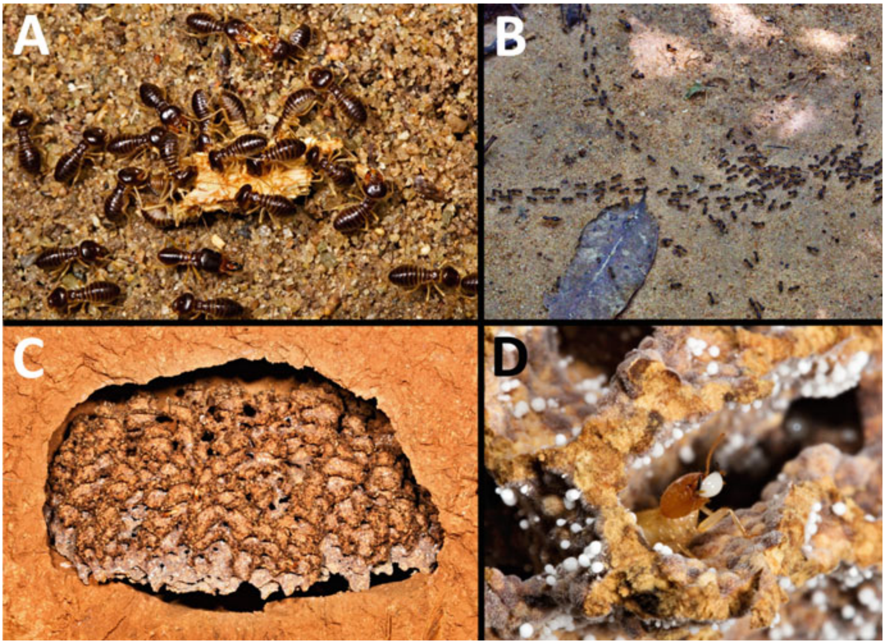

Fig. 1.5 Examples of Macrotermitinae (Termitidae), the fungus-growing termites. (**a**) *Macrotermes carbonarius* foraging on a small wood item on the ground, Thailand; (**b**) *Macrotermes carbonarius* (Hagen 1858) workers marching to the nest from a foraging trip (note trail-following behavior), Thailand; (**c**) fungus comb of *Odontotermes* sp., China; (**d**) soldier of *Odontotermes* sp. spitting the defensive labial gland secretion in response to disturbance (note the white nodules, conidia, growing from the fungus comb), China (All images by J. Šobotník)

(nodules). It also supplies the colony with cellulases that complement the innate enzymes of the host and greatly improve food digestion and detoxification (Hyodo et al. 2003; Nobre et al. 2011). Due to their symbioses with *Termitomyces*, macrotermitines are considered among the most efficient of all insects at decomposing dead wood and other plant matter (Schuurman 2005; Brune and Ohkuma 2011), processing 5–6 times more food per unit biomass than other termites (Bignell and Eggleton 2000).

1.2.3.4 Predators

Predators make up a large proportion of the insect biodiversity associated with dying and dead wood. For example, predators accounted for about 41% of all saproxylic beetle species collected in a recent study conducted in Germany (Wende et al. 2017). While some saproxylic predators opportunistically prey upon a wide range of species present in dead wood, many others exhibit a high degree of host specificity. This is especially true among parasitoids that are predatory as larvae and, unlike parasites, ultimately kill their hosts (Godfray 1994). Most parasitoids belong to the order Hymenoptera (major saproxylic families include Braconidae, Ichneumonidae, etc.) (Hilszczański 2018; see Chap. 6) although there are some notable groups of dipteran (e.g., Tachinidae) and coleopteran parasitoids (e.g., Bothrideridae and Passandridae) as well. Parasitoids typically specialize on particular life stages, with some attacking only eggs, larvae, or pupae. An important distinction can be made between parasitoids that do (idiobionts) or do not (koinobionts) paralyze their hosts at the time of oviposition. Hosts parasitized by koinobionts continue to feed until they are ultimately killed by the larvae feeding within. Parasitoids can also be categorized as endo- or ectoparasitoids depending on whether they feed from the outside or within their hosts. Endoparasitoids tend to be more host-specific than ectoparasitoids, with some ectoparasitoids known to attack an extremely wide range of host species. The habitat associations of parasitoids are typically more narrow than those of their hosts. For example, larval parasitoids that attack hosts hidden under bark can be limited by the length of their ovipositor, being unable to penetrate thick bark (Abell et al. 2012; Berisford 2011). Although few species are strictly saproxylic, ants are often extremely abundant in dead wood, especially toward the tropics, and no doubt play an important role in structuring saproxylic insect communities (King et al. 2018; see Chap. 8).

1.2.4 Specialization and Succession

The huge diversity of saproxylic insects can largely be attributed to the fact that many saproxylic insect species specialize on particular species of wood, wood positions (standing/suspended or fallen), wood diameters, environmental conditions (sun exposure, temperature, and humidity), etc. There is also a predictable succession of insects as decomposition proceeds, with some species occurring only during the phloem stage or while there is bark, whereas others colonize wood only after it has become highly decomposed by fungi. Although these successional patterns have been described in multiple studies (Ulyshen and Hanula 2010; Hövemeyer and Schauermann 2003; Muñoz-López et al. 2016; Lee et al. 2014; Grove and Forster 2011; Derksen 1941), the insects associated with the last stages of decomposition remain very poorly characterized (Ferro 2018; see Chap. 22). This highly degraded and fungus-rich substrate is known to support a unique fauna (Grove 2007), however, including some of the largest and most visually stunning species. A wide variety of Scarabaeoidea breeds only in highly decomposed wood (including the material that collects in tree hollows), for example, including lucanids (Huang 2018; see Chap. 4), passalids (Ulyshen 2018a; see Chap. 3), and the scarab subfamilies Dynastinae, Cetoniinae, and Rutelinae (Fig. 1.6). These groups appear to be especially diverse and numerous in the tropics where they process large amounts of woody material [e.g., 1.5 kg per individual in the case of *Megasoma elephas* (F.)] and are thought to strongly influence decomposition (Morón 1985; Morón and Deloya 2001). Because highly decomposed wood is slow to develop and can be

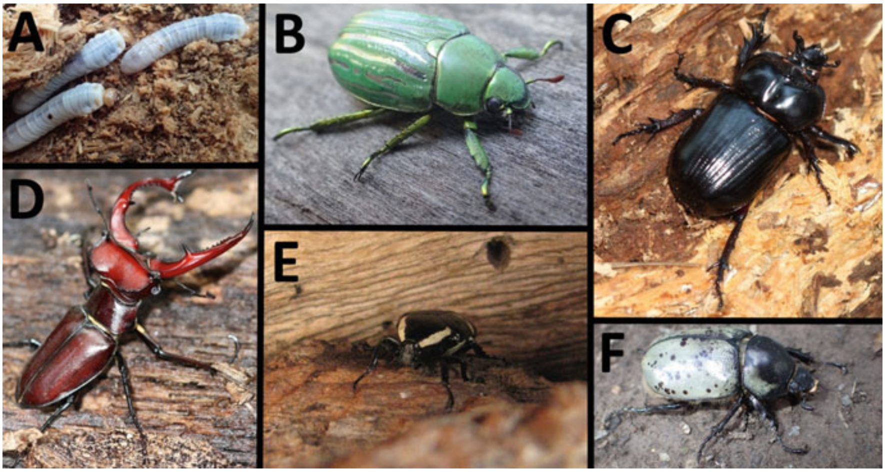

Fig. 1.6 North American examples of Scarabaeoidea associated with highly decomposed wood. (**a**) Passalid larvae (*Odontotaenius disjunctus* (Illiger), Georgia); (**b**) ruteline scarab (*Chrysina gloriosa* LeConte, Arizona); (**c**) dynastine scarab (*Phileurus truncatus* (Beauvois), Florida); (**d**) lucanid (*Lucanus elaphus* L., Mississippi); (**e**) cetoniine scarab (*Gymnetina cretacea* (LeConte)) emerging from oak tree hollow, Arizona; (**f**) dynastine scarab (*Dynastes granti* Horn, Arizona) (Images (**a**–**d**) and (**f**) by Michael D. Ulyshen, image (**e**) by Michael L. Ferro)

easily destroyed during timber operations (McCarthy and Bailey 1994), it is typically more common in older less-disturbed forests, except in the case of legacy debris from a previous stand (Carmona et al. 2002; McCarthy and Bailey 1994; Idol et al. 2001). Similar patterns have been shown for insects that depend on highly decomposed wood. Lucanids, for example, are among the insects most sensitive to forest disturbance (Lachat et al. 2012) but can persist after a harvest if an adequate amount of wood is left behind (Michaels and Bornemissza 1999).

1.2.5 Global Diversity Patterns with a Focus on Social Insects

Although the four main functional groups described above occur in all forest types, the composition of these communities varies greatly among the regions of the world as dictated by the biogeography of the different taxa. One of the biggest differences concerns the uneven distribution of eusocial groups like termites (Bignell 2018; see Chap. 11) and ants (King et al. 2018; see Chap. 8) and subsocial groups like the beetle family Passalidae (Ulyshen 2018a; see Chap. 3). These groups tend to be more diverse and abundant toward the tropics compared to more temperate regions (King et al. 2013; Schuster 1978). It remains largely unknown whether or not the diversity patterns of nonsocial saproxylic insect groups also become more diverse toward the tropics. Most organisms exhibit this pattern, however, and it seems likely to hold true for most groups of saproxylic insects considering tropical forests support a much larger number of tree genera than temperate or boreal forests. Tropical forests also tend to be much older, especially compared to those occurring in areas that were glaciated just several thousand years ago, and this may also contribute to a higher insect diversity. Few studies have specifically focused on saproxylic insect biodiversity in tropical forests, however, although it is clear from work by Grove (2002a, c) that a high diversity of saproxylic beetles (>500 species) can be found in the rainforests of tropical Australia. An analysis of saproxylic hemipteran diversity by Gossner and Damken (2018; see Chap. 9) shows these insects are more diverse in tropical and subtropical forests. A related question concerns whether the proportion of species that is saproxylic differs among regions. Hanski and Hammond (1995) were among the first to broach this topic, noting that the proportion of beetles that are "wood-associated" is about equally as high in the rainforests of Sulawesi (33%) as in the forests of Finland (35%). Because Sulawesi has many times more beetle species overall than Finland, this suggests the number of saproxylic beetle species should be an equal degree higher in Sulawesi.

On the other hand, the tremendous abundance of social insects in tropical forests could potentially cause other saproxylic insects to be less diverse in tropical forests than expected. Due to their large colonies, for example, termites may meaningfully reduce the amount of resources available to other insects. The Sulawesi example mentioned above does not rule this out given the relatively low diversity of termites there compared to other tropical regions. Indeed, termites richness varies greatly within the tropics, firstly being more diversified at the southern hemisphere and secondly being both more diverse and abundant in the Afrotropics followed by the Neotropics, the Indomalayan region, and Australasia (Davies et al. 2003). While these patterns are probably a consequence of historical events, such as the origin of the most successful termite family, Termitidae, in the rainforests of Africa (Bourguignon et al. 2017b; Aanen and Eggleton 2005), the same pattern of abundance calls for a different, yet-unknown, explanation. If termites do negatively influence the number of saproxylic species present in a forest, the strongest effect might be seen in places like west Africa where the "higher" termites originated and termite diversity and abundance remain the highest. While this has never been formally tested, observations from Cameroon and other tropical locations suggest that fewer saproxylic insect species are encountered where termites are most active (JS, pers. obs.).

Ants are also extremely abundant on the forest floor, especially in the tropics where they have been shown to be the major agents of resource removal (Griffiths et al. 2018). Ants are among the most important predators of termites (King et al. 2018; see Chap. 8) and are likely to reduce the populations of other insects found within dead wood as well. There is limited information on this question in the literature, however. In Puerto Rico, Torres (1994) attributed the low beetle diversity in logs in part to the presence of many ant species. Stronger evidence that ants negatively influence insects in dead wood comes from Jackson et al. (2012) who showed the probability of log occupancy by a species of passalid beetle in Louisiana to be higher when ants were absent. In Portugal, by contrast, Henin and Paiva (2004) found no evidence that an aggressive species of ant reduced the ability of a bark beetle to colonize logs. Their study found that attempts by the ants to attack the beetles were not successful and the ants were also unable to access the galleries under the bark, possibly due to the plug of dust surrounding the boring hole. Insects have been evolving in the presence of ants for a long time, and many morphological and/or behavioral adaptations may exist for surviving encounters with these predators. This certainly seems to be the case for termites which are known to often coexist in wood with ants (Shelton et al. 1999).

1.3 Wood in Human History

> *But who really owns the tree stump? The bark beetle that gnaws tunnels inside it? The ants that travel through the tunnels? The earwig that sleeps under its bark? Or the bear that uses it to sharpen her claws? Does it belong to the titmouse that flies down upon it? The frog that find shelter in one of its holes? Or the man who believes he owns the forest? Maybe the stump belongs to all- the beetle and the ants, the bear and the titmouse, the frog, the earwig, and even the man. All must live together.*
>
> Romanova (1985)

The quote above, translated from the Russian children's book "Чей э́то пень?" (i.e., Whose stump?), nicely captures the conflict between human demand for woody resources and the importance of those resources to many other species. It also recognizes our inherent appreciation for biodiversity and desire to protect it. Throughout most of human history, however, demand drove the relationship between humans and wood, with wood playing a key role in our quality of life and technological progress. Perlin (1989) summarized this particularly well:

> It may seem bold to assert wood's crucial place in the evolution of civilization. But consider: throughout the ages trees have provided the material to make fire, the heat of which has allowed our species to reshape the earth for its use. With heat from wood fires, relatively cold climates became habitable; inedible grains were changed into a major source of food; clay could be converted into pottery, serving as useful containers to store goods; people could extract metal from stone, revolutionizing the implements used in agriculture, crafts, and warfare; and builders could make durable construction materials such as brick, cement, lime, plaster, and tile for housing and storage facilities. Charcoal and wood also provided the heat necessary to evaporate brine from seawater to make salt; to melt potash and sand into glass; to bake grains into bread; and to boil mixtures into useful products such as dyes and soap. Transportation would have been unthinkable without wood. Until the nineteenth century every ship, from the Bronze Age coaster to the frigate, was built with timber. Every cart, chariot, and wagon was also made primarily of wood. Early steamboats and railroad locomotives in the United States used wood as their fuel. Wooden ships were tied up to piers and wharves made from wood; carts, chariots and wagons made of wood crossed wooden bridges; and railroad ties, of course, were wooden. Wood was also used for the beams that propped up mine shafts and formed support for every type of building. Water wheels and windmills—the major means of mechanical power before electricity was harnessed—were built of wood. The peasant could not farm without wooden tool handles or wood plows; the soldier could not throw his spear or shoot his arrows without their wooden shafts, or hold his gun without its wooden stock. What would the archer have done lacking wood for his bow; the brewer and vintner, without wood for their barrels and casks;

> or the woolen industry, without wood for its looms? Wood was the foundation upon which early societies were built.

Whereas many regions were extensively forested for thousands or even millions of years prior to human colonization, most forests now growing in developed regions are just decades or centuries old and exist in scattered patches (Speight 1989). These patches are also known to contain less dead wood in terms of both abundance and variety compared to the least disturbed old-growth remnants (Stenbacka et al. 2010b). It is ironic but also encouraging to consider that the wood- and coal-fueled technological progress that gave rise to modern civilization and resulted in drastic changes in forest cover may have given us the opportunity as a species to stop and consider how our actions have affected forest ecosystems over time. As it became apparent, near the end of the twentieth century, that saproxylic organisms were being lost from intensively managed forests, the conservation of these organisms became a major research focus in places like Europe, Australia, and North America. There has been dramatic change in how foresters view dead wood in forests over the past half century or so. Spaulding and Hansbrough (1944) captured the sentiment held by many foresters in the mid-twentieth century as follows: "Those who harvest forest trees are faced with the problem of the disposal of the resulting logging slash. It has been termed the "garbage" of the woods. Because of its ubiquity in the exploited forest, however, the tendency has been to accept it as a necessary evil, one about which little or nothing can be done in a practical way." Today, by contrast, the value of woody debris to biodiversity and nutrient cycling is widely recognized although it should be noted that there is some concern about the role woody debris can play in increasing certain pest populations. In Europe, for example, major inputs of dead wood (e.g., severe wind damage) have been shown to briefly (for 1–2 years) increase the outbreak risk of the bark beetle, *Ips typographus* L. (Schroeder and Lindelöw 2002). Examples from other parts of the world are lacking, but, because most forest-damaging pests (e.g., bark beetles and various wood borers) are associated with dying or freshly killed trees, wood at later stages of decay (i.e., after the phloem layer is gone) poses little threat in this regard.

1.4 History of Research on Saproxylic Insects

Sharp divisions exist in the saproxylic insect literature along both taxonomic and biogeographical lines. Examples include separate bodies of literature on primarily tropical groups like eusocial termites, subsocial passalid beetles, and other nonsocial insect assemblages. Although understandable, these divisions are unfortunate given the fact that many or all of these groups, depending on the region, interact extensively within their shared substrate. Moreover, progress in a number of research directions has been limited by this divided view of saproxylic insect communities. Efforts to quantify the role of insects in decomposition historically focused on termites, for example, without regard for the activities of other insects. Artificial wooden substrates such as machined wooden blocks have been and continue to be used in these studies despite the fact that they exclude entire guilds of insects (e.g., phloem feeders and others associated with the subcortical space) known to facilitate fungal colonization and have strong but indirect effects on levels of decomposition. Indeed, it is clear from recent research that ignoring the effects of bark coverage and phloem-feeding beetles can yield highly unrealistic information on rates of wood decomposition and the contributions of insects (Ulyshen et al. 2016). As stated earlier, a major goal of this book is to take steps toward uniting the literature on nonsocial saproxylic insects and wood-dwelling social insects (including saproxylic termites as well as ants which are mostly non-saproxylic). The global diversity and ecology of saproxylic insects cannot be understood without achieving this unified perspective. As the two largest bodies of literature, brief histories of research on nonsocial saproxylic insects and research on wood-feeding termites are provided in the following sections.

1.4.1 Research on Nonsocial Saproxylic Insects

The diversity of wood borers and other species associated with freshly dead woody material was noted by many early naturalists. At a single small location over a 2-month period in Singapore, for instance, the Victorian-era naturalist Alfred Russell Wallace (1869) collected at least 700 species of beetles, including 130 distinct kinds of wood-boring cerambycids, which he attributed in large part to the felling of trees in the area. Townsend (1886) similarly reported collecting 34 species from the dead trunks of *Tilia americana* L. in North America, and Davis and Leng (1912) collected 42 species of beetles in just 2 hours from a recently felled longleaf pine in Florida. Shelford (1913) recognized the value of dead wood to animal life in his big book on temperate American zoology. Blackman and Stage (1924) were among the first researchers to consider the succession of insects throughout the decomposition process. They published an extremely detailed study of insects and other organisms associated with the bark and wood of dead hickories in New York, including information on successional patterns over a period of 6 years. The following year, Graham (1925) published an article entitled “The felled tree trunk as an ecological unit” in which he carefully described how nutrition, moisture, and temperature vary within and among dead trees and how these factors influence early insect colonists. Other notable contributions from that decade include those of Richards (1926) and Krogerus (1927). The 1930s saw the publication of a major effort by Savely (1939) on the ecology of arthropods associated with dead pine and oak in North Carolina. Several excellent papers were published in German in the 1940s on the succession of insects in decomposing wood. Derksen (1941) studied the insect communities associated with beech stumps, for example, and Eidmann (1943) investigated the succession of wood-dwelling insects in West Africa. In the 1950s, Howden and Vogt (1951) surveyed the insect communities associated with standing dead pine in

Maryland, and Wallace (1953) studied the ecology of insects in pine stumps in Britain.

This growing body of literature along with his own research in England led Elton (1966) to conclude that "dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and if fallen timber and slightly decayed trees are removed the whole system is impoverished of perhaps more than a fifth of its fauna." Yet it would be some time before the importance of dead wood to biodiversity would be widely recognized by the community of researchers and foresters. For example, Stubbs (1972) remarked that "many of those who manage woodlands for amenity and conservation, and many conservationists themselves, appear to be uninformed of the immense value of dead and dying wood for the conservation of a variety of wildlife." Indeed, for many land managers, dead wood represented waste, lost revenue, or risk from pest outbreak—concerns still held by some today. Beginning in the late 1970s, researchers in the northwestern United States were among the first to fully recognize the value of dead wood to terrestrial and aquatic ecosystems. Teskey (1976) compiled a list of Diptera known to utilize dying and dead wood in North America. Thomas et al. (1979) reviewed the importance of snags to cavity-nesting birds, while Maser et al. (1979) reviewed dead and downed woody material utilization by vertebrates. Maser and Trappe (1984) reviewed the properties of dead wood and discuss their ecological importance in both forests and streams. An even more detailed treatment was provided several years later by Harmon et al. (1986). In addition to discussing forests and freshwater systems, Maser et al. (1988) also included lengthy sections on the ecology of dead wood in estuaries, in the sea, and on coastal beaches.

The modern era of research aimed specifically at conserving insect biodiversity in dead wood largely began in 1980 when the Council of Europe initiated a project aimed at using insects dependent on dead wood to compile a list of high-quality forests and to assess the health of the terrestrial decomposer community (Speight 1989). Before this effort was undertaken, as written by Speight (1989), "the plight of the saproxylics (i.e., species reliant on dead or dying wood) had not been recognized, the significance of their role in natural forest had been ignored and only a handful of European forests supporting a recognizably diverse saproxylic community had been secured for protection." The committee began by developing a list of insect species that were thought to be associated with mature forests and highly localized in their distribution. They then sent this list to specialists across Europe, requesting information on forests likely to be important to such species. The results from the project were compiled by Speight (1989) who began his report by defining the term "saproxylic" as species "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics." Their survey efforts resulted in a list of approximately 150 forests throughout Europe with potential conservation value, some of them as little as 40 hectares in size. They were found to be largely concentrated in mountainous regions, whereas lowland and valley forests were noticeably lacking, and alluvial forests were almost totally absent from the list (Speight 1989). According to Speight (1989), these remaining high-value forests, all hundreds or even thousands of years old and quite isolated from one another, “have effectively become islands within a sea of hostile terrain too vast for saproxylics to successfully traverse.” Perhaps more than any other previous work, Speight’s report brought attention to the challenges facing saproxylic organisms in Europe after millennia of deforestation, fragmentation, and intensive management.

The years following Speight’s publication have seen a dramatic increase of interest in the ecology of dead wood, especially regarding the conservation of saproxylic organisms. The number of papers using the keyword “saproxylic” in titles and abstracts, for instance, has been increasing at a rate of about 5 per year since the year 2000 (source: Scopus, accessed 29 October 2017). This timeline was punctuated by some major review articles and books aimed at compiling the growing body of evidence and guiding conservation-oriented management. Samuelsson et al. (1994) wrote an excellent book outlining the importance of dead and dying trees to biodiversity in both terrestrial and aquatic environments. McComb and Lindenmayer (1999) outlined spatiotemporal patterns of dead and dying trees in forests, with particular attention given to the importance of tree cavities to many species. A paper by Siitonen (2001) reviewed the state of knowledge for Northern Europe. The following year Grove (2002b) published another excellent review, also largely focused on the European case but also including some of his findings from Australia. Another review article by Bunnell and Houde (2010) focused on vertebrates associated with dead wood in the Pacific Northwest of North America. Most recently, Stokland et al. (2012) published their book on *Biodiversity in Dead Wood* which is perhaps the most ambitious effort ever undertaken to produce a comprehensive synthesis of this vast and multidisciplinary topic.

1.4.2 Research on Wood-Feeding Termites

> *Such however are the extraordinary circumstances attending their economy and sagacity, that it is difficult to determine, whether they are more worthy of the attention of the curious and intelligent part of mankind on these accounts, or from the ruinous consequences of their depredations, which have deservedly procured them the name of Fatalis or Destructor.*
>
> Smeathman (1781)

The above quote came from a letter written by Henry Smeathman to Sir Joseph Banks of the Royal Society in which he reported his observations of termites in and around Sierra Leone, Africa. Although termites have been written about since at least 1350 BC (Snyder 1956), Smeathman’s letter stands among the earliest efforts to accurately report on the natural history of termites, so much so that Smeathman worried about whether readers would even believe his accounts of these “wonderful insects.” The first family description, of Termitidae, took place in 1802 (Latreille 1802), and the order Isoptera (in Greek “equally winged”) was introduced by Brullé (1832). Many important early observations were summarized in a three-volume book *Monographie der Termiten* by Hagen (1855, 1858, 1860). Observations on the nesting biology of Indo-Malayan termites were introduced by Haviland (1898), and the relationships between termites and their social parasites were described by Wasmann (1893). Pioneering work on Asian termites was published by Holmgren (1909, 1911, 1912) in his extensive descriptions of termite biology, and perhaps the first modern monograph on termites describing the biology of a single species, *Archotermopsis wroughtoni* (Desneux), was published by Imms (1919). A taxonomic survey of African termites was published by Sjöstedt in 1926. Research by Emerson and Snyder on termite evolution, biogeography, and taxonomy was especially influential in directing the progression of termite research, and Grassé and Noirot made many important pioneering observations on termite biology, nesting and feeding habits, ontogenetic patterns, and communication. Several landmark books have been published on termites in the past 50 years, including the two-volume *Biology of Termites* (Krishna and Weesner 1969, 1970) and the multivolume compendium on termite biology by Grassé (1982, 1984, 1986). More recent reviews of termite ecology include the books by Abe et al. (2000) and Bignell et al. (2011), and an excellent survey of termite systematics, including all relevant resources, was recently published by Krishna et al. (2013).

As urban pests, termites globally have an estimated annual cost of $40 billion (Rust and Su 2012) and also greatly reduce the value of timber in forests by hollowing out the centers of living trees (Werner and Prior 2007; Apolinário and Martius 2004). According to Rust and Su (2012), about 6.1% of the ~3000 termite species globally are considered pests, and only about 2.8% (~80 species) cause severe damage to wooden structures or furniture. These most damaging urban pests have received the majority of attention from researchers, however. Among these are termites that have been introduced into new areas. According to Evans et al. (2013), there are 28 species of termites worldwide considered to be invasive outside their native ranges, all of which are wood feeders. The most serious invasive termite pests are the kalotermitids *Cryptotermes brevis* (Walker) and *C. havilandi* (Sjöstedt); the rhinotermitids *Reticulitermes flavipes* (Kollar), *Coptotermes formosanus* Shiraki, and *C. gestroi* (Wasmann); and the nasutitermitine termitid *Nasutitermes corniger* (Motschulsky) (Evans et al. 2013). The introduction of these particular invasives can have major economic consequences and may also have strong effects on native ecosystems although the latter question has received little attention to date. While the negative effects of termites have long been a primary focus of termite research, resulting in the production of books with titles like *Termites and Termite Control* (Kofoid 1934), *Our enemy the termite* (Snyder 1948), or *Termites—a world problem* (Hickin 1971), the treatment of termites and other wood-dwelling insects has expanded over time to include all aspects of their ecology and even concerns about their conservation. Termite researchers have long speculated about the key functions termites perform in nutrient cycling and in aerating and turning over the soil (Noyes 1937; Snyder 1948; Kofoid et al. 1934; Grassé 1984; Ulyshen 2016), and appreciation for the ecosystem services provided by termites has grown over time. Indeed, it is now widely acknowledged that termites are among the most important ecosystem engineers of all invertebrates (Lavelle et al. 1997; Bignell and Eggleton 2000), with the role they play in promoting decomposition and nutrient cycling being of particular interest (see Sect. 1.5).

One of the most fundamental facts and key discoveries about termites is that they can function as decomposers only in partnership with endo- or ectosymbionts. Although initially mistaken for parasites (Leidy 1881), the flagellate protists found in the guts of non-termitid termites and C*ryptocercus* cockroaches were among the first endosymbionts of wood-feeding invertebrates to be discovered by researchers. Cleveland (1923) provided the first experimental evidence that protists play a key role in the digestion of wood, showing that "lower" termites quickly die of starvation in the absence of their symbionts. The traditional distinction between "lower" (basal taxa) and "higher" (Termitidae only) termites is based on the presence of gut flagellates in the former and absence in the latter (both groups contain bacterial endosymbionts). Although this separation is artificial from a phylogenetic point of view, it is often helpful from an ecological perspective. Like *Cryptocercus*, all "lower" termites are wood feeders, with the exception of Hodotermitidae, which feed on dry grasses, and *Serritermes* (Serritermitidae), which is the sole inquiline among "lower" termites and feeds on *Cornitermes* spp. (Termitidae: Syntermitinae) nest material (Emerson and Krishna 1975). By contrast, not all termitid species are wood feeders, with some feeding instead on microepiphytes, grasses, leaf litter, highly decayed wood, upper soil layers, and bare soil and within the nests of other termites or ants. Indeed, given the diversity of Termitidae, only about 26% of termite genera overall feed on wood, 59% are soil feeders, and the rest feed on grass, leaf litter, or microepiphytes (Bignell 2016; Krishna et al. 2013).

After being assigned to their own order (Isoptera) for over 150 years, recognition that termites are in fact eusocial cockroaches (Blattodea: Termitoidae), with *Cryptocercus* wood roaches being their sister group, is another landmark finding in the history of termite research (Lo et al. 2000; Inward et al. 2007). This fact was suspected long before it was proven molecularly due to the many similarities (e.g., endosymbionts, sociality, xylophagy, etc.) between *Cryptocercus* and "lower" termites (Cleveland et al. 1934). Several important classification schemes have been developed for understanding the ecology of termites. Combined evidence from termite anatomy and gut content led Donovan et al. (2001) to recognize four distinct feeding groups, generally corresponding to wood feeders, litter feeders (including dried grass, dung, etc.), soil/wood feeders (including humus), and soil feeders (including mound walls) (Bignell 2018; see Chap. 11). More recent work utilizing carbon and nitrogen stable isotopes, however, suggests termites can be meaningfully separated into just two broad groups: wood feeders and soil feeders (Bourguignon et al. 2011). Another classification system based on where termites nest in relation to their food substrate was first developed by Abe (1987) who distinguished between termites that feed within the same piece of wood ("one-piece nesters") and those that forage away from their nests ("separate-piece nesters"). There are also "intermediate nesters" that nest and feed within the same substrate but also forage outside the limits of that substrate. One-piece nesting is probably the ancestral condition, whereas separate-piece nesting is exemplified by mound-building termitids. An additional category, the inquilines, was introduced by Shellman-Reeve (1997) for species feeding on the nest material or stored food of a separate-piece nester host.

Working in Nigeria, Wood et al. (1977) were perhaps the first to show that termites, similar to other saproxylic taxa, are highly sensitive to land-use changes. In fact, soil-feeding termites are negatively influenced by faint changes, such as selective logging, and deforestation leads to almost immediate disappearance of the vast majority of soil-feeding taxa. Although wood-feeding guilds are in general less affected by these man-made perturbations, many specialists quickly disappear, and only the most resistant segment of the local fauna can survive habitat alterations (Bourguignon et al. 2017a). The most resilient taxa consist primarily of species capable of forming large colonies, controlling their environment by bringing water from distant sources, and building well-defined centralized nest. Examples include *Coptotermes* (Rhinotermitidae), *Odontotermes* (Termitidae: Macrotermitinae), *Microcerotermes* (Termitidae: Termitinae), or *Nasutitermes* (Termitidae: Nasutitermitinae). The ability to acquire water from air humidity is common only in several species of *Cryptotermes* (Kalotermitidae). Wood-feeding species, of course, cannot persist for long in deforested areas which are commonly colonized by specialized grass-feeding taxa from neighboring habitats (Eggleton et al. 2002; Jones et al. 2003; Krishna et al. 2013).

1.5 Valuing and Conserving Saproxylic Insects

1.5.1 Importance to Decomposition, Nutrient Cycling, and Productivity

Given their taxonomic and functional diversity as well as the abundance of many species, saproxylic insects may provide important ecosystem services in forests. One of the most commonly assumed, but rarely quantified, functions provided by these insects is accelerating wood decomposition. Wood decomposition is largely driven by fungi in most forested ecosystems, but saproxylic insects may also contribute significantly to this process (Ulyshen 2016). Termites are thought to be particularly influential in this regard, as supported by estimates of wood-processing rates and various experimental approaches. An excellent review of termite contribution to organic matter turnover, focused mostly on grasses and leaf litter, was provided by Bignell and Eggleton (2000). The importance of termites for wood mineralization has received less attention but is thought to be higher in dry habitats (but see Cheesman et al. in press), where microbial decomposition is slow. Findings from studies using a variety of estimates and experimental approaches suggest the amount of wood consumed by termites varies greatly among locations, ranging from $<10\%$ of wood consumed to nearly all of it (Ulyshen 2016). Studies in Africa have reported some of the largest effects of termites, and macrotermitines stand out as being particularly important (Buxton 1981; Collins 1981; Schuurman 2005). Despite being a topic of investigation for over 50 years, estimates of the contributions of termites to wood decomposition suffer from a number of limitations. First, studies using a combination of field-based estimates of termite density and lab-based measurements of feeding rates may yield highly inaccurate estimates given that termites exist within complex communities of microbes and other insects that cannot be recreated under laboratory conditions and wood quality changes as decomposition proceeds. Past experimental approaches in which chemical or physical methods were used to exclude termites and other insects are also problematic because most exclusion methods are known to affect microbial activity (Ulyshen and Wagner 2013). Open-topped pans with screened bottoms may largely overcome this challenge, at least for studies primarily targeting termites (Ulyshen et al. 2016). Another shortcoming of decomposition studies is the frequent and continued use of machined wooden blocks which represent an unnecessary and misleading simplification of naturally occurring wood. Using wood without the natural bark layer, for instance, has been shown to greatly underestimate decay rates and excludes an entire guild of saproxylic insects (Ulyshen et al. 2016).

In addition, because most experimental decomposition studies have been short in duration (<3 years), thus covering only the early stages of the process, it is not currently possible to determine whether termites provide more than a short-term acceleration of wood decomposition. Termites consume large amounts of wood but are known to focus their feeding on the least dense and most nutritious parts of wood, leaving the most recalcitrant fractions behind. It thus remains possible that termites have no net accelerative effect on decomposition over the entire process (Ulyshen et al. 2014). Long-term studies that extend over almost the entire decomposition process and allow for interactions among species under field conditions are needed to adequately address this question. A related question and one of particular relevance to forest managers concerns the role saproxylic insects play in accelerating nutrient release from decomposing wood and stimulating tree growth. This question was recently tested in the southeastern United States where subterranean termites are known to significantly speed up wood decomposition, but termites were found to have no effect on tree growth after more than 4 years of decomposition in that study (Ulyshen et al. 2017).

Although much of the research addressing the value of saproxylic insects to decomposition has focused on termites, nonsocial taxa are also likely to influence the process. In addition to those that directly facilitate decomposition by consuming and digesting wood, saproxylic insects are likely to have a variety of indirect effects on decomposition. These include promoting fragmentation by scavenging vertebrates, creating tunnels that facilitate the movement of fungi into wood, and vectoring fungi and other decay organisms on or within their bodies (Ulyshen 2016). It is also important to recognize that insects can have both accelerative and inhibitory effects on the overall decomposition process. By providing a food source for woodpeckers, for example, insects can hasten the loss of bark which can greatly reduce how quickly wood decomposes (Ulyshen et al. 2016).

1.5.2 Importance as Predators

As discussed earlier, a large proportion of saproxylic insect species are predators, including parasitoids, and this guild has the potential to reduce economically damaging pest populations associated with dying or recently dead trees. The best evidence for this comes from the extensive literature on bark beetles. For example, a species of monotomid beetle, *Rhizophagus grandis* Gyllenhal, has been shown to greatly reduce numbers of *Dendroctonus micans* (Kugelann) in Europe (Fielding and Evans 1997) and *D. valens* LeConte in China (Yang et al. 2014), often below economically damaging levels. Several fly taxa are also major predators of bark beetles, with *Medetera* and *Lonchaea* (Dolichopodidae and Lonchaeidae, respectively) being particularly influential. *Medetera* was the only predator significantly associated with *Ips typographus japonicus* Niijima mortality in Japan, for example (Lawson et al. 1996). *Medetera* was also one of the two most important predators (the other being *Enoclerus sphegeus* Fab.) of *Dendroctonus* in Western North America, contributing to over 90% mortality in some trees (Hopping 1947).

Although high rates of mortality have been reported for many parasitoid species as well, parasitoids are generally expected to play a less important role than predators in reducing pest populations (Wegensteiner et al. 2015). This is because a parasitoid larva is confined to a single host, whereas a predatory larva commonly kills multiple hosts. In some cases, including some lonchaeid and pallopterid flies, predators are known to kill more hosts than they consume (Wegensteiner et al. 2015). Parasitoids have been shown to impact pest populations, however. In North America, Duan et al. (2015) showed that both introduced and native larval parasitoids played a part in significantly reducing population growth rates of the emerald ash borer, *Agrilus planipennis* Fairmaire. The effectiveness of parasitoids at reducing host populations is often limited by the lengths of their ovipositors, however, with parasitism rates decreasing with increasing bark thickness (Berisford 2011; Abell et al. 2012).

As reviewed by Wegensteiner et al. (2015), efforts to measure the overall impact of predators and parasitoids on bark beetle populations suggest a high degree of variability, with studies reporting mortality rates of between 23 and 90%. They conclude that natural enemies play an essential role in controlling forest pest populations and stress the importance of having a diversity of predatory taxa. More research is needed to understand the role predation and other interspecific interactions play in structuring saproxylic insect assemblages (Brin and Bouget 2018; see Chap. 14).

1.5.3 Conserving Saproxylic Insect Diversity in Managed Forests and Beyond

Forest clearance and degradation are the two main processes by which dead wood has been lost from many landscapes, resulting in a patchwork of forest stands of varying size, age, and quality surrounded by a matrix of other land uses. In some parts of the world, these disturbances happened so long ago that the appearance and composition of the original forests can only be guessed (Speight 1989). Fragments of old-growth forests, for which there is no history, records, or suspicion of clearance or major disturbance, provide invaluable insights into the amount and variety of dead wood as well as the diversity and composition of saproxylic insects in the absence of human activity (Lachat and Müller 2018; see Chap. 17). Many studies indicate that old-growth forests contain a greater volume and variety of dead wood than younger managed forests from the same region (Siitonen 2001; Stenbacka et al. 2010a). In addition to containing larger volumes of dead wood, old-growth forests support a greater variety of dead wood than most managed forests. In Sweden, for example, Siitonen et al. (2000) reported the average number of dead trees greater than 40 cm in diameter to be 25 and 35 times higher in old-growth forests compared to mature managed forests for coniferous and deciduous species, respectively. Similarly, Spies et al. (1988) reported twice as many logs exceeding 60 cm in diameter in old-growth forests as compared to those of intermediate age in northwestern North America. Old-growth forests also contain more wood at advanced stages of decomposition.

Given these large differences in the amount and variety of dead wood, it is perhaps not surprising that many studies have highlighted the importance of relatively undisturbed old-growth forests to saproxylic insect communities. Indeed, numerous studies have shown a positive correlation between saproxylic insect diversity and dead wood volume (Grove 2002c; Vanderwel et al. 2006; Økland et al. 1996; Martikainen et al. 2000). Moreover, Grove (2002c) showed that the basal area of large-diameter trees can be used as an indicator of ecological integrity for saproxylic beetles in Australian rainforests. Old trees are particularly valuable because they frequently contain tree hollows which are required by some of the most vulnerable species. Floren and Schmidl (2008) estimated that approximately 86% of beetle species dependent on tree hollows in Germany are threatened, for example. Species with limited dispersal abilities or dependence upon microhabitats characteristic of old forests are often much more common at locations with a long history of forest cover. In Germany, for example, Buse (2012) showed that flightless saproxylic weevils are restricted to "ancient" forests (at least 220 years old). The relict status of these small-twig feeders is due to their inability to disperse long distances rather than a dependence on old-growth features. Other species are largely restricted to old-growth forests due to the absence or rarity of suitable microhabitats in younger forests. Tree hollows, for example, typically require a long time to develop and become more common as forests age. A number of hollow-dependent insect species are thus more common in older forests, although these species can be supported in other contexts when efforts are taken to protect veteran trees. Indeed, although old-growth forests play a central role in maintaining populations of sensitive species, second-growth forests are known to support diverse assemblages as well, including vulnerable species, provided that efforts are taken to provide an adequate abundance and continuity of critical microhabitats. How much wood is necessary remains an open question and is perhaps less critical than the variety of wood provided (Seibold and Thorn 2018; see Chap. 18). It is well-known that different saproxylic species utilize different tree genera and also differentiate between wood that is either standing or suspended in the canopy and wood in contact with the forest floor (Berkov 2018; see Chap. 16). Fire also plays an influential role in providing resources for specialist species (Hjältén et al. 2018; see Chap. 20). In addition, species separate into groups defined by their preferences for particular stages of decomposition. Whereas some species attack only trees that are dying or recently dead, colonization by others occurs only near the end of the process. These patterns suggest that efforts to maximize the number of tree species, wood postures, and stages of decomposition will be the most successful at maintaining diverse saproxylic insect assemblages.

Another key question concerns how much spatial and temporal continuity is needed. Many studies indicate that spatial and temporal continuity of dead wood is more important than the amount or variety of dead wood at any particular time and place (Similä et al. 2003; Sverdrup-Thygeson et al. 2014; Schiegg 2000a, b). In France, for example, Brin et al. (2016) found forests >200 years old to support a higher richness of saproxylic beetles, including more large-bodied species, than younger forests despite having less volume and variety of dead wood. These patterns may be due in large part to differences in dispersal ability among species (Feldhaar and Schauer 2018; see Chap. 15), with large-bodied species being generally less capable of flying long distances (Ranius and Hedin 2001) and/or having shorter flight periods (Gillespie et al. 2017) than smaller species. The same is of course also true for flightless species (Buse 2012). Many species with the weakest dispersal abilities are associated with persistent habitats such as tree hollows, whereas species associated with ephemeral habitats such as phloem or small-diameter wood tend to be relatively strong dispersers (Nilsson and Baranowski 1997). Although site history is important (Goßner et al. 2008) and large blocks of old forest have the highest conservation value (Irmler et al. 2010; Grove 2002a), it is important to recognize the value of smaller and younger forest patches in supporting a subset of the saproxylic fauna (i.e., the strong dispersers), especially within the context of metapopulation dynamics. One example of this comes from the wheat-farming region of western Australia where Abensperg-Traun (2000) found that even small and disturbed patches of *Eucalyptus* imbedded within an agricultural matrix supported wood-feeding termites. Termite species richness increased with tree number (patch size), but distance from other source populations had no effect, probably due to the ability of termites to disperse over long distances. Similarly, studies on the tree-hollow specialist, *Osmoderma eremita* (Scopoli), in Europe show that even scattered trees in highly managed landscapes can promote the conservation of certain species. In managed forests, strategies such as retention harvesting, where a certain number of trees are left behind either in a dispersed or aggregated arrangement, may improve spatial connectivity, thus softening the impact of harvest operations for many species (Lee et al. 2018; see Chap. 19).

The relationship between saproxylic insect diversity and canopy openness is another question of high relevance to managers. Naturalists have long recognized that many saproxylic insect groups, especially many of the large and colorful taxa most prized by collectors (e.g., cerambycids, buprestids, etc.), are more readily

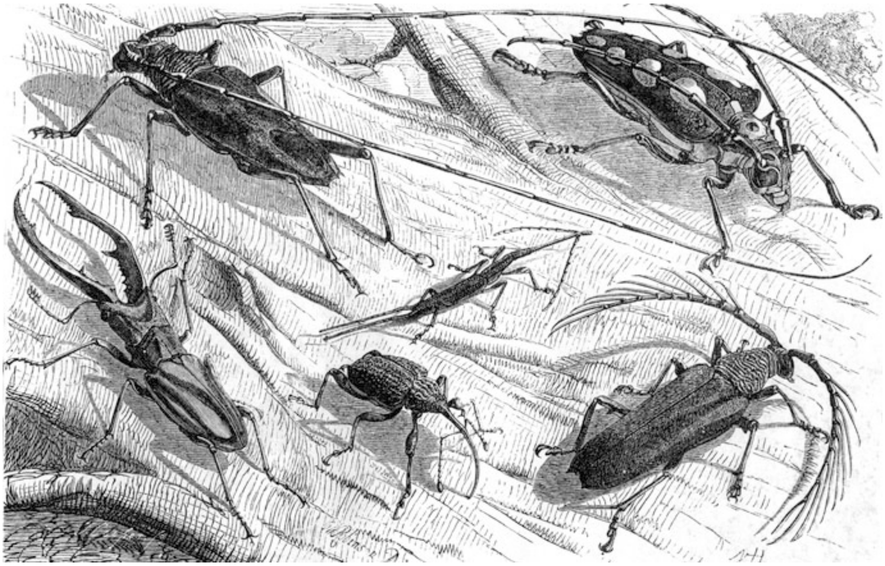

Fig. 1.7 Examples of “remarkable” saproxylic beetles collected by Alfred Russel Wallace (1869) in Borneo

collected in sunny areas. In his 12 years of collecting insects in the tropics, for example, Alfred Russel Wallace (1869) found recently cleared areas of forest to be by far the most productive, with one such place in Borneo yielding nearly 2,000 species of saproxylic beetles (Fig. 1.7). Studies using passive trapping techniques (e.g., flight intercept traps) have shown this to be true for a wide range of taxa although many others prefer shady conditions. In Germany, for example, Seibold et al. (2016b) found that 105 and 57 species of beetles collected in flight intercept and pitfall traps were significantly associated with sunny and shady plots, respectively. Lachat et al. (2016) compared saproxylic beetle assemblages present in the centers and on the edges of canopy gaps as well as under closed canopy conditions away from the gaps in an old-growth Ukrainian beech forest. They found beetle abundance to be higher and beetle composition to be different in the centers of the gaps compared to the forest but found no difference in species richness. The findings from passive trapping have the potential to exaggerate the importance of sunny conditions, however, as many insects are more active and thus more readily captured in sunny areas. Few studies have addressed this question using emergence traps although Gossner et al. (2016) reported a positive correlation between the number of beetle species emerging from dead wood and canopy openness in Germany. More emergence-trap studies are needed to better understand these patterns, and studies targeting less commonly studied insect orders would be particularly informative. Flies, for example, are dependent on moist or wet substrates, and may be particularly sensitive the drying effects of more open forest conditions (Ulyshen 2018b; see

Chap. 5). The needs of such species should be taken into consideration when developing management plans.

In addition to the effects of forest clearance and degradation, saproxylic insects are likely to be impacted by the intentional or accidental introduction of nonnative tree species into many of the remaining forested areas. Invasive trees and shrubs are a growing problem in many regions, and plantations of nonnative trees are planted over vast expanses of land that once supported native forests. The quality of these highly modified forests to saproxylic insects, especially the most vulnerable species, remains uncertain (Ulyshen et al. 2018; see Chap. 23). The value of urban environments to saproxylic insects is also an increasingly important question, representing both a challenge and opportunity for community engagement (Horák 2018; see Chap. 24). Although many questions remain about how best to conserve saproxylic insects in managed landscapes, there can be little doubt that these decisions can have important and lasting consequences for this major fraction of our biodiversity.

1.6 Aims and Scope of This Book

The 25 chapters included here are in-depth considerations of prioritized topics but are united by several broad objectives that collectively aim to provide the most global and inclusive synthesis of current knowledge possible. These objectives include (1) incorporating information from regions outside of Europe, (2) recognizing the key roles social insects (e.g., termites, ants, and passalid beetles) play in saproxylic assemblages, (3) highlighting some of the less commonly studied taxa, and (4) addressing the value of highly decomposed wood. The book is organized into four sections. The first section, titled "Diversity," includes chapters addressing particular taxonomic groups. Insect orders are presented in decreasing order of estimated global saproxylic diversity. The three chapters on Coleoptera are thus presented first, followed by Diptera, Hymenoptera, Hemiptera, Lepidoptera, and Isoptera. The second section, titled "Ecology," contains chapters on insect-fungal interactions, nutrient dynamics in decomposing wood, biotic interactions among saproxylic insects, dispersal of saproxylic insects, and seasonality and stratification of saproxylic beetles in tropical forests. The third section is titled "Conservation" and includes chapters on the importance of primary forests to saproxylic insects, the importance of dead wood amount and variety, saproxylic insect conservation under variable retention harvesting, saproxylic insects and fire, saproxylic insects and tree hollows, insects in highly decomposed wood, utilization of nonnative wood by saproxylic insects, and the role of urban environments for saproxylic insects. The fourth section, titled "Methodological advancements," contains a single chapter on molecular tools for assessing saproxylic diversity.

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Part I
Diversity

Chapter 2
General Overview of Saproxylic Coleoptera

Matthew L. Gimmel and Michael L. Ferro

Abstract A broad survey of saproxylic beetles (Coleoptera) from literature and personal observations was conducted, and extensive references were included to serve as a single resource on the topic. Results are summarized in a table featuring all beetle families and subfamilies with saproxylicity indicated for both adults and larvae (where known), along with information on diversity, distribution, habits, habitat, and other relevant notes. A discussion about the prevalence of and evolutionary origins of beetles in relation to the saproxylic habitat, as well as the variety of saproxylic beetle habits by microhabitat, is provided. This initial attempt at an overview of the entire order shows that 122 (about 65%) of the 187 presently recognized beetle families have at least one saproxylic member. However, the state of knowledge of most saproxylic beetle groups is extremely fragmentary, particularly in regard to larval stages and their feeding habits.

2.1 Introduction to Beetles

There are nearly 400,000 described species of beetles, which comprise 40% of all described insect species (Zhang 2011). In fact, one in every four *animal* species (from jellyfish to Javan rhinos) is a beetle. The dominance of this group in terrestrial ecosystems can hardly be overstated—and the dead wood habitat is no exception in this regard. The largest (see Acorn 2006), longest-lived, and geologically oldest beetles are saproxylic. Of the roster of saproxylic insect pests in forests, beetles

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dominate in terms of sheer number of species and, arguably, economic losses (Furniss and Carolin 1977; Solomon 1995).

Beetles (order Coleoptera) fall within the Endopterygota (Holometabola) and therefore undergo so-called complete metamorphosis, passing through anatomically and behaviorally disparate larval, pupal, and adult stages. This temporal division of labor—in which the primary directive of the larval stage is to eat and grow and the function of the adult is to disperse and reproduce, often in a habitat quite different from the larva—is thought to be a key innovation within the insect tree of life. Indeed, although the Endopterygota contains less than half of the 29 extant insect orders, it contains over 80% of described insect species [numbers derived from Zhang (2011)]. When considering saproxylicity among beetle species, the disparate nature of life stages is a key discussion topic, since a frequent strategy among beetles is to have a saproxylic larva and a non-saproxylic adult (see Table 2.1).

The anatomy of beetles is peculiar among insects, making them one of the most distinctive major orders. The most salient feature of beetles is the presence of elytra, mesothoracic wings modified and corneous and not generally used for flight, which most often completely cover the dorsal portions of the meso-metathorax (including flight wings) and abdomen (but can be significantly shortened in some families) and usually meet in a straight line middorsally. Hardened elytra confer obvious protection against would-be attackers. As adults, beetles are often heavily armored throughout and exhibit an ability to retract appendages in defense of predators or to assist in the ability to squeeze into tight spaces. These adaptations are also related to protection from pathogens and from water loss in arid habitats (Lawrence and Newton 1982; Grimaldi and Engel 2005). The general anatomical direction of beetles has been one of fusion and increased sclerotization; however, there are many notable exceptions (e.g., Staphylinidae and many Elateroidea).

2.2 Early Evolution of Beetles in Dead Wood

Perhaps no major order of insects typifies the saproxylic habit more than beetles. Of the “big four” holometabolous insect groups, beetles express the highest diversity in dead wood habitat in terms of both number of taxa present as well as microhabitat diversity. They are probably the only order of Endopterygota that can attribute their evolutionary origins and unique morphology to the dead wood habitat (Hamilton 1978).

During their initial period of diversification, taking place prior to the Early Permian, beetles experienced major anatomical modifications. Most obvious among these was the hardening of the forewings into protective elytra. Other adaptations included dorsoventral flattening of the body, migration of the antennal insertions laterally (lower) on the head, non-projection of the coxae, rotation of the mouthparts into a prognathous aspect, reduction of the mesothorax and its fusion with the metathorax (with concomitant loss of mesothoracic flight muscles), and fusion of the hind coxae with the metathorax (see Grimaldi and Engel (2005) for a good overview).

Based on Lubkin and Engel (2005), the two Early Permian "beetle" families are Tshekardocoleidae (from Tshekarda, Russia) and Oborocoleidae (from Obora, Czech Republic); even though the latter are older (268 Ma), they are only known from scattered elytra. Tshekardocoleidae are conclusively placed as beetles based on mesothoracic structure (Kukalová 1969). Late Permian beetle families include Permocupedidae, Asiocoleidae, Rhombocoleidae, and Schizocoleidae. Before *Permocoleus* (Lubkin and Engel 2005), no Permian beetles were known from North American deposits. These families, collectively referred to as Protocoleoptera (sensu Lawrence and Ślipiński 2013: 4), are distinguished from one another based on the morphology of the elytra. All possess varying degrees of apparent sclerotization of the elytra as visualized through the relative area proportion of "window punctures" (presumably the original wing membrane) versus the principal and interstitial veins separating them.

Recently, however, the fossil beetle *Coleopsis archaica* (Kirejtshuk et al. 2014) has come to light from the earliest Permian of Germany (ca. 295 Ma), which was classified in the Tshekardocoleidae; additionally, the authors synonymized Uralocoleidae and Moravocoleidae with this family. This fossil in part led Toussaint et al. (2017) to re-calibrate and re-date the beetle tree of life dataset of McKenna et al. (2015), shifting the origin of Coleoptera about 80 million years older to approximately 333 Ma (95% CI: 349 to 317 Ma)—a Late Carboniferous origin for the order. An excellent summary of the fossil history of beetles can be found in Lawrence and Ślipiński (2013: 4–8).

Whether the morphological changes outlined above developed in association with saproxylicity is not known with certainty, though present-day forms adapted to this habitat possess these features in particular. The Permian experienced a rapid rise in the dominance of the gymnosperms, while tree lycopods typical of the Carboniferous went extinct, probably in connection with Northern Hemisphere desertification and Southern Hemisphere glaciation (Shear and Kukalová-Peck 1990). Ponomarenko (2003) concluded that the beetle ancestral habit was "xylomycetophagy," with xylophagy and rhizophagy not appearing until later (Jurassic) times. At the very least, evolution of these Protocoleoptera preadapted beetles to a saproxylic lifestyle, allowing them to squeeze into bark crevices without damaging flight wings and other appendages [although Permian Protocoleoptera tended to have more complete wing venation, suggesting that folding mechanisms had not yet developed; see Crowson (1975)]. Additionally, fossils of trees whose bark was probably prone to sloughing were present in the same deposits as these early beetles (Crowson 1981). Unfortunately there are no known fossils of beetle larvae or wood borings in these deposits, so this evidence remains strictly circumstantial. Since larvae lack the same dispersal abilities as adults and are generally tied to their habitats more intimately, form is generally much more closely tied to habits in this life stage. Consequently, larval evidence would go a long way toward informing the habits of the world's first beetles. However, Crowson (1981: 660) believed, based on the presumed groundplan of larval beetle mouthparts, that the first beetle larva was more likely to have been a mold-feeding type than a wood-boring type. Even so, this potentially places the protocoleopteran larvae on or around decaying wood. Although most of the Permian forms are currently grouped into the extinct suborder Protocoleoptera, they are quite similar morphologically to many members of the extant order Archostemata, which contains almost exclusively saproxylic members today.

One report of Carboniferous wood-boring activity by Cichan and Taylor (1982) is suggestive of early beetles in a (presumably aerial) root of a gymnosperm and consists of 0.3–0.6 mm-diameter burrows with accompanying frass. However, it is not until Triassic fossils that we have unambiguous evidence of wood-inhabiting activity in beetles. The remarkable published findings of Walker (1938) based on numerous examples of fossilized wood of *Araucarioxylon arizonicum* Knowlton (Araucariaceae) in the Petrified Forest of Arizona exhibit a wide range of boring patterns, whose similarity to modern boring behavior of Buprestidae and Scolytinae (Curculionidae) was noted. Tapanila and Roberts (2012) later reported ichnofossils of pupation in wood that probably represented early beetles from similar deposits (Late Triassic Chinle Formation of southern Utah). Based on the foregoing evidence, both fossil and ichnofossil, it seems likely that saproxylic beetles have existed since at least the Permian, for nearly 300 million years.

2.3 Habits and Habitats of Saproxylic Beetles

Saproxylic beetles can be conceptually divided up along a variety of axes, including but not limited to (1) taxonomic, (2) feeding type, (3) succession, and (4) microhabitat. Division along the taxonomic axis is accomplished in Table 2.1. As the study of saproxylic beetles progresses, in the future it would be perhaps more biologically useful to divide up these taxa along the feeding type axis—categories might be, e.g., mycophagy, myxomycophagy, xylophagy, predatory, saprophagy, and parasitoids. However, given the incomplete nature of this knowledge at present and the difficulty of ascertaining such information through detailed life history studies and careful labwork, we can only indicate these feeding types where known. An additional axis related to feeding types is succession, in a sense treating the dead log as a forensic entomologist treats a dead body; categorizing beetles as early, middle, and late (veteris) in relation to the death of the tree; and recognizing important differences related to “carcass” size, position, geography, tree species, and macrohabitat. For the discussion below we divide up saproxylic beetles into categories based on microhabitat, for this can be directly and unambiguously observed in the field. The flow of categories below progresses (roughly) from the interior of a dead log to the periphery of dead-wood-dependent habitats, with a discussion of aquatic dead-wood habitats appearing at the end. For a lengthy discussion of the European saproxylic beetle fauna by habitat, see Merkl (2016).

2.3.1 Wood-Inhabiting Taxa

This subcategory is typified by classic wood-boring taxa, which tend to sport strong, stout mandibles in whichever stage actively tunnels through wood. Larvae that are borers are more prevalent than adults and tend to be more or less cylindrical and have a poorly sclerotized cuticle, and the head capsule tends to be retracted into the thorax. Some adults, however, are wood-boring and include Bostrichidae, Ptinidae, and Curculionidae (Lawrence and Ślipiński 2013). Beetles in the first two groups are often pests of wood inside houses (Lewis and Seybold 2010). Other groups include certain Curculionidae (Platypodinae and Scolytinae: Xyleborini), Cerambycidae, Passalidae, Buprestidae, Lymexylidae, Ptinidae, and Bostrichidae. For a more detailed discussion of the ambrosia beetles (Curculionidae: Platypodinae and certain Scolytinae), see Sect. 2.3.7.

Cerambycidae, which contain an enormous number of wood-borers ("round-headed borers"), whose adults do not tunnel through wood, typically start as larvae by boring subcortically and then bore directly into sapwood and heartwood as they develop (Evans 1975). Buprestidae larvae ("flat-headed borers") often have similar habits, boring through wood just under the cambium before plunging into the wood toward the center of the log to finish larval development and to pupate.

As woody debris reaches an advanced stage of decay, it plays host to a distinct fauna. Especially rotten wood is known to be a classic habitat for scarabaeoid grubs, particularly of the families Lucanidae, Passalidae, and Scarabaeidae (chiefly the subfamilies Cetoniinae and Dynastinae), a fact well-known among enthusiasts of those groups, while larvae of Callirhipidae are typical of white-rotted wood in an advanced decay stage (Lawrence and Ślipiński 2013). However, Ferro et al. (2012a) demonstrated a distinct fauna of smaller beetles within the final decay stage of hardwood logs in an eastern North American forest (Ferro 2018, see Chap. 22). For an in-depth discussion of the habits of Passalidae and Lucanidae, see Ulyshen (2018) and Huang (2018) (Chaps. 3 and 4, respectively).

Some beetles seem to be typical of red-colored rotten wood. Notable examples include *Micromalthus debilis* LeConte (Micromalthidae); *Schizophilus subrufus* (Randall) of the Eucnemidae (Otto and Young 1998); members of the small family Prostomidae, which prefer wood with a mud- or clay-like consistency (Lawrence 1991; Klimaszewski and Watt 1997; Lawrence and Ślipiński 2013); the Nearctic *Priognathus monilicornis* (Randall) (Pythidae) (Pollock 2002a); and certain terrestrial larvae of Scirtidae from the Southern Hemisphere (Lawrence and Ślipiński 2013).

2.3.2 Subcortical Taxa, Including Phloem Feeders

The subcortical group is dominated, both in terms of number of species and abundance, by the "bark beetles" of the subfamily Scolytinae (Curculionidae). An extremely wide variety of other beetle groups, however, are typical of this habitat. Cucujidae, Laemophloeidae, and Silvanidae, collectively known as "flat bark beetles," contain adults and larvae often highly flattened and specialized for living under bark. Their habits are not entirely clear, but many are at least facultative predators and are probably opportunistic scavengers or saprophages. Predatory beetles typical of this habitat, and often associated with Scolytinae, are the Histeridae, Trogossitidae (Trogossitinae), Carabidae (Bembidiini: Tachyina), Synteliidae, Chaetosomatidae, Thanerocleridae, Cleridae, Brentidae, larvae of Brachypsectridae, Cantharidae, Lampyridae, Rhadalidae, adults of Elateridae, Bothrideridae, and certain Zopheridae (Colydiinae). Parasitoid beetles include Bothrideridae and Passandridae. Other taxa present in this microhabitat, probably feeding upon fungal mycelium, are Biphyllidae, Cerylonidae, Cryptophagidae, Endomychidae, Teredidae, Carabidae (Rhysodinae), Euxestidae, Jacobsoniidae, Eupsilobiidae, Boridae, Pythidae, Pyrochroidae, Salpingidae, Monotomidae, Myraboliidae, Nitidulidae, Curculionidae (Cossoninae), larvae of Synchroidae, Mycteridae, and Scraptiidae.

Since microclimates on even a single log can differ greatly (Evans 1975: 159, from Geiger 1950: 235, also Chauvin 1967), their beetle faunas correspondingly differ. The wet, waterlogged parts of the wood-bark interface have a distinctive beetle fauna, apparently most diverse in the Southern Hemisphere, which may contain Hydrophilidae (especially Cylominae) and larvae of Scirtidae (M. Fikáček, pers. com.; MLG, pers. obs.).

2.3.3 Dead Wood Surface (Including Contact with Substrate)

A large number of beetles find optimum shelter under dead logs, since they provide a relatively stable microclimate along the ground surface, with much lower thermal conductivity than rocks and with high moisture retention properties. In addition to those beetles obligately associated with wood-rotting fungi (which often reach their peak toward the more moist underside), adult and larval beetles typical of this habitat include in particular Carabidae, Leiodidae (Camiarinae), Staphylinidae, Tenebrionidae, and Zopheridae.

A large number of adult beetles occur on the surface of dead wood at night; some of these are predacious (e.g., Carabidae), but many of these graze on lichens and microfungi and may include certain Tenebrionidae (especially Stenochiinae), Cerambycidae, Erotylidae, and Chalcodryidae. Adults of Buprestidae are also typical of this habitat but are mostly diurnal. Some larvae of Cryptocephalinae (Chrysomelidae) graze the outer layer of dead twigs (Chamorro 2014). Among predacious Carabidae, remarkable larval examples include tiger beetles of the genera *Collyris*, *Ctenostoma*, *Therates*, and some *Tricondyla*, which occupy tunnels opening to the bark surface, from which they hunt prey nocturnally (Balduf 1935; Trautner and Schawaller 1996; Pearson and Vogler 2001; excellent illustrations of burrows in Zikan 1929).

An interesting community of beetles is also associated with wounded parts of living trees (sap flows and slime fluxes), a microhabitat often infected with bacteria, yeasts, and other microfungi. Members of the family Nosodendridae are perhaps the most strikingly adapted beetles in this peculiar habitat, the larvae possessing mostly dorsal spiracles, with the last pair being located at the apex of an elongated terminal abdominal segment, allowing the larvae to be totally immersed in the slime flux (Crowson 1981; Leschen and Beutel 2010b). The larvae also possess a rough dorsal surface which allows debris to adhere and causes the larvae to virtually disappear in their habitat. Other taxa typical in the sap flow or slime flux microhabitat include *Peltastica* (Derodontidae; Leschen and Beutel 2010a), Sphaeritidae (Newton 2016a), some Histeridae (Kovarik and Caterino 2016), adult Lucanidae (Scholtz and Grebennikov 2016), *Euderia* (Bostrichidae; Klimaszewski and Watt 1997), and many Nitidulidae (Jelínek et al. 2010).

Tree holes (or tree hollows) with an accumulation of woody debris and other organic matter represent unique environments with a distinct community. These habitats are covered in detail by Micó (2018, see Chap. 21). Coleoptera species in these habitats are dominated by certain Histeridae, Ptiliidae, Staphylinidae (especially Pselaphinae), Hybosoridae, Scarabaeidae, Elateridae (larval), Ciidae, Tenebrionidae, and Curculionidae (Park et al. 1950; Park and Auerbach 1954; pers. obs.).

2.3.4 Wood-Rotting Fungal Bodies and Slime Molds

Inhabiting fungal fruiting bodies on a dead wood substrate is one of the largest single categories of saproxylicity in beetles, and many beetle families possess this habit (Crowson 1981; Lawrence 1989). Perhaps most typical of this habit are the families Staphylinidae (especially subfamilies Aleocharinae, Oxyporinae, and Tachyporinae) and Erotylidae. Significant numbers or percentages of Tetratomidae, Tenebrionidae, Zopheridae, Ciidae, Ptiliidae, Anthribidae, Nitidulidae, Endomychidae, Anamorphidae, Latridiidae, Discolomatidae, Endecatomidae, Phloiophilidae, Mycetophagidae, Hobartiidae, Cryptophagidae, Lamingtoniidae, and Leiodidae also occur in this habitat. Gilled mushrooms (Agaricales) and polypore-style basidiomycetes harbor the greatest number of beetles, though significant associations occur in other wood-inhabiting fungi (including Ascomycetes, see Crowson 1984) as well. Certain members of *Derodontus* (Derodontidae) are partial to the "tooth fungi" (Hydnaceae) (Leschen 1994) and members of *Litochropus* (Phalacridae) inhabit and consume the woody galls of *Daldinia* (Ascomycota: Xylariales) (Gimmel 2013). Lawrence (1977) reported on a broad collection of beetles from *Hypoxylon* on dead oak and discussed this habitat in detail. For an excellent summary of mycophagy among Coleoptera, see Lawrence (1989).

Inhabitants of myxomycetes (slime molds), which are most often associated with woody debris, include certain Leiodidae (particularly Leiodinae: Agathidiini) (Newton 1984), certain Carabidae, Staphylinidae, Clambidae, Eucinetidae, Cerylonidae, and Latridiidae (Forrester and McHugh 2010). Perhaps most intimately tied to this habitat are members of the family Sphindidae, whose members are known to feed and develop only in myxomycetes, both as larvae and adults.

2.3.5 Other Woody Plant Parts

Other woody or corky plant tissues (cones, galls, woody carps, etc.) are inhabited by a variety of small beetles, including a number of Scolytinae and Ptinidae. Scolytines often found in fallen woody carps include *Araptus* and *Hypothenemus* species; species of *Conophthorus* develop in cones of *Pinus*; one species of *Spermophthorus* has been reported from a gall (Wood 1982). Members of one spondylidine cerambycid genus, *Paratimia*, develop in pine cones (Svacha and Lawrence 2014b). As for Ptinidae, species of *Ernobius* can be found inhabiting cones of conifers (Ruckes 1957), while *Ozognathus* larvae inhabit oak galls (Philips and Bell 2010). Ommatidae are suspected of developing in underground roots, though this has not been confirmed (Hörnschemeyer and Beutel 2016). Root-feeding larvae in woody plants are typical of many Scarabaeidae, Elateridae, Cerambycidae and Curculionidae (Evans 1975), and certain termitophilous beetles are associated with termites whose nests occupy such roots (e.g., *Anorus* of the Dascillidae; Lawrence 2016b).

2.3.6 Aquatic Saproxylic Habitats

2.3.6.1 Waterlogged and Submerged Woody Debris

Several families of beetles are typical of wood submerged in lentic or lotic environments, including Amphizoidae (adults and larvae), Lutrochidae (adults and larvae), Cneoglossidae (larvae only), some Elmidae (adults and larvae), some Dryopidae (adults only), some Hydraenidae (adults only), some Psephenidae (larvae only), and some Eulichadidae (larvae only; Ivie 2016). Larvae of certain Lutrochidae and Elmidae may even burrow into submerged wood (Valente-Neto and Fonseca-Gessner 2011). Waterlogged wood may harbor larvae of Oedemeridae and larvae of some Ptilodactylidae (Ptilodactylinae) (Lawrence and Ślipiński 2013: 237). Many larvae of Scirtidae also forage on submerged wood (Lawrence 2016a). Larvae of Oedemeridae may inhabit intermittently buried pieces of driftwood (Kriska 2002); the so-called wharf borer, *Nacerdes melanura* (Linnaeus), even inhabits wood pilings and other structural timber inundated by seawater and has the potential to be a minor pest (Arnett 1951). As indicated by Dudley and Anderson (1982), wood-degrading activity of aquatic beetles is relatively minor, at least in temperate regions.

2.3.6.2 Water Trapped in Tree and Log Holes

These peculiar habitats play host to a few aquatic Coleoptera, primarily including larvae of Scirtidae and adults and larvae of Dytiscidae. A summary of beetles recorded from container habitats (including water in saproxylic environments) was provided by Kitching (2000, Table A.13). Scirtidae larvae are actively moving detritus feeders mostly present among debris in the hole but also crawling inverted just under the water surface (Lawrence 2016a). Dytiscidae are predacious, primarily on other invertebrates, as both adults and larvae, and are active swimmers through the water column. A few genera of this family are present in phytotelmata broadly, including tree and log holes, and the fauna of these habitats is distinctive (Miller and Bergsten 2016); however, most of these are probably not restricted to particular types of phytotelmata. A remarkable southeast Asian species of Nitidulidae, *Amphicrossus japonicus* Reitter, is an aquatic predator of mosquito larvae in injured bamboo culms and stumps that have filled with water. Adults seize mosquito larvae with their front legs (Kovac et al. 2007).

2.3.7 Ambrosia Beetles

2.3.7.1 Saproxylic Beetle Agriculture

Three major groups of beetles may be referred to as “ambrosia beetles”: Lymexylidae; Curculionidae, Scolytinae (various tribes); and Curculionidae, Platypodinae. The nature of the ambrosia habit in Lymexylidae is not nearly as developed as in the curculionid lineages, but they were probably the first group to evolve such habits (Wheeler 1986). In this family, it is pouches in the female genitalia that act as mycangia, transporting fungal inoculum to the site of egg laying. The fungus (which belongs to Ascoidaceae), while containing nutrients consumed by the larvae, probably serves to condition the wood for tunneling by the larvae (Wheeler 1986).

Unlike their relatives that create two-dimensional superficial galleries under bark, most ambrosia beetles in Scolytinae and Platypodinae bore directly into wood, across the grain, where the larvae feed not on the wood itself but exclusively on fungi cultivated in the tunnels by the adults. These specialized fungi (primarily Ophiostomales and Microascales) are delivered using mycangia, which are cuticular invaginations on the beetle cuticle that transport fungal inoculum. Three types of mycangia are known in Xyleborini: mandibular, mesothoracic, and elytral (Cognato et al. 2011) (for a discussion of the distribution of mycangia among beetles, see Grebennikov and Leschen 2010). As the fungi grow, they form a dark carpet of conidia that are then fed upon by the larvae (Jordal and Cognato 2012). Not only are the beetles totally dependent on the fungus for food, but they apparently also cannot complete development without the presence of certain fungal steroids (Jordal and Cognato 2012).

About 2000 species of Scolytinae have evolved to use these cultivated fungi as a primary food source, apparently at least ten separate times, represented by the following lineages: Corthylini, Corthylina (460 spp.); Scolytini, *Camptocerus* (30 spp.); Bothrosternini, *Bothrosternus* and *Eupagiocerus* (16 spp.); Xyleborini (1300 spp.); Xyloterini (24 spp.); Scolytoplatypodini (32 spp.); Hyorrhynchini

(15 spp.); Premnobiini (25 spp.); and one species each of *Hypothenemus* (Cryphalini) and *Scolytodes* (Hexacolini) (Jordal and Cognato 2012). Xyleborini are the most widespread and dominant group and comprise about 30 genera and 1300 species that are concentrated in tropical regions but contain a number of temperate species as well (Cognato et al. 2011; Jordal and Cognato 2012). The habit of fungus cultivation among Scolytinae is apparently less than 50 million years old, with Xyleborini developing this trait only about 20 million years ago. This is corroborated by both a dated phylogenetic hypothesis (Jordal and Cognato 2012) and lack of presence of Xyleborini in Dominican amber which, however, does contain inclusions of Corthylina and Platypodinae (Bright and Poinar 1994).

The Platypodinae ("pinhole borers"), the other main beetle group with advanced fungus-cultivating habits, is probably the oldest such group of insects, estimated at around 80 ma or older (Jordal 2015), and presumably the habit evolved only once within the group. All except two of the about 1400 described species are ambrosia beetles, and they occur primarily in tropical areas (Jordal 2015). However, unlike the Xyleborini, all Platypodinae are monogamous and not haplodiploid and do not engage in parthenogenesis. The only known eusocial beetle is the Australian platypodine species *Austroplatypus incompertus* (Schedl) (Kent and Simpson 1992).

Ambrosia beetles have a number of advantages through their specialized habits. The beetles are able to attack a wide variety of tree hosts since their fungi have wide tolerances, a particular advantage in hyper-diverse tropical regions. In addition, the Xyleborini have evolved haplodiploidy, with the flightless dwarf (haploid) males from unfertilized eggs being rarely produced, and matings occurring primarily between siblings. The fact that a colony can be started by a single female allows them to colonize rapidly and efficiently (Cognato et al. 2011). Because they tend to be so widespread and abundant and among the first colonizers of newly created saproxylic habitats, ambrosia beetle populations in wood generally bring with them or otherwise attract a veritable ecosystem of associates, including mutualists, predators, and commensals. Interestingly, ambrosia beetles are much less likely to kill healthy host trees than certain scolytine bark beetle counterparts which spread so-called blue-staining pathogenic fungi (Evans 1975; Crowson 1981; see above), with a few exceptions, such as Fusarium dieback associated with shot-hole borers (*Euwallacea* spp.).

2.3.8 Notable Unique Structures, Adaptations, and Mysteries

2.3.8.1 Unique Structures

One extraordinary adaptation of a few saproxylic beetles that deserves mention is the possession of infrared-sensitive pits on the adult cuticle. These structures are located in the thoracic sclerites or abdomen and apparently serve as detectors for beetles seeking to oviposit in fire-killed wood. The structures are known to occur in two phylogenetically distant families: Buprestidae [represented by *Melanophila* (s.str.)

and *Merimna atrata* (Gory and Laporte)] and Acanthocnemidae (containing only *Acanthocnemus nigricans* Hope). In *Melanophila* (s.str.), each of a pair of pits is located on the metaventrite, adjacent to the mesocoxal cavity. Each pit contains a number of spherical sensillae (Evans 1966). In *Merimna atrata*, these organs are similar, but 1–3 pairs occur laterally on abdominal ventrites 2–4 (Mainz et al. 2004). In *Acanthocnemus nigricans*, each of a pair of pits is located along the notosternal suture of the prothorax (anterior to procoxae) and is made up of a flat disc overlying a small airspace. A large number of sensillae are located on the surface of the disc, and the type of infrared receptor is quite different from that of the buprestids (Kreiss et al. 2005).

Larvae of the family Eucnemidae are unique among Coleoptera for several structures: (1) non-opposing mandibles that curve outward rather than inward (also possessed by some Elateridae: Cardiophorinae), (2) microtrichial patches on most body segments, and (3) areoles (median oval shiny structures) on most body segments (Muona and Teräväinen 2008). All of these structures appear to be adaptations for squeezing through hard, often fluid-filled wood. When the mandibular muscles contract, the mandibular apices move away from each other (Van Horn 1909). The microtrichial patches serve as cuticular anchors as the legless larva creeps forward using waves of internal fluid pressure, while the areoles apparently drain excess water from the larva (Muona and Teräväinen 2008).

As a group, beetles are well-known for their tendency to evolve elaborate weaponry as adults, usually horns or other cuticular projections, especially among males. Interestingly, this occurs primarily in saproxylic taxa, especially those specializing on well-decayed wood, sap flows, or wood-decaying fungi, though it also occurs in taxa associated with other habitats (e.g., dung). Saproxylic taxa possessing this trait include Scarabaeidae (several subfamilies), Lucanidae, Staphylinidae (Piestinae), Ptinidae, Ciidae, and Tenebrionidae. One explanation for this phenomenon is that habitats that are highly localized and defendable (e.g., those listed above), in combination with unrestricted terrain for fighting, such as the surface of a log or tree trunk, provide selection pressure to evolve fight-performance-related structures (see Emlen (2008) for an extensive discussion).

2.3.8.2 Parasitoids

There are not many parasitoids among beetles, but two saproxylic families are exclusively ectoparasitoid as larvae, Bothrideridae and Passandridae, the former being parasitic on larvae and pupae of wood-boring beetles, as well as Hymenoptera, Xiphydriidae and Apidae (*Xylocopa*). Passandridae are also parasites of various wood-boring beetles (especially Phytophaga) and larval Hymenoptera. The most advanced forms, however, are represented by the endoparasitoid larvae of Ripiphoridae, of which members of two of the five subfamilies (Hemirhipidiinae and Pelecotominae) are known to attack wood-boring beetle larvae, particularly of the families Ptinidae and Cerambycidae (Lawrence et al. 2010b).

As pointed out by Crowson (1981: 555), the dividing line between predators and parasitoids is a blurry one, particularly in saproxylic forms. Brentidae and Zopheridae contain some species inhabiting brood burrows of Scolytinae; Cleridae (e.g., *Orthopleura*) contain more-or-less parasitic forms on wood-boring beetle larvae (Crowson 1981: 555). Intermediate forms between predators and parasitoids exist among members of the zopherid genus *Colydium*, which are often present with *Platypus*, and *Aulonium* which is associated with *Scolytus* (Crowson 1981: 556). Adults of *Lasconotus* (Zopheridae) often have a concave dorsal surface, presumably to assist in squeezing past obstacles among the burrows of Scolytinae (MLG, pers. obs.).

2.3.8.3 Sociality

Eusociality and even subsociality are quite rare among beetles, but it is notable that these traits are only known to occur in saproxylic species. The most widespread and well-known among these taxa are within the Passalidae (Ulyshen 2018, see Chap. 3). Less well-known subsocial species are the passalid-looking members of the genus *Phrenapates* (Tenebrionidae: Phrenapatinae) (Lawrence and Ślipiński 2013). As mentioned previously, the only known eusocial beetle is *Austroplatypus incompertus* (Schedl) (Curculionidae: Platypodinae), which lives in galleries in the heartwood of *Eucalyptus* trees in southeastern Australia (Kent and Simpson 1992).

2.3.8.4 A Mystery

The family Trictenotomidae contains some of the largest adult beetles in the world, which are among the most popular collectors' items in Coleoptera. There are two genera (*Autocrates* and *Trictenotoma*) that occur in southern and eastern Asia. However, the presumed saproxylic larva has apparently only been found once, in Java in association with "débris of pupae and imagines" of *Trictenotoma childreni* Gray. This remarkable larva measured 12 cm long (Gahan 1908). Unfortunately the whereabouts of this specimen are currently unknown, and additional collecting efforts have so far not been fruitful (M. Barclay, pers. com.). For further notes on the life history of Trictenotomidae, see Pollock and Telnov (2010).

2.4 Overview of Saproxylic Beetles (Table 2.1)

While a few families of saproxylic beetles are dominant on the research radar of most dead wood entomologists, one of the primary purposes of this chapter, Table 2.1 in particular, is to highlight some lesser-known but biologically or numerically significant groups. Well-known groups with large numbers of well-studied species include Carabidae, Scarabaeoidea, Buprestidae, Elateridae, Bostrichidae, Cleridae,

Table 2.1 Annotated checklist of all world beetle families and subfamilies [modified from Beutel and Leschen (2016a)], with saproxylic groups indicated

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Suborder Archostemata (4)									All known L assoc with fungus-infected wood
1	**Ommatidae**	X	6	Most	Aus, SAm	Away	Unk	In WD	Sapro	Habits very poorly known, but apparently saproxylic
	Tetraphalerinae	X	2	Most	SAm	Away	Unk	In WD	Sapro	May live on roots or stems of shrubs; L unk (Hörnschemeyer and Beutel 2016)
	Ommatinae	X	4	Most	Aus	Away	Unk	In WD	Sapro	L assoc with dead wood or tree roots; only one presumed L known (Hörnschemeyer and Beutel 2016)
2	**Crowsoniellidae**									L and habits unk
3	**Micromalthidae**	X	1	All	NW, adv WW	In WD	Sapro	In WD	Sapro	Entire life cycle takes place in red rotten wood (Pollock and Normark 2002)
4	**Cupedidae**	X	31	All	WW exc Eur	In WD; away	Poll	In WD	Sapro	Subcortical; all known L feed on fungus-infected wood; pupation takes place in wood (Snyder 1956; Neboiss 1968)
	Priacminae	X	3	All	NW	In WD; away	Unk	In WD	Sapro	L habits unstudied, certainly saproxylic
	Cupedinae	X	28	All	WW exc Eur	In WD; away	Poll	In WD	Sapro	Subcortical; all known L feed on fungus-infected wood; pupation takes place in wood (Snyder 1956; Neboiss 1968)
	Suborder Myxophaga (4)									

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
5	**Lepiceridae**									Aquatic, grazers
6	**Torridincolidae**									Aquatic, algae grazers
7	**Hydroscaphidae**									Aquatic, algae grazers
8	**Sphaeriusidae**									Aquatic, algae grazers
	Suborder Adephaga (10)									
9	**Gyrinidae**									Aquatic, pred
	Non-saproxylic subfamilies: Gyrininae, Heterogyrinae, Spanglerogyrinae									
10	**Haliplidae**									Aquatic omnivores
11	**Trachypachidae**									Ground dwelling, probably pred
12	**Meruidae**									Aquatic in rock seepages
13	**Noteridae**									Aquatic omnivores
	Non-saproxylic subfamilies: Noterinae, Notomicrinae									
14	**Amphizoidae**	X	5	Most	Hol	On WD	Pred	On WD	Pred	A and L cling to aquatic woody debris (Dettner 2016; MLG, pers. obs.)
15	**Aspidytidae**									Aquatic, pred
16	**Hygrobiidae**									Aquatic, pred
17	**Dytiscidae**	X	4300	Few	WW	Water-filled tree holes	Sapro, pred	Water-filled tree holes	Sapro, pred	A few spp. occur in water-filled tree holes
	Laccophilinae	X	200	Few	WW	Water-filled tree holes	Pred	Water-filled tree holes	Pred	Data from Miller and Bergsten (2016)

	Copelatinae	X	700	Few	WW	Water-filled tree holes	Pred	Water-filled tree holes	Pred	Data from Miller and Bergsten (2016)
	Hydroporinae	X	2200	Few	WW	Water-filled tree holes	Pred	Water-filled tree holes	Pred	Data from Miller and Bergsten (2016)
	Non-saproxylic subfamilies: Agabinae, Colymbetinae, Coptotominae, Dytiscinae, Hydrodytinae, Lancetinae, Matinae									
18	**Carabidae**	X	40,000	Few	WW	In WD	Pred	In WD	Pred	Subcortical, many spp. may seek shelter under bark, few are consistently there
	Paussinae	X	750	Some	WW	In WD	Pred	In WD	Pred	L and A found under bark, in rotting wood, or on trees at night (Moore 2008); L may construct galleries in wood (Moore and Di Giulio 2006)
	Cicindelinae	X	2000	Few	WW	Away	Pred	In WD	Pred	Rarely L in rotten wood (Arndt et al. 2016); L of some found in tunnels in bark (Zikan 1929; Balduf 1935; Trautner and Schawaller 1996; Pearson and Vogler 2001)
	Carabinae	X	1300	Few	WW	In WD	Pred	Away	Pred	A of especially *Scaphinotus* can be found under bark or in rotten wood or tree hollows or under driftwood (Erwin 2007)
	Rhysodinae	X	170	All	WW	In WD	Myxo, myco	In WD	Myxo, myco	Subcortical; A and L found in logs, stumps, or roots, probably feed on slime molds (Beutel 2016)
	Psydrinae	X	6	Some	Nea, Aus, Africa, w Pal	In WD	Pred	Unk	Unk	*Psydrus piceus* found under bark of large coniferous trees (Bousquet 2012)

(continued)

Table 2.1 (continued)

#	Taxon	Sap^a	#Spp^b	% S^c	Regions^d	Adult found^e	A food^f	Larva found^e	L food^f	Notes
	Siagoninae	X	100	Most	Africa, Pal, SAm	In WD	Pred	?	Unk	Subcortical, esp *Cymbionotum*, *Siagona*, *Enceladus*
	Trechinae	X	4000	Few	WW	In WD	Pred	?	Unk	Subcortical, esp certain Tachyina (*Tachys* and relatives)
	Pseudomorphinae	X	500	Most	Aus, Or	In WD	Pred	In ant or termite nests in soil or canopy	Unk	A subcortical (Arndt et al. 2016)
	Harpalinae	X	20,000	Some	WW	In WD	Pred	In WD		A subcortical, esp Morionini, Platynini, and many Pterostichini (MLG, pers. obs.)
	Non-saproxylic subfamilies: Apotominae, Brachininae, Broscinae, Cicindinae, Clivininae, Elaphrinae, Gehringiinae, Hiletinae, Loricerinae, Melaeninae, Migadopinae, Moriomorphinae, Nebriinae, Nototylinae, Omophroninae, Promecognathinae, Scaritinae									
	Suborder Polyphaga									
	?Series ?Super-family (1)									
19	**Jurodidae**									L and habits unk
	Series Scirtiformia									
	Superfamily Scirtoidea (4)									
20	**Decliniidae**									A apparently poll, L unk
21	**Eucinetidae**	X	40	All	WW	In WD	Myxo, myco	In WD	Myxo, myco	A and L in rotting wood; at least some myxo and myco (Leschen 2016a)
22	**Clambidae**	X	150	Some	WW	In WD	Myco, myxo	In, on WD	Myco, myxo	A and L fungus feeding in various habitats (Leschen 2016b)

	Calyptomerinae	X	4	All	Hol (adv Aus, Afr)	On WD	Myco	In, on WD	Myco	A of *Calyptomerus* found on dead/dying spruce in New Mexico (Hinson and Buss 2014)
	Acalyptomerinae	X	4	Some	Neo, Afr, Or	In, on WD	Myco	In, on WD	Myco	A collected from rotten palm litter, under log, and from *Auricularia* mushrooms (Endrödy-Younga 1998)
	Clambinae	X	130	Some	WW	On WD	Myco, myxo	In, on WD	Myco, myxo	A of *Sphaerothorax* found on tree stumps, in heap of *Eucalyptus* branches, in cut bamboo (Klimaszewski and Watt 1997)
23	**Scirtidae**	X	800	few	WW	Away	Pred, non	Water-filled tree holes	Sapro	Some L in tree and log holes (Kitching 2000), pupation of some in upper dryer parts of tree holes; L of other aquatic spp. forage on submerged wood (Lawrence 2016a)
	Scirtinae	X	800	few	WW	Away	Pred, non	Water-filled tree holes	Sapro	Some L in tree and log holes, pupation of some in upper dryer parts of tree holes; L of other aquatic spp. forage on submerged wood (Lawrence 2016a); other L terrestrial in wood (Ruta et al. 2017)
	Non-saproxylic subfamilies: Nipponocyphoninae, Stenocyphoninae									
	Series Derodontiformia									
	Superfamily Derodontoidea (1)									
24	**Derodontidae**	X	37	Some	Hol, STem	On fungi, sap flows	Myco	On fungi, sap flows	Myco	A few spp. assoc with woody debris

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Peltasticinae	X	2	All	Hol	At sap flows	Myco	At sap flows	Myco	*Peltastica* A and L feed on fungi and suspended nutrients in ferm sap (Leschen and Beutel 2010a)
	Derodontinae	X	14	Some	Hol, STem	On fungi	Myco	On fungi	Myco	Some *Derodontus* A and L on wood-dec fungi (Leschen 1994; Leschen and Beutel 2010a)
	Non-saproxylic subfamily: Laricobiinae (pred on Adelgidae or on sooty molds on living trees)									
	?Series ?Superfamily (1)									
25	**Jacobsoniidae**	X	20	Most	WW	In WD	Sapro	in WD	Sapro	*Saphophagus* subcortical (Lawrence and Leschen 2010a; MLG, pers. obs.), other gen may be found in rotten wood (Lawrence and Leschen 2010a)
	Series Staphyliniformia									
	Superfamily Hydrophiloidea (9)									
26	**Helophoridae**									Aquatic omnivores
27	**Epimetopidae**									Aquatic omnivores
28	**Georissidae**									Aquatic omnivores
29	**Hydrochidae**									Aquatic omnivores
30	**Spercheidae**									Aquatic omnivores
31	**Hydrophilidae**	X	2932	Few	WW	In WD	Sapro	In WD	Sapro	Most spp. aquatic; terrestrial forms assoc with rotting material; in tree holes in southern Aus (Kitching 2000)

	Cylominae	X	48	Few	Aus, Neo, Afr	In WD	Sapro	In WD	Sapro	Some spp. occur in dec logs (M. Fikáček, pers. com.; MLG, pers. obs.)
	Sphaeridiinae	X	950	Few	WW	In WD	Sapro	In WD	Sapro	Smetana (1978) recorded *Cercyon assecla* Smetana, *Cryptopleurum subtile* Sharp, and *Cryptopleurum minutum* (Fabricius) from “fresh wood-cuttings soaked with sap”; Costa et al. (1988) recorded *Dactylosternum subrotundatum* (Fabricius) from well-rotted and wet fallen logs; some *Cercyon* assoc with beach driftwood
	Non-saproxylic subfamilies: Acidocerinae, Chaetarthriinae, Enochrinae, Hydrophilinae									
32	**Sphaeritidae**	X	5	Few	Hol	On WD	Pred	On WD	Pred	A and L from sap flows of dying/dead trees and stumps (Newton 2016a)
33	**Synteliidae**	X	9	Most	E Asia, CAm	In WD	Pred	In WD	Pred	Subcortical in dec logs, some at sap flows, others in moist interior of dec columnar cacti; pred on diptera; pupate under bark (Newton 2016b)
34	**Histeridae**	X	3900	Some	WW	In WD	Pred	In WD	Pred	Subcortical, some in tree holes or wood boring beetle tunnels, fungal spore feeders in older dead trees and rotting wood, or assoc with bracket and polypore fungi
	Niponiinae	X	21	All	Pal, Or	In WD	Pred	In WD	Pred	In wood-boring beetle tunnels (Kovarik and Caterino 2016)
	Chlamydopsinae	X	180	Few	Or, Aus	In WD	Pred	?	Unk	One sp. known from termite nest in Aus (Kovarik and Caterino 2016)
	Onthophilinae	X	80	Some	WW	In WD	Pred, myco	In WD	Pred	One *Onthophilus* known from ferm sap, *Epiechinus* myco in rotten wood (Kovarik and Caterino 2016)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Dendrophilinae	X	460	Some	WW	In WD	Pred, myco	In WD	Pred	Many under bark of fresh wood (esp. Paromalini), a few in tree holes (*Bacanius*, *Dendrophilus*), some in bark beetle galleries (*Paromalus*), in rotten wood (*Bacanius*, *Cyclobacanius*) (Kovarik and Caterino 2016)
	Abraeinae	X	440	Most	WW	In WD	Pred, myco	In WD	Pred	Some in tree holes (*Abraeus*, *Chaetabraeus*), some in bark beetle tunnels (Plegaderini, Teretriini), some in rotten wood (*Aeletes*, *Acritus*) (Kovarik and Caterino 2016)
	Trypeticinae	X	110	All	Afr, Or, Aus	In WD	Pred	In WD	Pred	Many in bark beetle tunnels, one *Pygocoelis* in rotten wood (Kovarik and Caterino 2016)
	Trypanaeinae	X	75	All	Neo	In WD	Pred	In WD	Pred	In wood-boring beetle tunnels (Kovarik and Caterino 2016)
	Saprininae	X	620	Few	WW	In WD	Pred	In WD	Pred	*Gnathoncus* in tree holes, some coastal *Hypocaccus* under driftwood (Kovarik and Caterino 2016)
	Tribalinae	X	215	Few	WW	In WD	Pred, myco	In WD	Pred	*Epierus* in wood-boring beetle tunnels and in rotten wood, *Tribalus* and *Parepierus* in rotten wood (Kovarik and Caterino 2016)
	Histerinae	X	1950	Some	WW	In WD	Pred, myco	In WD	Pred	Many under bark of fresh wood (esp. Hololeptini), some in tree holes, some at sap fluxes, some in bark beetle tunnels, some in rotten wood (Kovarik and Caterino 2016)

	Haeteriinae	X	330	Few	WW	In WD	Pred	In WD	Pred	Some assoc with wood-inhabiting ants and termites (Kovarik and Caterino 2016)
	Superfamily Staphylinoidea (6)									
35	**Hydraenidae**	X	1300	Few	WW	On WD	Sapro?	Away	Unk	Aquatic A of *Hydraena vandykei* saproxylic (Dudley and Anderson 1982)
	Hydraeninae	X	1000	Few	WW	On WD	Sapro?	Away	Unk	Aquatic A of *Hydraena vandykei* saproxylic (Dudley and Anderson 1982)
	Non-saproxylic subfamilies: Ochthebiinae, Orchymontiinae, Prosthetopinae									
36	**Ptiliidae**	X	600	Some	WW	In WD	Myco	In WD	Myco	Some A in rotten wood, polypore fungi (Hall 2016)
	Ptiliinae	X	400	Some	WW	In WD	Myco	In WD	Myco	Tree-related niches, tree holes, rotting logs, etc., also wood-related habitats near social insects
	Nanosellinae	X	100	Most	WW	In fungi	Myco	In fungi	Myco	Usu assoc with polypore fungi (Newton 1984)
	Non-saproxylic subfamilies: Acrotrichinae (primarily leaf litter, ant refuse piles), Cephaloplectinae (myrmecophiles)									
37	**Agyrtidae**	X	61	Some	WW exc Aus, Afr	In WD	Myco, sapro	In WD	Myco, sapro	Several spp. assoc with woody debris (Newton 2016c)
	Agyrtinae	X	25	Some	Hol, Or	In WD	Myco, sapro	In WD	Myco, sapro	*Ipelates latus* A assoc with dec logs and fungi (Newton 2016c)
	Non-saproxylic subfamilies: Necrophilinae, Pterolomatinae									
38	**Leiodidae**	X	3460	Some	WW	In WD	Myco, sapro, myxo	In WD	Myco, sapro, myxo	Maj sapro and myco inhabitants of the forest floor including dead logs
	Camiarinae	X	90	Some	STem	On WD	Myxo, myco	On WD	Myxo, myco	*Neopelatops* is myxo (Lawrence and Ślipiński 2013)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Catopocerinae	X	50	Some	Hol, STem	In WD	Myco	In WD	Myco	Present in highly decomposed wood (Ferro et al. 2012a)
	Leiodinae	X	1780	Some	WW	On WD	Myco, myxo, Sapro	In, on WD	Myco, myxo, Sapro	Some are myxo, others are assoc with gilled, fleshy [wood-rotting] fungi (Peck and Newton 2017)
	Cholevinae	X	2040	Few	WW	In WD	Sapro	In WD	Sapro	Generally assoc with dec matter, some members found in rotten wood (Ferro et al. 2012a)
	Non-saproxylic subfamilies: Coloninae (saprophages and mold feeders), Platypsyllinae (assoc with mammal nests and fur)									
39	**Silphidae**									Carrion; sometimes incidental on rotten wood-rotting fungal fruiting bodies (Newton 1984)
	Non-saproxylic subfamilies: Nicrophorinae, Silphinae									
40	**Staphylinidae**	X	62,000	Some	WW	In, on WD; away	Myco, sapro, pred	In, on WD	Myco, sapro, pred	Enormous diversity of habits and habitats, even within individual subfamilies (Thayer 2016)
	Glypholomatinae	X	8	Some	STem	In WD	Myco, sapro	In WD	Myco	Assoc with “logs” (Thayer 2016)
	Microsilphinae	X	4	Some	STem	In, on WD	Myco	Unk	Myco?	Assoc with “logs”; L poorly known (Thayer 2016)
	Omaliinae	X	1400	Some	WW	In, on WD; away	Myco, sapro, Pred	In WD	Myco	Assoc with “logs,” fungi, and fermenting plant material (Thayer 2016); several genera reported as subcortical (Newton et al. 2000)
	Empelinae	X	1	All	Nea	On WD	Myco	Unk	Unk	A on gilled fungi on aged cedar (MLF, pers. obs.)

	Proteininae	X	190	Some	WW	On WD	Myco, sapro, Pred	In WD	Myco, sapro	Assoc with “logs,” fungi, and fermenting plant material (Thayer 2016); some under bark, in rotten wood (Newton et al. 2000)
	Micropeplinae	X	80	Some	Hol, Neo, Afr, Or	In, on WD	Myco	In, on WD	Myco	Assoc with “logs” (Thayer 2016)
	Dasycerinae	X	17	Most	Hol, Or	In, on WD	Myco	Away	Myco	Assoc with fungi or dec wood; L in litter (Wheeler 1984)
	Pselaphinae	X	10,000	Some	WW	In, on WD	Pred	In WD	Pred	Assoc with “logs” (Thayer 2016); maj of gen in leaf litter but many reported from rotten wood, tree holes or under bark (Newton et al. 2000)
	Phloeocharinae	X	5	Some	Hol, Neo, STem	In WD	Pred	In WD	Pred	Assoc with “logs” (Thayer 2016); A and L of *Charhyphus* found together under bark (Newton et al. 2000)
	Olisthaerinae	X	2	All	Hol	In WD	Pred	In WD	Pred	Assoc with “logs” (Thayer 2016); under bark of dead conifers (Newton et al. 2000)
	Tachyporinae	X	1520	Some	WW	In, on WD	Myco, sapro, pred	In WD	Myco	Assoc with “logs” (Thayer 2016); a few gen under bark of dead trees, in wood-rotting fungal fruiting bodies, wood debris (Newton et al. 2000)
	Trichophyinae	X	16	Few	Hol, Neo, Or	?	Myco, pred	?	Myco	Assoc with “logs” (Thayer 2016); A and L only reported from forest litter in Ashe and Newton (1993)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Habrocerinae	X	22	Some	WW	In WD	Myco, sapro, pred	In WD	Myco, sapro	Assoc with "logs" (Thayer 2016); in litter, wood debris and fungi (Newton et al. 2000)
	Aleocharinae	X	13,000	Some	WW	In, on WD	Myco, sapro, pred	In WD	Myco, sapro, pred	Assoc with "logs" (Thayer 2016); many gen under bark, a few assoc with termites, fallen logs or wood-dec fungal fruiting bodies (Newton et al. 2000)
	Trigonurinae	X	10	All	Hol, Or	In WD	Sapro	In WD	Sapro	Assoc with "logs" (Thayer 2016); A and L under bark, especially of conifer logs (Newton et al. 2000)
	Apateticinae	X	25	Some	Pal, Or	?	Sapro	?	Sapro	Assoc with "logs" (Thayer 2016)
	Scaphidiinae	X	1450	Most	WW	In, on WD	Myco, sapro, Myxo	In, on WD	Myco, sapro, myxo	Assoc with "logs" (Thayer 2016); *Baeocera* myxo, other genera on logs with polypores or other mushrooms (Newton et al. 2000)
	Piestinae	X	110	Most	Hol, Neo, STem	In WD	Myco, sapro	In WD	Myco, sapro	Assoc with "logs" (Thayer 2016); maj under bark of dec trees (Newton et al. 2000)
	Osoriinae	X	2100	Most	WW	In WD	Myco, sapro, pred	In WD	Myco, sapro, pred	Assoc with "logs" (Thayer 2016); maj under bark or in rotting wood, others in soil (Newton et al. 2000)
	Oxytelinae	X	2000	Few	WW	In WD	Myco, sapro, pred	In WD	Myco, sapro, pred	Assoc with "logs," fungi, and fermenting plant material (Thayer 2016); maj assoc with wet rotting material and riparian areas, but a few, e.g., *Syntomium*, assoc with rotting logs (Newton et al. 2000)

	Oxyporinae	X	122	Most	Hol, Neo, Or	On WD	Myco	On WD	Myco	Obligate associates of fleshy mushrooms as A and L, most of which are produced by wood-rotting fungi (Hanley and Goodrich 1995)
	Megalopsidiinae	X	165	Most	WW	In, on WD	Pred	In, on WD	Pred?	Assoc with “logs” (Thayer 2016); usu found in association with dec trees and fungusy logs, biology, and L poorly known (Newton et al. 2000)
	Scydmaeninae	X	4600	Some	WW	In WD	Pred	In WD	Pred	Some assoc with rotting wood (Jałoszyński 2016)
	Steninae	X	2250	Few	WW	In, on WD	Pred	In, on WD	Pred	Assoc with “logs” (Thayer 2016); may be found on or in forest debris (Newton et al. 2000)
	Euaesthetinae	X	760	Few	WW	In WD	Pred	In WD	Pred	Assoc with “logs” (Thayer 2016); maj assoc with forest leaf litter (Newton et al. 2000)
	Pseudopsinae	X	55	Few	WW exc Aus, Afr	In WD	Pred	In WD	Pred?	Assoc with “logs,” fungi, and fermenting plant material (Thayer 2016); maj in litter or riparian, a few *Pseudopsis* in fungi (Newton et al. 2000)
	Paederinae	X	6100	Some	WW	In, on WD	Pred	In, on WD	Pred	Assoc with “logs,” fungi, and fermenting plant material (Thayer 2016); many in forest litter, some on fungus or under bark (Newton et al. 2000)
	Staphylininae	X	6900	Some	WW	In, on WD	Pred	In, on WD	Pred	Assoc with “logs,” fungi, and fermenting plant material (Thayer 2016); many in dec matter, some under bark, in log litter, tree holes or on fungi (Newton et al. 2000)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Non-saproxylic subfamilies: Neophoninae (L poorly known), Protopselaphinae (habits poorly known, L unk), Solieriinae (habits and L unk), Leptotyphlinae (deep soil and leaf litter inhabitants)									
	Series Scarabaeiformia									
	Superfamily Scarabaeoidea (12)									The ancestor of this superfamily was probably assoc with dead wood (Beutel and Leschen 2016a)
41	**Pleocomidae**									L are root feeders
42	**Geotrupidae**									L eat dung, humus, fungi
	Non-saproxylic subfamilies: Bolboceratinae, Geotrupinae, Taurocerastinae									
43	**Belohinidae**									L and habits unk
44	**Passalidae**	X	680	All	WW	In WD	Sapro	In WD	Sapro	A and L spend entire life cycle in dead wood (Scholtz and Grebennikov 2016)
	Aulacocyclinae	X	?	All	Or, Aus	In WD	Sapro	In WD	Sapro	Ulyshen (2018)
	Passalinae	X	?	All	WW	In WD	Sapro	In WD	Sapro	Ulyshen (2018)
45	**Trogidae**									A and L feed on carrion
46	**Glaresidae**									Habits and L unk
47	**Diphyllostomatidae**									Habits and L unk
48	**Lucanidae**	X	1250	All	WW	On WD; away	Phyto, non	In WD	Sapro	Most L develop in CWD, A feed at sap flows and flowers (Scholtz and Grebennikov 2016)
	Aesalinae	X	?	All	Hol, Neo, Or	On WD; away	Phyto, non	In WD	Sapro	See Huang (2018)

	Nicaginae	X	?	All	Hol	On WD; away	Phyto, non	In WD	Sapro	See Huang (2018)
	Ceratognathinae	X	?	All	Neo, Or, Aus	On WD; away	Phyto, non	In WD	Sapro	See Huang (2018)
	Syndesinae	X	?	All	WW exc Afr	On WD; away	Phyto, non	In WD	Sapro	See Huang (2018)
	Lampriminae	X	?	All	Neo, Aus	On WD; away	Phyto, non	In WD	Sapro	See Huang (2018)
	Lucaninae	X	?	Most	WW	On WD; away	Phyto, non	In WD	Sapro	All except South African genus *Colophron* develop in dead wood (Scholtz and Grebennikov 2016)
49	**Ochodaeidae**									Poorly known; possibly underground fungus feeders
	Non-saproxylic subfamilies: Chaetocanthinae, Ochodaeinae									
50	**Hybosoridae**	X	600	Some	WW	In, on WD; away	Sapro, pred, Myco	In WD	Sapro, myco, Pred	A and L feed on carrion and decomposing plant material, some may be predatory
	Ceratocanthinae	X	366	Most	WW exc Eur	In, on WD	Myco	In WD	Myco	A and L found in rotten wood, adult mouthparts indicate fungal feeding (Scholtz and Grebennikov 2016)
	Non-saproxylic subfamilies: Anaidinae, Dynamopodinae (habits and L unk), Hybosorinae, Liparochrinae, Pachyplectrinae									
51	**Glaphyridae**									L feed on detritus, A visit flowers
52	**Scarabaeidae**	X	27,000	Some	WW	In WD, away	Sapro, phyto, poll, nec	In WD	Sapro	Extremely diverse habits

(continued)

Table 2.1 (continued)

#	Taxon	Sap^a	#Spp^b	% S^c	Regions^d	Adult found^e	A food^f	Larva found^e	L food^f	Notes
	Aphodiinae	X	3300	Few	WW	In WD	Sapro	?	Sapro?	Aulonocnemini under bark (Lawrence et al. 1999a)
	Orphninae	X	200	Few	WW exc Aus, Nea	Away	Sapro	In WD	Sapro	L of *Aegidium cribratum* under rotting logs (Scholtz and Grebennikov 2016)
	Dynastinae	X	1500	Some	WW	Away	Phyto	In WD	Sapro	Some L are borers (Scholtz and Grebennikov 2016)
	Cetoniinae	X	3270	Few	WW	Away	Poll, nec	In WD	Sapro	Valgini L develop in rotting wood (Scholtz and Grebennikov 2016)
	Euchirinae	X	12	All	Asia	Away	Phyto	In WD	Sapro	L in rotten wood (Scholtz and Grebennikov 2016)
	Non-saproxylic subfamilies: Aclopinae (habits and L unk), Allidiostomatinae (habits and L unk), Phaenomeridinae (habits and L unk), Melolonthinae (A and L phytophagous), Rutelinae (A and L phytophagous), Scarabaeinae (dung beetles)									
	?Series ?Superfamily (1)									
53	**Nosodendridae**	X	50	All	WW	On WD	Sapro, myco	On WD	Sapro, myco	A and L at slime flux from tree wounds (Leschen and Beutel 2010b)
	Series Elateriformia									
	Superfamily Dascilloidea (2)									
54	**Dascillidae**	X	80	Few	NHem	In WD	Unk	In WD	Unk	Root-feeding, some may be assoc with termites (Lawrence 2016b)
	Karumiinae	X	20	Some	WW	In WD	Unk	?	Unk	Flightless female *Anorus* was found in a dead root of *Acacia greggii* in AZ (Lawrence 2016b)

	Non-saproxylic subfamily: Dascillinae									
55	**Rhipiceridae**									L are parasites of Cicadidae
	Superfamily Buprestoidea (2)									
56	**Schizopodidae**									External root feeders
57	**Buprestidae**	X	14,600	Most	WW	Away	Phyto, poll, nec	In WD	Sapro	Maj of L are wood-borers, feeding on inner bark and outer wood of roots, trunks, and branches (Lawrence 1991)
	Polycestinae	X	1250	Most	WW	Away	Poll, nec	In WD	Sapro	Many wood borers
	Galbellinae	X	85	All	Afr, Or, Pal	Away	Unk	In WD	Sapro	L in twigs and wood of *Acacia* and *Phillyrea* (Volkovitsh and Bílý 2001)
	Chrysochroinae	X	2700	Most	WW	Away	Phyto, poll, nec	In WD	Sapro	Many wood borers
	Buprestinae	X	3300	Most	WW	Away	Phyto, poll, nec	In WD	Sapro	Many wood borers
	Agrilinae	X	7120	Most	WW	Away	Phyto, poll, nec	In WD	Sapro	Many wood borers; a significant number (>2000 spp.) are leaf miners (Evans et al. 2015)
	Non-saproxylic subfamily: Julodinae (external root feeders)									
	Superfamily Byrrhoidea (12)									
58	**Byrrhidae**									A and L phytophagous on mosses and other plants

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Non-saproxylic subfamilies: Amphicyrtinae, Byrrhinae, Syncalyptinae									
59	**Elmidae**	X	1500	Few	WW	On WD	Sapro	In, on WD	Sapro	Aquatic, some A and L assoc with woody debris
	Larainae	X	160	Most	WW	On WD	Sapro	In, on WD	Sapro	*Potamophilus* dwell on submerged wood; *Lara avara* L feed on dec wood; both probably get nutrients from algae, microbes, and dec wood (Kodada et al. 2016a)
	Elminae	X	1350	Few	WW	On WD	Sapro	In, on WD	Sapro	*Graphelmis* and some *Macronychus* are strictly assoc with wood (Kodada et al. 2016a); *Stegoelmis* bore into wood as L (Valente-Neto and Fonseca-Gessner 2011)
60	**Dryopidae**	X	280	Few	WW	On WD	Sapro	In WD	Sapro	Generally eat dec plant matter; A (aquatic) and L (mostly terrestrial) live on and under dead wood, some *Dryops* larvae observed to chew on dead wood (Kodada et al. 2016b)
61	**Lutrochidae**	X	15	all	NW	On WD	sapro	In WD	Sapro	Aquatic, A and L on wood; *Lutrochus germari* bore into wood as L (Valente-Neto and Fonseca-Gessner 2011)
62	**Limnichidae**									Poorly known, L may eat algae
	Non-saproxylic subfamilies: Cephalobyrrhinae, Hyphalinae, Limnichinae, Thaumastodinae									
63	**Heteroceridae**									A and L in wet sand

	Non-saproxylic subfamilies: Elythomerinae, Heterocerinae									
64	**Psephenidae**	X	272	Few	WW	Away	Non	On WD	Sapro	Some L are xylophagous on submerged logs, some pupate in dead wood (Lee et al. 2016)
	Psephenoidinae	X	30	Some	Afr, Or, Pal	Away	Non	On WD	Sapro	*Xylopsephenoides* L xylophagous on submerged logs (Lee et al. 2016)
	Eubrianacinae	X	50	Some	Hol, Afr, Or	Away	Non	On WD	Sapro	*Jaechanax* and *Mubrianax* L xylophagous on submerged logs (Lee et al. 2016)
	Non-saproxylic subfamilies: Afroeubriinae (on stones in water), Eubriinae (generally on stones in water, though some may pupate in holes and crevices in dead logs), Psepheninae (generally on stones in water)									
65	**Cneoglossidae**	X	8	All	Neo	Away	Unk	In WD	Sapro	Apparently aquatic L have emerged from submerged rotting brushwood (Costa et al. 2016)
66	**Ptilodactylidae**	X	500	Some	WW	Away	Myco	In WD	Sapro	Some L in wet or submerged rotten wood (Lawrence 2016c)
	Anchytarsinae	X	?	?	?	?	?	?	?	L live in or on submerged wood (Ivie 2002)
	Ptilodactylinae	X	?	?	?	?	?	?	?	L from moist leaf litter and rotten logs (Ivie 2002)
	Non-saproxylic subfamilies: Aploglossinae (L and habits unk), Araeopidiinae [L at margins of streams (Ivie 2002)], Cladotominae [L with known habits assoc with gravel, mud, or rock faces (Lawrence 2016c)], Podabrocephalinae (L and habits unk)									
67	**Chelonariidae**	X	300	Some	Ptrop	Away	Unk	In WD	Unk	Possibly assoc with ants or termites; L sometimes found under bark (Beutel and Leschen 2016b)
68	**Eulichadidae**	X	22	Few	Nea, Or	Away	Unk	On WD	Sapro	L aquatic, feeding mostly on rotting detritus and roots; gut of one *Eulichas* contained wood particles (Ivie 2016)
69	**Callirhipidae**	X	16	Most	WW	In, on WD; away	Unk	In WD	Sapro	L are borers, primarily in wood with white rot fungi (Lawrence 2016d)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Superfamily Elateroidea (17)									
70	**Artematopodidae**									Probably moss-feeding
	Non-saproxylic subfamilies: Allopogoniinae, Artematopodinae, Electribiinae									
71	**Rhinorhipidae**									Habits poorly known, L possibly in soil
72	**Brachypsectridae**	X	6	All	Hol, Or, Aus, WI	Away	Non?	In WD	Pred	L and rarely A subcortical (Neck 1993; Costa et al. 2010a; Petrzelkova et al. 2017)
73	**Cerophytidae**	X	21	Some	Hol, Neo	Away	Phyto?	In WD	Sapro	L from wood infested with brown rot (Costa et al. 2010b)
74	**Eucnemidae**	X	1500	Most	WW	On WD	Non?	In WD	Sapro	L wedge their way through wood, and probably have extra-oral digestion (Muona 2010)
	Pseudomeninae	X	2	All	Nea, Aus	In WD	Unk	In WD	Sapro	L of *Schizophyllus* in oak in red rotten stage (Otto and Young 1998)
	Palaeoxeninae	X	1	All	Nea	In WD	Unk	In WD	Sapro	In stumps of incense cedar (Muona 2000)
	Anischiinae	X	6	Most	Neo, Ausas	On WD	Unk	In WD	Unk	On wood-dec fungi, rotten wood, and dead branches (Lawrence et al. 2007); presumed L in rotten wood (Lawrence et al. 2007)
	Melasinae	X	?	Most	?	In WD	Unk	In WD	Sapro	Maj in dead logs (Muona 1993)
	Eucneminae	X	?	Most	?	In WD	Unk	In WD	Sapro	Maj in dead logs (Muona 1993)
	Macraulacinae	X	?	Most	?	In WD	Unk	In WD	Sapro	Maj in dead logs (Muona 1993)

	Non-saproxylic subfamilies: Perothopinae [L develop in soil (Muona 2010)], Phyllocerinae [L develop in soil (Muona 1993, 2000, 2010)], Phlegoninae [biology unk (Muona 1993)]									
75	**Throscidae**	X	150	Some	WW	Away	Unk	In WD	Sapro	Some L in soft rotten wood, in logs (Muona et al. 2010); L and A may be extraordinarily abundant in fresh WD (Ferro et al. 2012b)
76	**Elateridae**	X	10,000	Some	WW	Away	Phyto	In WD	Sapro, pred	Diverse habits, but all L liquid feeders (Costa et al. 2010c)
	Cebrioninae	X	?	Few	WW exc Aus	In WD	Phyto	Away	Unk	A *Euthysanius* found under pine bark (Evans and Hogue 2006); otherwise L in soil (Lawrence et al. 1999a)
	Agrypninae	X	2500	Some	WW	Away	Phyto	In WD	Sapro, pred	Some Tetralobini live in termite nests in wood (Costa et al. 2010c); some gen in wood, under bark (Becker and Dogger 1991)
	Thylacosterninae	X	45	Most	Neo, Afr, Ausas	Away	Phyto	In WD	Sapro, pred	In wood logs (Vahtera et al. 2009)
	Lissominae	X	150	Some	WW	In WD	Phyto	In WD	Sapro, pred	A of *Drapetes* under loose bark, L saproxylic under loose bark or within dec wood (Johnson 2015)
	Semiotinae	X	92	Some	Neo	Away	Phyto	In WD	Pred	L usu in moist, sappy areas under bark (Lawrence et al. 1999b)
	Pityobiinae	X	20	All	Nea, Neo, STem	Away	Phyto	In WD	Pred	Some gen in wood, under bark (Becker and Dogger 1991); L pred in rotten wood (Costa et al. 2010c)
	Dendrometrinae	X	1500	Some	WW	Away	Phyto	In WD	Pred, phyto	Some gen in wood, under bark (Becker and Dogger 1991; Lawrence et al. 1999a)
	Elaterinae	X	3500	Most	WW	Away	Phyto, nec	In WD	Pred	Some gen in wood, under bark (Becker and Dogger 1991)
	Cardiophorinae	X	800	Few	WW	Away	Phyto	In WD	Pred	L in soil or rotten wood (Costa et al. 2010c)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Non-saproxylic subfamilies: Campyloxeninae (habits and L unk), Hemiopinae [L unk (Costa et al. 2010c)], Eudicronychinae [L unk (Costa et al. 2010c)], Morostomatinae (habits and L unk), Negastriinae (L in leaf litter and soil, often riparian), Oestodinae (habits and L unk), Oxynopterinae (habits and L unk), Parablacinae (habits and L unk), Physodactylinae [L unk (Costa et al. 2010c)], Subprotelaterinae (habits and L unk)									
77	**Plastoceridae**									L and habits unk
78	**Omalisidae**									Pred on millipedes
79	**Iberobaeniidae**									A collected from pitfall traps and sweeping vegetation (Kundrata et al. 2017)
80	**Lycidae**	X	4600	Some	WW	Away	Nec, non	In, on WD	Sapro	L in dead wood in various stages, less often in forest litter and soil (Bocak and Matsuda 2003); not pred but feed on soft or fluid material assoc with rotting wood (Lawrence 1991)
	Dictyopterinae	X	?	Some	Hol, Ausas	Away	Nec, non	In, on WD	Sapro	A of *Dictyoptera* found overwintering under pine bark (Bocak and Bocakova 2008); L presumably saproxylic
	Lyropaeinae	X	?	Some	Or	Away	Nec, non	In, on WD	Sapro	L of *Platerodrilus* is known to be saproxylic (Bocak and Matsuda 2003; as *Duliticola*)
	Lycinae	X	?	Most	WW	Away	Nec, non	In, on WD	Sapro	Maj are probably saproxylic (Bocak and Matsuda 2003)
	Non-saproxylic subfamilies: Ateliinae (L unk), Dexorinae (L unk), Libnetinae (L unk)									
81	**Telegeusidae**									Habits, females, and L unk
82	**Phengodidae**									L pred on millipedes

	Non-saproxylic subfamilies: Mastinocerinae, Penicilliphorinae, Phengodinae									
83	**Rhagophthalmidae**									L predacious in soil and litter
84	**Lampyridae**	X	2000	Few	WW	Away	Pred	In, on WD	Pred	L may be found "in rotten logs" (Branham 2010)
	Lampyrinae	X	1000	Few	WW exc Aus	Away	Pred	In, on WD	Pred	*Ellychnia* and *Lucidota* L inhabit rotting logs (Lloyd 2002)
	Non-saproxylic subfamilies: Luciolinae (L aquatic or subaquatic), Ototretinae (L in leaf litter and soil), Photurinae (L general pred of snails and soft-bodied insects on surface of soil), Psilocladinae, Pterotinae (L in leaf litter and soil)									
85	**Omethidae**									L unk
	Non-saproxylic subfamilies: Driloniinae, Matheteinae, Omethinae									
86	**Cantharidae**	X	5083	Some	WW	Away	Poll, nec, pred	In, on WD	Pred	Some L may be subcortical, on dec wood debris (Ramsdale 2010); possibly not obligate
	Saproxylic habits by subfamily unk: Cantharinae, Chauliognathinae, Dysmorphocerinae, Malthininae, Silinae									
	Series Elateriformia: ?family (1)									
	Cydistinae									L unk
	Series Bostrichiformia									
	Superfamily Bostrichoidea (4)									
87	**Dermestidae**	X	1000	Few	WW	Away	Poll, nec, sapro	In WD	Sapro	A, L occasionally in dry woody debris (Lawrence and Ślipiński 2010)
	Orphilinae	X	10	Most	WW	Away	Poll, nec	In WD	Sapro, myco	*Orphilus* and possibly *Orphilodes* L assoc with dead wood (Lawrence and Ślipiński 2005, 2010a)
	Non-saproxylic subfamilies: Attageninae, Dermestinae, Megatominae, Thorictinae, Trinodinae									
88	**Endecatomidae**	X	4	All	Hol	In, on fungi	Myco	In, on fungi	Myco	A and L bore into polypores and other wood-dec fungi on dead wood (Lawrence 2010a)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
89	**Bostrichidae**	X	570	All	WW	In WD	Sapro, phyto	In WD	Sapro	Most A and L wood borers (Liu et al. 2008; Lawrence 2010b); some in cones
	Dysidinae	X	2	All	Or, Neo	In WD	Sapro	In WD	Sapro	A have been found in dead softwood board (Lawrence et al. 1999b)
	Polycaoninae	X	28	All	Or, NW	In WD	Sapro, phyto	In WD	Sapro	*Polycaon* and *Melalgus* may attack living tissue (Lawrence 2010b); former may attack dead trunks or branches of *Eucalyptus* (Liu et al. 2008)
	Bostrichinae	X	450	All	WW	In WD	Sapro, phyto	In WD	Sapro	Maj bore into dying or dead trees (Lawrence et al. 1999b); *Dinapate* attacks living trees
	Psoinae	X	13	All	Hol, Afr, Or	In WD	Sapro, phyto	In WD	Sapro	*Psoa* attacks shrubs (Tilden 1953)
	Dinoderinae	X	50	Most	WW exc Aus	In WD	Sapro	In WD	Sapro	Non-wood-feeding grain borers belong to this group; others wood-boring, including *Stephanopachys* in conifers (Liu et al. 2008)
	Lyctinae	X	32	All	WW	In WD	Sapro	In WD	Sapro	Primary group of powder-post beetles, includes pests of furniture and cane (Lawrence 2010b)
	Euderiinae	X	1	All	NZ	Away	Sapro	In WD	Sapro	L from moist or sappy bark of dead or injured trees (Klimaszewski and Watt 1997)
90	**Ptinidae (=Anobiidae)**	X	2200	Most	WW	In, on WD; away	Sapro	In WD	Sapro	A and L found in dry woody debris (Philips and Bell 2010)

	Eucradinae	X	70	All	Hol, Afr, Or	In, on WD	Sapro	In WD	Sapro	Wood borers, L tunnel between bark and wood of mainly dead hardwoods (Arango and Young 2012)
	Ptininae	X	650	Some	WW	In, on WD	Sapro	In WD	Sapro	Most members feed on accumulated dried plant or animal material, but some members are wood borers (Philips 2002); *Ptinus fur* reported from cones of conifers (Arango and Young 2012)
	Dryophilinae	X	75	All	WW	In, on WD	Sapro	In WD	Sapro	Wood borers (Philips 2002)
	Ernobiinae	X	150	All	WW exc Aus	In, on WD	Sapro	In WD	Sapro	Bore beneath bark or into wood; some in cones of conifers (Arango and Young 2012)
	Anobiinae	X	400	Most	WW	In, on WD	Sapro	In WD	Sapro	Most are wood-boring, some are stored product pests (Arango and Young 2012)
	Ptilininae	X	65	All	WW exc Aus	In, on WD	Sapro	In WD	Sapro	*Ptilinus* are wood-feeding (Arango and Young 2012)
	Xyletininae	X	370	Most	WW	In, on WD	Sapro	In WD	Sapro	L of most bore into dead wood (Arango and Young 2012)
	Dorcatominae	X	670	Some	WW	In, on WD	Sapro, myco	In WD	Sapro, myco	L in woody (sometimes wood-dec) fungi, wood, branches twigs, vines, as well as puffballs and other mushrooms (Arango and Young 2012)
	Mesocoelopodinae	X	370	Some	WW	In, on WD	Sapro	In WD	Sapro	L habitats varied, including seeds, wood, branches, vines, galls, bark, kelp (Arango and Young 2012)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Non-saproxylic subfamily: Alvarenganiellinae (L and habits unk)									
	Series Cucujiformia									
	Superfamily Coccinelloidea (15)									
91	**Bothrideridae**	X	270	All	WW	In WD	Unk	In WD	Ecpar	L ecto of L and pupae of wood-boring Coleoptera and Hymenoptera (Ślipiński et al. 2010b)
92	**Murmidiidae**	X	12	Some	WW	In WD	Myco	In WD	Myco	Under bark, often of trees infested by fungi; otherwise in dec vegetation (Ślipiński 1990)
93	**Discolomatidae**	X	400	Some	Ptrop	In, on WD and fungi	Myco, sapro	In, on WD and fungi	Myco, sapro	Habits and L poorly known
	Aphanocephalinae	X	90	Some	Neo, Ausas, Sey	On WD	Myco	on WD	Myco	A of *Aphanocephalus* from fungi, including wood-dec polypores (Cline and Ślipiński 2010)
	Discolomatinae	X	40	Some	Neo, Afr	On WD	Myco	Unk	Unk	A of *Discoloma* from old twigs encrusted with lichens and various subcortical fungi (Cline and Ślipiński 2010)
	Non-saproxylic subfamilies: Cephalophaninae, Notiophyginae, Pondonatinae (only myrmecophilous?)									
94	**Teredidae**	X	120	Some	WW	In, on WD	Myco	In, on WD	Myco, pred	Habits various
	Teredinae	X	20	All	WW	In, on WD	Myco	In, on WD	Myco	L myco, some on Xylariaceae, some inhabit tunnels and galleries of Ptinidae, Cerambycidae, Curculionidae (Ślipiński et al. 2010b)

	Non-saproxylic subfamily: Anommatinae (L and A in dec vegetation, L habits unk)									
95	**Euxestidae**	X	62	Most	WW	In WD	Myco	In WD	Myco	Subcortical, often early stage of dec, but can be late
96	**Cerylonidae**	X	410	Most	WW	In WD	Myco	In WD	Myco, myxo	Subcortical, often early stage of dec, but can be late
	Ostomopsinae	X	2	All	Neo, Ausas, Sey	In WD	Myco	?	Unk	A assoc with rotten palm wood, under bark, or extracted from leaf/log litter (Ślipiński 1990)
	Loebliorylоninae	X	9	Some	Or	In WD	Myco	?	Unk	In leaf litter and rotten wood (Ślipiński 1990); L unk
	Ceryloninae	X	400	Most	WW	In WD	Myco	In WD	Myco, myxo	Habits various: A and L under bark, in rotten wood, leaf litter, probably feeding on wood juices, hyphae, and myxo (Ślipiński 1990)
97	**Latridiidae**	X	760	Some	WW	In, on WD	Myco	In, on WD	Myco	Generally myco and occasionally with woody debris, including fallen branches; L habits very poorly known (Hartley and McHugh 2010); in dec trunks and stumps, wood mold, cut branches, bracket fungi, among other habitats (Klimaszewski and Watt 1997)
	Latridiinae	X	258	Some	WW	In, on WD	Myco	In, on WD	Myco	Some members assoc with woody debris; habits poorly known
	Corticariinae	X	502	Some	WW	In, on WD	Myco	In, on WD	Myco	Some members assoc with woody debris (Plewa et al. 2017); habits poorly known
98	**Akalyptoischiidae**									Myco in leaf litter
99	**Alexiidae**	X	50	Some	w Pal	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Subcortical, on mushrooms (Ślipiński and Tomaszewska 2010)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
100	**Anamorphidae**	X	170	Some	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Many on wood-dec fungal fruiting bodies (Shockley et al. 2009)
101	**Corylophidae**	X	300	Some	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Generally myco on internal and external wood-dec fungi
	Periptyctinae	X	6	Some	Aus	On WD	Myco	On WD	Myco	*Pakalukodes* from logs (Ślipiński et al. 2009)
	Corylophinae	X	300	Some	WW	On WD	Myco	On WD	Myco	Many under bark (Ślipiński et al. 2010c)
102	**Endomychidae**	X	1585	Most	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Generally subcortical or on fungal fruiting bodies
	Pleganophorinae	X	24	Most	WW	On WD	Myco	On WD	Myco	*Trochoideus* on wood-dec Auriculariaceae fungi (Shockley et al. 2009)
	Leiestinae	X	15	Most	Hol	In, on WD	Myco	In, on WD	Myco	Many on wood-dec fungal fruiting bodies (Shockley et al. 2009)
	Xenomycetinae	X	2	All	Nea	On WD	Myco	On WD	Myco	L of *Xenomycetes rivesi* only known from softwood-dec *Paxillus atrotomentosus* (Johnson 1986)
	Danascelinae	X	2	All	Nea, Pakistan	In WD	Myco	Unk	Unk	One A of *Hadromychus chandleri* collected "sifting conifer log" (Bousquet and Leschen 2002); L unk

	Stenotarsinae	X	458	Some	WW	In, on WD	Myco	In, on WD	Myco	Some on wood-dec fungal fruiting bodies (Shockley et al. 2009)
	Endomychinae	X	94	Most	Hol, Or	In, on WD	Myco	In, on WD	Myco	Many on wood-dec fungal fruiting bodies (Shockley et al. 2009)
	Epipocinae	X	166	Some	Neo, Nea	In, on WD	Myco	In, on WD	Myco	Some on wood-dec fungal fruiting bodies (Shockley et al. 2009)
	Lycoperdininae	X	713	Most	WW	In, on WD	Myco	In, on WD	Myco	Many on wood-dec fungal fruiting bodies (Shockley et al. 2009)
	Non-saproxylic subfamily: Merophysiinae									
103	**Mycetaeidae**	X	7	Few	WW exc Aus	In, on WD	Myco	In, on WD	Myco	General myco, presence in woody debris possibly incidental
104	**Eupsilobiidae**	X	16	Some	NW, s Afr	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Many are social insect inquilines (Shockley et al. 2009)
105	**Coccinellidae**									Mostly pred, occasionally phyto or poll, myco
	Non-saproxylic subfamilies: Coccinellinae, Microweiseinae									
	Superfamily Tenebrionoidea (29)									
106	**Lymexylidae**	X	65	All	WW	In, on WD	Unk	In WD	Sapro, myco	L develop in fungal-infected wood and are wood borers; A *Elateroides dermestoides* inoculate wood with fungi for L to consume (Lawrence 2010c)
	Hylecoetinae	X	5	All	Hol, Or	In, on WD	Unk	In WD	Sapro, myco	A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c)
	Lymexylinae	X	4	All	Pal	In, on WD	Unk	In WD	Sapro, myco	A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Melittommatinae	X	25	All	WW	In, on WD	Unk	In WD	Sapro, myco	A may be found under bark, on wood surfaces or in rotten wood; L wood borers (Lawrence 2010c)
	Atractocerinae	X	30	All	Ptrop, Pal	Away	Unk	In WD	Sapro, myco	A active fliers; L wood borers (Lawrence 2010c)
107	**Mycetophagidae**	X	130	Few	WW	In, on WD	Myco, sapro	In, on WD	Myco, sapro	A and L in wood-dec fungi
	Esarcinae	X	10	Some	Pal	On WD	Myco	On WD	Myco	At least one *Esarcus* on Xylariaceae fruiting bodies (Lawrence 1991)
	Mycetophaginae	X	125	Most	WW	In, on WD	Myco, sapro	In, on WD	Myco, sapro	Maj feed on wood-dec fungi; some on ferns or stored products (Lawrence 1991)
	Non-saproxylic subfamily: Bergininae (pred, poll, or assoc with leaf litter and palms)									
108	**Archeocrypticidae**	X	50	Some	WW	In, on WD	Myco, sapro	In, on WD	Myco, sapro	Some Aus members on wood-dec polypores (Lawrence 2010d)
109	**Pterogeniidae**	X	24	Some	Asia	In, on fungi	Myco	In, on fungi	Myco	A and L of some gen in wood-dec polypores (Lawrence 2010e)
110	**Ciidae**	X	640	All	WW	In, on fungi	Myco	In, on fungi	Myco	A and L of all spp. in or on wood-dec fungi (Lawrence and Lopes-Andrade 2010)
	Sphindociinae	X	1	All	Nea	In WD, fungi	Myco	In WD, fungi	Myco	L bore into dry rotten wood at base of fruiting body of *Antrodia albida* (Lawrence and Lopes-Andrade 2010)
	Ciinae	X	640	All	WW	In, on fungi	Myco	In, on fungi	Myco	A and L of all spp. in or on wood-dec fungi (Lawrence and Lopes-Andrade 2010)

111	**Tetratomidae**	X	150	All	WW	In, on fungi	Myco	In fungi	Myco	Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f)
	Tetratominae	X	22	All	Hol	In, on fungi	Myco	In fungi	Myco	Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f)
	Piseninae	X	9	All	Hol, Or, s SAm	In, on fungi	Myco	In fungi	Myco	Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f)
	Penthinae	X	13	All	Hol, Or	In, on fungi	Myco	In fungi	Myco	Usu assoc with fruiting bodies of various wood-dec fungi, L feed internally (Lawrence and Leschen 2010f)
	Hallomeninae	X	17	All	Hol	In, on fungi	Myco	In fungi	Myco	L assoc with various wood-dec fungi, especially polypores (Lawrence 1991)
	Eustrophinae	X	86	All	WW exc Aus	In, on fungi	Myco	In fungi	Myco	Found in a wide variety of bracket fungi (Lawrence 1991)
112	**Melandryidae**	X	420	All	WW	In, on WD	Myco	In WD	Myco	L of maj inhabit dead wood of varying consistency (Lawrence 1991); maj are wood borers
	Melandryinae	X	400	All	WW	In, on WD	Myco	In WD	Myco	L of maj inhabit dead wood (Lawrence 1991)
	Osphyinae	X	35	All	Hol, Neo, Or	Away	Unk	In WD	Myco	L inhabit dead wood (Lawrence 1991)
113	**Mordellidae**	X	1500	Most	WW	Away	Poll, myco	In, on WD and fungi	Myco, sapro	L primarily in dead wood and rotten stems, some in polypores (Lawrence and Ślipiński 2010c)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Mordellinae	X	1500	Most	WW	Away	Poll, myco	In, on WD	Myco, sapro	L primarily in dead wood and rotten stems, some in polypores (Lawrence and Ślipiński 2010c)
	Non-saproxylic subfamily: Ctenidiinae (L and habits unk)									
114	**Ripiphoridae**	X	400	Some	WW	Away	Poll, non	In WD	Enpar	Endo on other insects, including wood-boring beetle larvae
	Pelecotominae	X	15	All	WW	Away	Unk	In WD	Enpar	Hosts are wood-boring beetle L (Lawrence et al. 2010b)
	Hemirhipidiinae	X	9	All	Ausas	Away	Unk	In WD	Enpar	Hosts are wood-boring beetle L (Lawrence et al. 2010b)
	Non-saproxylic subfamilies: Ptilophorinae (L and habits unk), Ripidiinae (endo of Blattodea), Ripiphorinae (endo of Hymenoptera)									
115	**Zopheridae**	X	1700	All	WW	In, on WD	Myco, pred	In, on WD	Myco, pred	Maj assoc with dead wood, on which L feed (Ślipiński and Lawrence 2010a)
	Colydiinae	X	1000	All	WW	In, on WD	Myco, pred	In, on WD	Myco, pred	Usu feed on dead plant material and assoc with rotten logs; some groups pred on scolytines (Ślipiński and Lawrence 2010a)
	Zopherinae	X	700	All	WW	In, on WD	Myco	In, on WD	Myco	Assoc with various fungi and dec plant material (Ślipiński and Lawrence 2010a)
116	**Ulodidae**	X	40	All	STem	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Maj assoc with dead wood and wood-dec fungi (Leschen and Ślipiński 2010)
117	**Promecheilidae**									Probably feed on mosses and lichens

118	**Chalcodryidae**	X	6	Some	NZ	On WD	Unk	In, on WD	Lichens?	L reported from "refuge galleries" in dead twigs and branches, A and L on moss/lichen-covered branches (Lawrence and Leschen 2010g)
119	**Tenebrionidae**	X	20,000	Most	WW	In, on WD	Myco, sapro, pred	In, on WD	Myco, sapro, pred	Large family with a wide variety of life histories; may be subcortical, on fungi, in rotten wood, or in bark beetle tunnels
	Zolodininae	X	2	All	NZ, Tasmania	In, on WD	Unk	In WD	Sapro	L under bark of logs and in rotten wood (Matthews et al. 2010)
	Lagriinae	X	?3000	Most	WW	In, on WD	Unk	In WD	Sapro	Maj in leaf litter and dead plant material; some Adeliini and Lupropini L feed internally in dead wood (Matthews et al. 2010)
	Nilioninae	X	40	All	Neo	On WD	Myco	On WD	Myco	L and A gregarious on fungus-infested branches (Matthews et al. 2010)
	Phrenapatinae	X	175	All	WW	In WD	Sapro	In WD	Sapro	All A and L live in and feed on rotten wood (Matthews et al. 2010)
	Tenebrioninae	X	?4000	Most	WW	In, on WD	Sapro, myco	In WD	Sapro, myco	Many feed as L in rotting wood (Matthews et al. 2010); includes former family Trachelostenidae, whose A have been collected under tight-fitting bark (Lawrence and Ślipiński 2010d)
	Alleculinae	X	?2000	Most	WW	On WD; away	Unk	In WD	Sapro	L either live in rotten wood or soil (Matthews et al. 2010)
	Diaperinae	X	?1500	Some	WW	In, on WD	Sapro, myco	In WD	Sapro, myco	Many subcortical or in dead wood as A and L, some A external feeders on fungi (Matthews et al. 2010)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Stenochiinae	X	?2500	All	WW	On WD; away	Sapro	In WD	Sapro	A on wood surfaces at night, L feed in rotting wood (Matthews et al. 2010)
	Non-saproxylic subfamily: Pimeliinae (ground-dwelling scavengers)									
120	**Prostomidae**	X	29	All	WW exc Neo	In, on WD	Myco	In WD	Myco	In soft, mud-like substrate in reddish rotten wood of large diameter logs (Seago and Beutel 2010)
121	**Synchroidae**	X	9	All	Hol, SE Asia	On WD	Unk	In WD	Myco	L feed on rotten cambium of deciduous trees (Ślipiński and Lawrence 2010b)
122	**Stenotrachelidae**	X	21	All	Hol	Away	Poll, non	In WD	Myco	L reported from well-rotted, brown rot, “lucanid stage of decomposition” wood (Lawrence and Ślipiński 2010e)
	Stenotrachelinae	X	6	All	Hol	Away	Poll, non	In WD	Myco	L of *Stenotrachelus aeneus* under bark or in wood of dead angiosperm trees (Lawrence and Ślipiński 2010e)
	Nematoplinae	X	4	All	Hol	Away	Poll, non	In WD	Myco	L of *Nematoplus semenovi* typical of wood in “lucanid stage” of decomposition (Lawrence and Ślipiński 2010e)
	Cephaloinae	X	9	All	Hol	Away	Poll, non	In WD	Myco	L of *Cephaloon* collected from old brown-rot-infected conifer logs (Lawrence and Ślipiński 2010e)
	Stoliinae	X	2	All	Pal	Away	Poll, non	Unk	Unk	L and habits unk; presumed saproxylic

123	**Oedemeridae**	X	1500	Most	WW	On WD; away	Poll, nec	In WD	Sapro, phyto, myco?	L in moist rotting wood, including driftwood
	Calopodinae	X	35	Most	Hol, Neo, Or	Away	Poll, nec	In WD	Sapro, phyto	L *Calopus* known to damage living trees (Lawrence and Ślipiński 2010f)
	Oedemerinae	X	1500	Most	WW	On WD; away	Poll, nec	In WD	Sapro, phyto, myco?	L in dec wood, including logs, stumps, roots, driftwood, structural timber (Lawrence and Ślipiński 2010f)
	Non-saproxylic subfamily: Polypriinae (L and habits unk)									
124	**Meloidae**									A phyto, L pred; *Eletica wahlbergi* oviposits under bark; L of *Eletica* and *Iselma* (Eleticinae) possibly saproxylic pred (Bologna et al. 2010)
	Non-saproxylic subfamilies: Eleticinae (see note above), Meloinae, Nemognathinae, Tetraonychinae									
125	**Mycteridae**	X	170	Some	WW	On WD; away	Poll, nec	In WD	Myco	Poorly known, but L appear to be subcortical, myco
	Mycterinae	X	16	All	Hol, Afr, Or	Away	Poll, nec	In WD	Unk	*Mycterus curculioides* L found under dead pine bark (Pollock 2010a)
	Eurypinae	X	120	Most	WW	On WD; away	Unk	In WD	Myco	Maj of L under bark; *Stilpnonotus postsignatus* in tunnels perpendicular to long axis of logs (Pollock 2010a)
	Non-saproxylic subfamily: Hemipeplinae (L and A assoc with grasses and unopened palm fronds)									
126	**Boridae**	X	4	All	Hol, Aus	In, on WD	Unk	In WD	Unk	L subcortical in conifers, especially fire-killed trees (Pollock 2010b)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Borinae	X	3	All	Hol	In, on WD	Unk	In WD	Unk	L subcortical in conifers, especially fire-killed trees (Pollock 2010b)
	Non-saproxylic subfamily: Synercticinae (L and habits unk)									
127	**Trictenotomidae**	X	14	Unk	Se Pal	On WD	Unk	Unk	Unk	A collected on WD, subcortically, and on tree fungi; L poorly known (Pollock and Telnov 2010)
128	**Pythidae**	X	22	Most	WW exc Afr	Away	Unk	In WD	Myco	Subcortical, one sp. in red rotten wood of conifers (Pollock 2010c)
129	**Pyrochroidae**	X	200	Most	WW	Away	Unk	In WD	Myco	L subcortical
	Tydessinae	X	2	All	Hol	Away	Poll?	In WD	Myco	L under bark of various hardwoods (Young and Pollock 2010)
	Pilipalpinae	X	37	All	SHem	In WD; away	Unk	In WD	Myco	L under bark of dead trees (Young and Pollock 2010)
	Pyrochroinae	X	100	All	Hol, Or	Away	Unk	In WD	Myco	L mostly subcortical, some within dec wood (Young and Pollock 2010)
	Non-saproxylic subfamilies: Agnathinae (L from dry, dec vegetation and dung), Pedilinae (most L unk, but known spp. in soil and dec vegetation)									
130	**Salpingidae**	X	350	Most	WW	In, on WD; away	Unk	In WD	Myco, sapro, pred	L often subcortical, some assoc with scolytines (Lawrence et al. 2010c)
	Othniinae	X	50	All	WW	Away	Unk	In WD	Unk	L collected under pine bark (Pollock 2002b)
	Prostominiinae	X	30	Most	Ptrop	On WD	Unk	In WD	Myco, sapro	Usu under bark; some in rotten leaf axils of tree ferns or palms (Lawrence et al. 2010c)

	Inopeplinae	X	75	All	WW	In, on WD	Unk	In WD	Unk	L and A usu under bark (Lawrence et al. 2010c)
	Salpinginae	X	150	Most	WW	In, on WD; away	Unk	In WD	Myco, sapro, pred	L in dec logs, branches or twigs; some assoc with scolytines (Lawrence et al. 2010c); a few phyto
	Non-saproxylic subfamilies: Aegialitinae (A and L under intertidal rocks), Agleninae (A and L from manure and dec vegetation), Dacoderinae (under stones, myrmecophiles)									
131	**Anthicidae**	X	3000	Few	WW	On WD; away	Myco, sapro, pred	In WD	Myco, sapro, pred	Some L have been reported from beneath bark of dead trees (Chandler 2010)
	Lemodinae	X	40	Most	Aus	On WD	Unk	In WD	Myco	A and L of *Lemodes* assoc with rotten logs (Telnov 2007); *Trichananca* L found under bark (Lawrence et al. 1999a)
	Non-saproxylic subfamilies: Anthicinae [maj of L in moist soil or organic debris (Chandler 2010)], Copobaeninae (L and habits unk), Eurygeniinae (L have been collected from a cranberry bog), Macratriinae (presumed L collected in forest litter), Notoxinae (some may bore into tubers), Steropinae (L and habits unk), Tomoderinae (L collected in forest litter)									
132	**Aderidae**	X	1000	Most	WW	Away	Unk	In WD	Sapro	L usu occur in rotten wood, leaf litter, or under bark; L *Megaxenus* assoc with termites (Lawrence and Ślipiński 2010g)
133	**Scraptiidae**	X	400	Some	WW	Away	Poll	In WD	Myco?, pred?	L usu subcortical in dead trees, some in leaf litter (Lawrence and Ślipiński 2010h)
	Scraptiinae	X	100	Most	WW	Away	Poll	In WD	Myco?, pred?	L usu subcortical; some in litter, with ants or in moldy hay (Lawrence and Ślipiński 2010h)
	Non-saproxylic subfamily: Anaspidinae (only known L habits are feeding on lichens on a rock (Lawrence and Ślipiński 2010h); possibly not saproxylic)									
134	**Ischaliidae**	X	37	Most	Asia, NAm	Away	Unk	In WD	Myco	L of *Ischalia vancouverensis* feed on fungal mycelium assoc with dec stumps or logs (Lawrence et al. 2010d)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Superfamily Tenebrionoidea: ?family (3)									
	Lagrioidinae	X	5	Most	Aus, NZ, s SAm	On WD	Unk	Away	Sapro	A may be found under logs or driftwood (Lawrence et al. 2010d; MLG, pers. obs.), but L feed on rotting vegetation
	Rhizonium antiquum	X	1	All	NZ	In WD	Unk	In WD	Unk	A and L in dead fronds of tree ferns and dec wood (Lawrence et al. 2010d; MLG, pers. obs.)
	Non-saproxylic subfamily: Afreminae (L, females and habits unk)									
	Superfamily Cleroidea (14)									
135	**Byturidae**									A and L fruit and poll
	Non-saproxylic subfamilies: Byturinae, Platydascillinae									
136	**Biphyllidae**	X	200	Most	WW	In, on WD	Myco	In, on WD	Myco	Maj under bark of dead trees or fallen branches (Cline and Shockley 2010)
137	**Phloiophilidae**	X	1	All	Eur	On fungi	Myco	On fungi	Myco	A and L eat basidiomycete fungi, L also on dead *Quercus* branches (Lawrence and Leschen 2010b)
138	**Trogossitidae**	X	634	Most	WW	In, on WD	Myco, pred	In, on WD and fungi	Myco, pred	Maj assoc with dead wood, either pred or myco
	Peltinae	X	33	Most	WW exc Afr	In, on WD	Myco	On fungi	Myco	L mostly in dec wood or on fungi, A under bark or on fungi (Kolibáč and Leschen 2010a)
	Lophocaterinae	X	117	Most	WW	In, on WD; away	Myco, poll	In WD	Myco, pred	Some in leaf litter or on flowers or stored products, but maj under bark or in dec wood (Kolibáč and Leschen 2010a)

	Trogossitinae	X	484	Most	WW	In, on WD	Pred	In WD	Pred, myco	Maj subcortical as A and L, some in rotten wood or in galleries of wood-boring insects (Kolibáč and Leschen 2010a)
139	**Acanthocnemidae**	X	1	All	Aus (adv WW)	On WD	Unk	Unk	Sapro?	A attracted to burning dead wood, probably pyrophilous (Lawrence and Leschen 2010c)
140	**Chaetosomatidae**	X	12	All	NZ, Mad	In, on WD	Unk	In WD	Sapro	L and A in woody debris, including tunnels of wood-boring beetles and moths (Leschen 2010)
141	**Metaxinidae**									In sooty mold on living trees, L pred
142	**Thanerocleridae**	X	30	All	WW	In, on WD	Pred	In, on WD	Pred	Pred on wood-boring or myco beetles (Kolibáč and Leschen 2010b)
143	**Cleridae**	X	3400	Some	WW	On WD	Pred, poll	In WD	Sapro, pred	Many pred on wood-boring beetles
	Tillinae	X	600	Some	WW exc SAm	On WD; away	Pred	In WD	Pred	At least some L are xylophilous pred in tunnels of wood-boring insects (Foster and Lawrence 1991a)
	Korynetinae	X	700	Some	WW	On WD; away	Pred	In WD	Pred	At least some L are xylophilous pred in tunnels of wood-boring insects (Foster and Lawrence 1991a)
	Hydnocerinae	X	600	Some	WW exc Eur	On WD; away	Pred, poll	In WD	Pred	At least some *Phyllobaenus* in woody habitats (Foster and Lawrence 1991a)
	Clerinae	X	1500	Most	WW	On WD	Pred	In WD	Pred, poll	Maj of A pred on wood-boring insects on trunks and branches; L within galleries (Kolibáč 2010)
	Non-saproxylic subfamily: Epiclininae (poll as A; L unk)									
144	**Phycosecidae**									A and L scavengers in marine littoral zones

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
145	**Prionoceridae**	X	158	Few	Pal, Or, Afr, Aus	Away	Poll	In WD	Sapro?, pred?	*Idgia* L may be found under bark (Lawrence and Leschen 2010d)
146	**Mauroniscidae**									Habits poorly known, L unk
147	**Rhadalidae**	X	250	Some	WW	Away	Poll, pred	In WD	Pred	L of *Rhadalus* known from rotting yucca stems (Foster and Lawrence 2010); L of *Aplocnemus* under bark, pred; *Trichoceble* L may develop in pine and fir cones (Kolibáč et al. 2005)
148	**Melyridae**	X	6000	Few	WW	Away	Poll, pred	In WD	Sapro, phyto, pred, myco	L mostly pred, with many occurring in dec wood
	Dasytinae	X	1300	Some	WW	Away	Poll, pred	In WD	Sapro, phyto, pred, myco	L in rotting stems or wood, under bark, in cerambycid galleries, in polypore fungi or cones (Kolibáč et al. 2005)
	Malachiinae	X	4000	Some	WW	Away	Poll, pred	In WD	Pred	*Anthocomus*, *Hypebaeus*, and *Malachius* L found under bark (Foster and Lawrence 1991b)
	Non-saproxylic subfamily: Melyrinae (known L soil-inhabiting, feeding on seeds; A poll)									
	Superfamily Cucujoidea (25)									
149	**Boganiidae**									A and L poll
	Non-saproxylic subfamilies: Boganiinae, Paracucujinae									
150	**Helotidae**	X	100	Most	Pal, Or, Afr	On WD	Ferm sap	In, on WD	Ferm sap	A and L assoc with sap flows from trees damaged by wood-boring insects (Lawrence et al. 2010a)

151	**Protocucujidae**									A and L probably living on vegetation or in leaf litter
152	**Sphindidae**	X	64	All	WW	In, on slime mold	Myxo	In, on slime mold	Myxo	A and L of all known members myxo (Forrester and McHugh 2010)
	Sphindinae	X	58	All	WW	In, on slime mold	Myxo	In, on slime mold	Myxo	A and L of all known members myxo
	Protosphindinae	X	2	All	Chile	In, on slime mold	Myxo	In, on slime mold	Myxo	A and L of all known members myxo
	Odontosphindinae	X	3	All	Hol	In, on slime mold	Myxo	In, on slime mold	Myxo	A and L of all known members myxo
	Sphindiphorinae	X	1	All	Afr	In, on slime mold	Myxo	In, on slime mold	Myxo	A and L of all known members myxo
153	**Cybocephalidae**									Pred of sternorrhynchine Hemiptera
154	**Monotomidae**	X	240	Most	WW	In, on WD	Myco, pred	In, on WD	Myco, pred	Generally myco, many under bark or in bark beetle galleries (Bousquet 2010)
	Rhizophaginae	X	50	Most	Hol, Or	In, on WD	Myco, pred	In, on WD	Myco, pred	Some *Rhizophagus* pred on scolytines (Bousquet 2010)
	Monotominae	X	190	Most	WW	In, on WD	Myco, pred	In, on WD	Myco, pred	Several gen reported from under bark of dead trees (Bousquet 2010)
155	**Erotylidae**	X	3500	Most	WW	In, on WD and fungi	Myco, sapro	In, on WD and fungi	Myco, sapro	Maj myco or sapro, but one major lineage (Languriinae) primarily phyto

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Xenoscelinae	X	10	Some	WW exc Nea	In, on WD	Unk	In, on WD	Unk	*Zavaljus*, *Protoloberus*, and perhaps *Xenoscelis* assoc with dead wood (Leschen 2003)
	Cryptophilinae	X	33	Some	WW	In WD	Myco, sapro	In WD	Myco, sapro	Some members found under bark; some Toramini on Xylariaceae (Leschen 2003)
	Erotylinae	X	2563	Most	WW	In, on WD and fungi	Myco, sapro	In, on WD and fungi	Myco, sapro	Most members assoc with wood-dec fungi (Leschen 2003)
	Non-saproxylic subfamilies: Languriinae (maj phyto on living tissues, some in leaf litter), Loberinae (assoc with leaf litter, rotting and live vegetation), Pharaxonothinae (on cycad cones, rotting vegetation or assoc with stored products)									
156	**Hobartiidae**	X	6	All	Aus, SAm	In, on WD and fungi	Myco	In, on WD and fungi	Myco	A and L from fungus-infested logs, often on soft fruiting bodies of basidiomycetes (Tomaszewska and Ślipiński 2010)
157	**Cryptophagidae**	X	600	Most	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Mostly myco
	Cryptophaginae	X	400	Some	WW	In, on WD and fungi	Myco, poll	In, on WD	Myco	Many spp. on wood-rotting macrofungi (Leschen 1996)
	Atomariinae	X	200	Some	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Some spp. of *Atomaria* assoc with wood-rotting macrofungi (Leschen 1996)

158	**Agapythidae**									In sooty mold on living trees, myco
159	**Priasilphidae**	X	11	Some	Aus, Chile, NZ	In, on WD	Myco	In, on WD	Myco	Have been collected in dec wood (Leschen and Lawrence 2010)
160	**Phloeostichidae**	X	6	Most	Pal, s SAm, Aus	In, on WD	Myco	In, on WD	Myco	A and L often found under bark of dead trees (Lawrence and Ślipiński 2010b)
161	**Silvanidae**	X	500	Most	WW	In, on WD	Myco	In, on WD	Myco	Mostly subcortical and myco (Thomas and Leschen 2010a)
	Brontinae	X	300	Most	WW	In, on WD	Myco	In, on WD	Myco	Mostly subcortical and myco (Thomas and Leschen 2010a)
	Silvaninae	X	200	Most	WW	In, on WD	Myco	In, on WD	Myco	Mostly subcortical and myco (Thomas and Leschen 2010a)
162	**Cucujidae**	X	48	All	WW exc Afr	In WD	Unk	In WD	Pred	L and A under bark of dead trees (Thomas and Leschen 2010b)
163	**Myraboliidae**	X	13	All	Aus	In WD	Unk	In WD	Unk	A and putative L found under bark of living *Eucalyptus* (Ślipiński et al. 2010a)
164	**Cavognathidae**									Assoc with bird nests
165	**Lamingtoniidae**	X	3	All	Aus	On fungi	Myco	On fungi	Myco	A and L in wood-rotting basidiomycete fungi (Lawrence and Leschen 2010e)
166	**Passandridae**	X	109	All	WW	In WD	Unk	In WD	Ecpar	Ecto on wood-boring insect L and pupae (Burckhardt and Ślipiński 2010)
167	**Phalacridae**	X	635	Few	WW	In WD	Myco	In WD	Myco	Generally myco, mostly on mold-forming fungi; others poll (Gimmel 2013)

(continued)

Table 2.1 (continued)

#	Taxon	Sap^a	#Spp^b	% S^c	Regions^d	Adult found^e	A food^f	Larva found^e	L food^f	Notes
	Phalacrinae	X	615	Few	WW	In WD	Myco	In WD	Myco	*Litochrus* L reported from rotten wood or bark, *Litochropus* A and L from wood-rotting *Daldinia* galls (Steiner 1984; Gimmel 2013)
	Non-saproxylic subfamily: Phaenocephalinae (assoc with hanging dead leaves or leaf litter).									
168	**Laemophloeidae**	X	470	Most	WW	In WD	Myco, pred	In WD	Myco, pred	Maj feed on subcortical fungi, though some pred on bark beetles in their burrows (Thomas and Leschen 2010c)
169	**Tasmosalpingidae**									Presumptive L fogged from bark of a living tree
170	**Cyclaxyridae**									In sooty mold on living trees, myco
171	**Smicripidae**									A assoc with palm flowers, L in litter
172	**Kateretidae**									L and A develop and feed in flowers
173	**Nitidulidae**	X	4500	Some	WW	In, on WD; away	Myco	In, on WD and fungi	Myco	Some A assoc with dead wood, either under bark or in wood-boring insect tunnels, others in fleshy fungi, some at tree wounds and ferm sap (Jelínek et al. 2010)
	Calonecrinae	X	3	All	Or	In, on WD	Myco	In, on WD	Myco	At tree wounds and ferm sap (Jelínek et al. 2010)
	Cryptarchinae	X	300	Most	WW	In, on WD	Myco	In, on WD	Myco	Often at tree wounds and ferm sap (Jelínek et al. 2010)
	Prometopiinae	X	?30	?	?	?	?	?	?	At least some at tree wounds and ferm sap (Jelínek et al. 2010)
	Epuraeinae	X	350	Some	Hol	In WD	Myco	In WD	Myco	Some subcortical (Jelínek et al. 2010)

	Carpophilinae	X	500	Some	Hol	In WD	Myco	In WD	Myco	Some subcortical (Jelínek et al. 2010)
	Amphicrossinae	X	41	Some	Hol	In WD	Myco, pred	In WD	Myco	One spp. aquatic and pred in bamboo culms and stumps (Kovac et al. 2007)
	Nitidulinae	X	1000	Most	WW	In, on WD	Myco	In, on WD	Myco	Maj in fleshy fungi, some assoc with tree wounds and ferm sap; some subcortical (Jelínek et al. 2010)
	Cillaeinae	X	450	Some	Ptrop	In, on WD	Myco	In, on WD	Myco	*Colopterus* at tree wounds and ferm sap; some subcortical (Jelínek et al. 2010)
	Non-saproxylic subfamilies: Maynipeplinae (habits and L unk), Meligethinae [primarily anthophiles and phyto (Jelínek et al. 2010)]									
	Superfamily Chrysomeloidea (7)									
174	**Oxypeltidae**									L develop in living *Nothofagus*
175	**Vesperidae**									L feed on living roots
	Non-saproxylic subfamilies: Anoplodermatinae, Philinae, Vesperinae									
176	**Disteniidae**	X	300	Most	WW exc Aus	Away	Nec, non	In WD	Unk	L subcortical and in sapwood of dead and dying trees and shrubs (Svacha and Lawrence 2014a)
177	**Cerambycidae**	X	35,000	Most	WW	In, on WD; away	Phyto, nec, non	In WD	Sapro, phyto	Maj of L in dead or dying wood; some L root feeders in soil, in living trees; one leaf miner (Svacha and Lawrence 2014b)
	Prioninae	X	1000	All	WW	Away	Non (most)	In WD	Sapro	Dead wood, occasionally dead parts of living trees, but not subcortical (Svacha and Lawrence 2014b)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Parandrinae	X	119	All	WW	In, on WD	Non	In WD	Sapro	Dead moist logs, dead wood of living trees; sometimes L mature in healed over tree hollows and resultant A reproduce without leaving the tree (Svacha and Lawrence 2014b)
	Spondylidinae	X	100	Most	WW (adv Aus)	Away	Non	In WD	Sapro, phyto	Maj of L are dead wood feeders, some within dead wood of living trees, few root feeders (Svacha and Lawrence 2014b)
	Lepturinae	X	1500	Most	WW exc Aus	Away	Poll (most)	In WD	Sapro, phyto	L in moist rotting wood, some subcortical, some in living tree, some root feeders (Svacha and Lawrence 2014b)
	Necydalinae	X	73	All	Hol, Or	Away	Poll (most)	In WD	Sapro, phyto	L in dead wood, occasionally in living trees (Svacha and Lawrence 2014b)
	Dorcasominae	X	300	Most	Or, Pal, Afr	Away	Poll (most)	In WD	Sapro, phyto	Some L in living host, most in dead wood, some subcortical, some in herbs or underground (Svacha and Lawrence 2014b)
	Cerambycinae	X	11,000	Most	WW	Away	Poll, non	In WD	Sapro	L do NOT occur in soft rotten wood, only firm dead wood; rarely subcortical (Svacha and Lawrence 2014b)
	Lamiinae	X	20,000	Most	WW	Away	Phyto, sapro, myco	In WD	Sapro, phyto	Typically develop in fresh or living hosts; spp. in dead wood require moist wood and fungi, rarely in strongly rotten wood (Svacha and Lawrence 2014b)

178	**Megalopodidae**									Exclusively phyt
	Non-saproxylic subfamilies: Megalopodinae, Palophaginae, Zeugophorinae									
179	**Orsodacnidae**									Exclusively phyto
	Non-saproxylic subfamilies: Aulacoscelidinae, Orsodacninae									
180	**Chrysomelidae**	X	35,000	Few	WW	Away	Phyto, poll	On WD; away	Sapro, phyto	Very few spp. are not exclusively phyto
	Cryptocephalinae	X	5300	Few	WW	Away	Phyto, poll	On WD	Sapro	Some L are general sapro, occasionally eating outer layer of dead twigs (Chamorro 2014)
	Non-saproxylic subfamilies: Bruchinae (L develop in seeds), Cassidinae (exclusively phyto), Chrysomelinae (exclusively phyto), Criocerinae (exclusively phyto), Donaciinae (exclusively phyto), Eumolpinae (exclusively phyto), Galerucinae (exclusively phyto), Lamprosomatinae (L feed on bark of living trees), Sagrinae (exclusively phyto), Spilopyrinae (exclusively phyto, with some feeding on bark), Synetinae (exclusively phyto)									
	Superfamily Curculionoidea (7)									
181	**Nemonychidae**									Exclusively phyto as L, poll as A
	Non-saproxylic subfamilies: Cimberidinae, Nemonychinae, Rhinorhynchinae									
182	**Anthribidae**	X	3861	Most	WW	In, on WD and fungi	Myco, sapro, phyto	In, on WD and fungi	Myco, sapro, pred	Most myco, some phyto (Mermudes and Leschen 2014)
	Anthribinae	X	3148	Most	WW	In, on WD and fungi	Myco, sapro, phyto	In, on WD and fungi	Myco, sapro, pred	Maj of spp. develop in bark or wood of trees affected by fungi (Mermudes and Leschen 2014)
	Choraginae	X	630	Most	WW	In, on WD and fungi	Myco	In, on WD and fungi	Myco	Maj of spp. myco as A and L, developing in fungus-infested wood (Mermudes and Leschen 2014)

(continued)

Table 2.1 (continued)

#	Taxon	Sap^a	#Spp^b	% S^c	Regions^d	Adult found^e	A food^f	Larva found^e	L food^f	Notes
	Non-saproxylic subfamily: Urodontinae (exclusively phyto)									
183	**Belidae**	X	350	Some	WW exc Eur	Away	Unk	In WD	Sapro, phyto	Most in reproductive structures of plants; some subcortical in fresh dead, dying branches (Marvaldi and Ferrer 2014)
	Belinae	X	145	Most	SHem	Away	Unk	In WD	Sapro, phyto	Borers in stems and branches of shrubs and trees (Marvaldi and Ferrer 2014)
	Oxycoryninae	X	200	Some	WW exc Pal	Away	Unk	In WD	Sapro, phyto	Usu develop in plant reproductive organs, but some (especially Aglycyderini) develop in stems or bark (Marvaldi and Ferrer 2014)
184	**Caridae**									Exclusively phyto
185	**Attelabidae**	X	2500	Few	WW	Away	Phyto	In WD	Sapro	Maj are phyto, some feed in dead twigs (Riedel 2014)
	Rhynchitinae	X	1700	Few	WW	Away	Phyto	In WD	Sapro	L of 3 spp. of *Lasiorhynchites* feed in young, dead twigs of trees (Riedel 2014)
	Non-saproxylic subfamily: Attelabinae									
186	**Brentidae**	X	4400	Some	WW	In, on WD; away	Sapro, pred	In WD	Sapro, pred, myco	Maj are phyto
	Brentinae	X	1760	Most	WW	In, on WD; away	Sapro, pred	In WD	Sapro, pred, myco	L are wood borers; some develop within Scolytinae and Platypodinae burrows (Sforzi et al. 2014)

	Non-saproxylic subfamilies: Apioninae (all are phyto), Eurhynchinae (L develop in living branches), Ithycerinae (L develop on cambium and phloem of tree roots), Microcerinae (L develop on herbaceous roots), Nanophyinae (all are phyto)									
187	**Curculionidae**	X	51,000	Few	WW	In, on WD; away	Myco, sapro, phyto	In WD	Myco, sapro, phyto	Most are phyto
	Dryophthorinae	X	1200	Some	WW	In WD	Sapro	In WD	Sapro	In dec and dying stems of cycads (*Phacecorynes* spp) and in dec and rotten wood (Anderson and Marvaldi 2014)
	Platypodinae	X	1400	All	WW	In WD	Myco	In WD	Myco	Nearly all spp. cultivate and consume fungi in tunnels in sapwood and heartwood (Jordal 2014c)
	Brachycerinae	X	1350	Few	WW	In WD	Unk	Unk	Unk	A few gen in Myrtonymini and Raymondionymini found in rotting wood, less than 20 spp. (Oberprieler 2014a)
	Cyclominae	X	1550	Few	WW	Away	Unk	In WD	Sapro	A few spp. of Aterpini with L that bore into dead wood (Oberprieler 2014b)
	Molytinae	X	8700	Some	WW	In, on WD; away	Sapro	In WD	Sapro	Some from dead wood, including subcortical, some wood borers, some twig or root borers, some on driftwood, some in old dead bamboo, some sap feeders (Lyal 2014a)
	Conoderinae	X	7571	Some	WW	Away	Myco, sapro	In WD	Myco, sapro	Many spp. borers in dead wood; *Phaenomerus* occupy platypodine tunnels (Prena et al. 2014)
	Cossoninae	X	1700	Most	WW	In, on WD	Sapro	In WD	Myco, sapro	Many L develop in fresh or rotten wood (Jordal 2014a)

(continued)

Table 2.1 (continued)

#	Taxon	Sap[a]	#Spp[b]	% S[c]	Regions[d]	Adult found[e]	A food[f]	Larva found[e]	L food[f]	Notes
	Scolytinae	X	6000	Most	WW	In, on WD	Myco, sapro	In WD	Myco, sapro	Most A and L bore into dying wood; about 300 spp. don't use traditional food sources, only a few dozen attack living trees (Jordal 2014b)
	Mesoptiliinae	X	200	Most	WW	Away	Unk	In WD	Sapro	L in living or dead wood of twigs and branches, in or under bark (Lyal 2014b)
	Non-saproxylic subfamilies: Curculioninae (all are phyto), Entiminae (L phyto, living freely in soil; A feed on leaves and flowers)									

[a] Sap, saproxylic

[b] World tally of species; numbers are approximate in most cases

[c] % S, estimate of the percent of taxa that are saproxylic, based on our interpretation of the literature: all, 90–100%; most, 50–90%; some, 10–50%; few, <10%

[d] Distribution of the group, without regard to saproxylicity; *adv* adventive, *Afr* Afrotropical, *Aus* Australia, *Ausas* Australasia, *CAm* Central America, *Eur* Europe, *exc* except, *Hol* Holarctic, *Mad* Madagascar, *NAm* North America, *Nea* Nearctic, *Neo* Neotropical, *NG* New Guinea, *NHem* Northern Hemisphere, *NW* New World, *NZ* New Zealand, *Or* Oriental, *OW* Old World, *Pal* Palearctic, *Ptrop* pantropical, *s*, southern, *se*, southeastern, *Sey* Seychelles, *SAm* South America, *SHem* Southern Hemisphere, *STem* Southern Temperate, *w* western, *WI* West Indies, *WW* Worldwide

[e] *Away* away from woody debris, *WD* woody debris

[f] Feeding habits, not limited to saproxylic taxa: *ecpar*, ectoparasitoid; *enpar* endoparasitoid, *ferm sap* fermenting sap flows, *myco* mycophagous, *myxo* myxomycophagous, *nec* nectar, *non* non-feeding, *phyto* phytophagous, *poll* pollen-feeding, *pred* predacious, *sapro* saprophagous, *unk* unknown

Other abbreviations: *A* adult(s), *L* larva(e), *assoc* associated, *dec* decayed/ing, *gen*, genus/genera, *maj* majority, *sp./spp.* species, *usu* usually

Cerambycidae, and Curculionidae. In our view, the most significant poorly studied groups in saproxylic habitats are the Leiodidae, Staphylinidae, Eucnemidae, Ptinidae, Trogossitidae, Laemophloeidae, Silvanidae, Erotylidae, Mordellidae, Melandryidae, Ciidae, Zopheridae, and Tenebrionidae.

Our working definition of saproxylic for this chapter is *any species that would no longer be present in a community if dead and dying woody material were no longer available (including dead and dying wood in live trees)*. This definition is similar to that of Alexander (2008) in that it includes such habitats as sap flows and slime fluxes. For this chapter, we elected to favor a more inclusive definition of saproxylic habitats when deciding about apparently borderline cases. The reason for this was to highlight taxa that have not been traditionally included in discussions of saproxylic organisms in the interest of a more complete survey of beetles associated with woody material. We feel we have provided ample information about the specific habits and habitats of such organisms (where known) so that researchers employing a more restricted definition will be able to unambiguously include or exclude taxa belonging to particular guilds according to whichever scheme is being followed. Additionally, we hope that this more inclusive approach helps encourage future researchers to investigate the true habits and habitat requirements of such nontraditional and otherwise overlooked taxa, particularly where their specific habits and habitats are currently unknown.

As suggested above, the state of knowledge of the habits and habitats of some beetle groups is exceedingly poor, so these numbers are certainly underestimates, though vast numbers of undescribed species are known to occur among both saproxylic and non-saproxylic Coleoptera. Saproxylicity among Coleoptera broadly is a vast and largely unexplored research area, and we encourage other researchers and observers to assist in refining our table of saproxylic beetles. As the core of this contribution, we have included a list of all beetle families and subfamilies, regardless of saproxylicity, in order to (1) facilitate the visualization of errors, omissions, or potential current discoveries, as well as (2) to appreciate the proportion of higher-level diversity with saproxylic members (Table 2.1). It should be clear based on the foregoing that lack of indication of saproxylic habits in the table should not be taken as a positive assertion that the group contains no saproxylic members—immature stages are still undescribed for most described species of beetles (see, e.g., Acorn 2006) and even among described immatures, habits are incompletely known. For groups with saproxylic members, we indicate approximate world species totals, an estimate of the percentage of members saproxylic, world distribution of the group, and more specific habits and habitats where known (by us) through literature surveys, personal observations, and communication with other workers. The primary sources of information for this table were the three volumes of the Handbook of Zoology, Coleoptera volumes {Volume 1: Beutel and Leschen (2005) [updated version: Beutel and Leschen (2016a)]; Volume 2: Leschen et al. (2010); Volume 3: Leschen and Beutel (2014)}, the two volumes of American Beetles [Volume 1: Arnett and Thomas (2000); Volume 2: Arnett et al. (2002)], the Coleoptera chapter of immature insects (Lawrence 1991), references contained within these sources, and a smattering of other sources cited in the text and "Notes" section of Table 2.1. Since the two active stages of beetles, larvae and adults, often have dramatically different habits or habitats, we created two different columns and indicate habits and habitats for both, even in the case of larval- or adult-only saproxylic taxa. Entries concerning habits and feeding types refer to the group as a whole and not just to saproxylic members. We hope this will be a helpful tool for those investigating the presence of particular saproxylic taxa, since indirect surveys can be a viable alternative to directly sampling saproxylic habitats.

The classification used here recognizes 187 beetle families, of which 122, or about 65%, contain at least one known saproxylic member (Table 2.1). Saproxylic beetles are represented in three of the four suborders of beetles—only Myxophaga lacks known saproxylic members. Our current state of knowledge indicates that there are 32 beetle families in which all or virtually all species (90–100%) would be considered saproxylic, 31 families in which most species (50–90%) are saproxylic, 35 families with some species (10–50%) that are saproxylic, 22 with a few (<10%) saproxylic species, and one family (Trictenotomidae) for which no estimate can be given. Adults of saproxylic species are found within woody debris in about 61 families, on woody debris or fungi in 64 families, and away from woody debris in 43 families (categories overlapping, not cumulative). Where known, adults are mostly (in descending order) mycophagous, saprophagous, and predacious, with a few that are phytophagous, non-feeding, pollen-feeding, nectar-feeding, sap-feeding, or myxomycophagous. Adult feeding is unknown for about 27 families. Larvae of saproxylic species are found within dead wood for about 100 families and on dead wood or fungi in about 49 families. Where known, larvae are mostly mycophagous, saprophagous, or predacious with a very few myxomycophagous, phytophagous, sap-feeding, or parasitic. Larval feeding is unknown for about seven saproxylic families.

2.5 Conclusion

The primary purposes of this chapter were twofold: firstly, to assemble what is known concerning the higher beetle taxa associated with the saproxylic habitat and provide a broad summary thereof. While we did not attempt an exhaustive review of the topic, we hope that the information and resources provided in this chapter provide sufficient ordnance to successfully storm the landscape of this topic and further interrogate particular saproxylic beetle groups.

Secondly, this chapter provides a map of sorts to parts of the saproxylic beetle landscape, highlighting those that are unknown, veiled, and beyond the wall of ignorance. Table 2.1 is bespotted with the term "unk" (i.e., unknown, 153 times!), to us evoking the spots that cover the fawn of a white-tailed deer—immature, gangly, and unsure of itself and the world. Our knowledge of saproxylic beetles is in much the same state, a long way from maturity. The reader is provided with a thin guide that we hope will be useful when marshalling resources and directing excursions into that mysterious realm. Every “unk” is an opportunity for future students of the topic to help piece together the complex tapestry of saproxylic beetle natural history.

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Chapter 3
Ecology and Conservation of Passalidae

Michael D. Ulyshen

Abstract Consisting of about 1000 species globally, beetles of the family Passalidae feed on decomposing wood in tropical and subtropical forests throughout the world. Passalids live in subsocial family groups within their galleries, characterized by overlapping generations, cooperative brood care, and a complex communication system involving stridulations. In what has been referred to as an “external rumen,” larval passalids feed on the microbe-rich frass and finely chewed wood paste produced by the wood-feeding adults. Endosymbionts found within the guts of passalids include a variety of microbes, including nitrogen-fixing prokaryotes and yeasts that aid in the digestion of wood. In addition to wood consumption, passalids fragment large amounts of wood in the process of creating extensive tunnel systems and are, among saproxylic insects, perhaps rivaled only by termites in their importance to wood decomposition. Although a number of laboratory studies have measured the amount of wood processed by various passalid species, no attempt has been made to quantify their contributions to wood decomposition under natural conditions. Passalids, along with their many microbial and invertebrate associates, are of considerable conservation concern given high levels of endemism and flightlessness. Many species appear sensitive to forest loss and disturbance and they have been used as indicator taxa in the creation of protected natural areas.

3.1 Introduction

Passalidae is a mostly tropical scarabaeoid family of shiny black beetles ranging from about 1 to 8 cm in length (Fig. 3.1). The family consists of two subfamilies [Aulacocyclinae (old world, two tribes) and Passalinae (pantropical, five tribes)] and approximately 1000 species (Boucher 2005). Each of the seven tribes recognized by Boucher (2005) is restricted to a particular region of the world. Passalini and

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Fig. 3.1 Museum specimens representing <3% (28 spp.) of global passalid diversity: *Aceraius grandis* (Burmeister) (Taiwan) (28); *Chondrocephalus* sp. (Guatemala) (3); *Heliscus tropicus* (Percheron) (Mexico) (4); *H. yucatanus* (Bates) (Mexico) (5); *Leptaulax* sp. (Philippines) (6); *Odontotaenius disjunctus* (Illiger) (USA) (31); *Od. striatopunctatus* (Percheron) (Honduras) (9); *Oileus sargi* (Kaup) (Honduras) (8); *Passalus bucki* (Luederwaldt) (Trinidad) (7); *Pas. caelatus* (Erichson) (Panama) (24); *Pas. elfriedae* (Luederwaldt) (Trinidad) (25); *Pas. interstitialis* (Eschscholtz) (Guatemala) (12); *Pas. punctatostriatus* (Percheron) (Panama) (13); *Pas. punctiger* (LePeletier and Serville) (Mexico) (1,2,16); *Pas. spiniger* (Bates) (Panama) (17); *Paxillus borellii* (Pangella) (Brazil) (20,30); *Pax. camerani* (Pangella) (Peru) (11); *Pax. jamaicensis* (Hincks) (Jamaica) (18); *Pax. leachi* (MacLeay) (Mexico) (19); *Proculus goryi* (Melly) (Guatemala) (14); *Pr. mniszechi* Kaup (Honduras) (15); *Ptichopus angulatus* (Percheron) (Mexico) (26); *Publius crassus* (Smith) (S. America) (10); *Spurius bicornis* (Truqui) (Mexico) (23); *Verres corticola* (Truqui) (Costa Rica) (27); *V. deficiens* Kuwert (Costa Rica) (29); *V. furcilabris* (Eschscholtz) (Trinidad) (21); *V. hageni* (Kaup) (Costa Rica) (22)

Proculini are restricted to the Americas, Solenocyclini are found in Africa and Madagascar, Ceracupini are found in Asia, Aulacocyclini and Macrolinini occur throughout Southeast Asia and eastern Australia, and Leptaulacini are found throughout Southeast Asia (Boucher 2005). Passalid richness typically decreases with increasing latitude or elevation, with the family being most diverse in moist lowland tropical forests (Schuster 1978; Moreno-Fonseca and Amat-García 2016; Castillo and Reyes-Castillo 2003). The number of passalid species present varies widely among locations within the tropics, ranging from 1 to 22 in Central and South

America, for example (Castillo and Reyes-Castillo 2003). Passalids exhibit high levels of endemism, including giant flightless species restricted to tropical cloud forests (Schuster et al. 2003), those occurring only in Andean foothills (Fonseca and Reyes-Castillo 2004), and species found only on particular islands (Jimenez-Ferbans et al. 2015) or at locations that were once islands separated from the mainland (Schuster 1994). Howden (1977) found passalids in driftwood on beaches in Australia, demonstrating the potential to colonize islands, and one island species consists almost entirely of females and has been shown to reproduce parthenogenetically (Boucher et al. 2015). Although passalid diversity is highest in tropical forests, a number of species occur in temperate zones, and these are among the best-studied taxa. These include *Odontotaenius disjunctus* (Illiger) in North America (extending as far north as Canada), *Cylindrocaulus* spp. in Japan and Northern China (Kon et al. 1999; Mishima et al. 2016), *Leptaulax koreanus* Nomura in Korea (Kim and Kim 2014), and *Pharochilus politus* (Burmeister) in Tasmania (Dibb 1938).

While a few species are known from other habitats [e.g., leaf-cutter ant nests, termite colonies, caves containing colonies of fruit-eating oilbirds, in detritus among the roots of epiphytes or from the decomposing debris of non-woody plants (Schuster 1978)], most passalid species are saproxylic, spending their entire life cycle within or beneath decomposing wood. Unlike the incredible diversity in form and coloration exhibited by other saproxylic scarabaeoid families (e.g., Lucanidae, Scarabaeidae), the body shape of passalids varies remarkably little among species (Arrow 1950) (Fig. 3.1). Moreover, whereas the males of many saproxylic lucanid and scarab (e.g., Dynastinae and Cetoniinae) species are famous for their exaggerated armaments (e.g., mandibles and horns), sexual dimorphism is largely absent among passalids. This may be due in part to the fact that passalids remain within decomposing logs as adults where giant mandibles and horns would be a hindrance to movement. The absence of sexual dimorphism in passalids may also be related to their monogamy and sociality, i.e., living in small family groups characterized by overlapping generations, cooperative brood care, and a complex communication system involving various stridulations. Compared to the amount of attention researchers have paid to passalid sociality, the importance of these insects to wood decomposition remains a relatively neglected topic. This is unfortunate considering that, among saproxylic insects, passalids are probably exceeded only by termites in their importance to decomposition in tropical and subtropical forests. These and other aspects of passalid biology are reviewed below, followed by some considerations for conservation.

3.2 Ecology

3.2.1 Subsocial Behavior

Passalids live in subsocial family groups within tunnels they excavate in moderately decomposed wood. Tunnel systems, or galleries, which often exceed a meter in length (Gray 1946; Galindo-Cardona et al. 2007), are initiated by a single female or male which is later joined by a member of the opposite sex. Copulation typically occurs within the galleries (Castillo and Reyes-Castillo 2009) although exceptions have been documented, e.g., MacGown and MacGown (1996) observed nuptial flights of *O. disjunctus* in Mississippi. Passalids are monogamous after gallery establishment, and both sexes contribute to the creation of galleries. These efforts result in the production of large amounts of fragmented wood, some of which gets pushed out of the log near the tunnel entrance (Fig. 3.2d). Eggs are laid upon a nest of finely chewed wood within the galleries and the adults attend to them. Larvae eat wood that is shredded and chewed by the adults as well as the frass of mature adults. In what Mason and Odum (1969) referred to as an "external rumen," the gut microbes associated with frass, as well as with the finely chewed wood paste that is used to line the walls of the galleries (Castillo and Reyes-Castillo 2009), continue the process of digestion outside the body, ultimately producing a more nutritious resource than the wood itself (Schuster and Schuster 1997; Rodriguez and Zorrilla 1986; Larroche and Grimaud 1988). Coprophagy is not uncommon among invertebrates that feed on decomposing plant matter (Szlávecz and Pobozsny 1995) and appears to be particularly important to passalids. It has been shown that *O. disjunctus* individuals quickly lose weight or even die in the absence of frass, for example (Pearse et al. 1936; Mason and Odum 1969; Mishima et al. 2016). The parents of at least one species of passalid, *Cylindrocaulus patalis* (Lewis) of Japan, go so far as to provision their larvae with trophic eggs, i.e., nonviable eggs which are consumed by the larvae (Ento et al. 2008).

The parents and their teneral and mature adult offspring assist larvae in the creation of a pupal case, constructed out of frass and providing protection for the vulnerable pupal stage (Schuster and Schuster 1997). Weeks or months are needed for teneral adults to change from reddish brown to black and to become sexually mature (Schuster and Schuster 1997). At that point [and sometimes before, see Jackson et al. (2009)], they either migrate to initiate a new colony [usually nearby, see Galindo-Cardona et al. (2007)] or excavate galleries off those created by their parents (Schuster and Schuster 1997). Migration typically takes place during particular parts of the year (e.g., at the beginning of the wet season in tropical areas) and, depending on the species, can involve flying and/or walking (Schuster and Schuster 1997). Passalids are known to communicate through tactile, chemical, and acoustic cues (Castillo and Reyes-Castillo 2009). Both larvae and adults produce a variety of sounds through stridulation, but the sounds produced by adults are louder and known to vary depending on the behavioral context. Schuster (1983) reported that the sounds produced by adult passalids can be separated into seven basic structural types and exist in 13 different behavioral contexts. The same study showed *O. disjunctus* to produce 14 different sound signals depending on the situation, representing perhaps the most complex repertoire of acoustic signals produced by any arthropod.

Social behavior is not uncommon among saproxylic insects, as evidenced by the high number of eusocial (e.g., termites) and subsocial (e.g., *Cryptocercus*) wood-feeding cockroaches, the eusocial ambrosia beetle *Austroplatypus incompertus* (Schedl) (Kent and Simpson 1992), subsocial stag beetles (Mori and Chiba 2009),

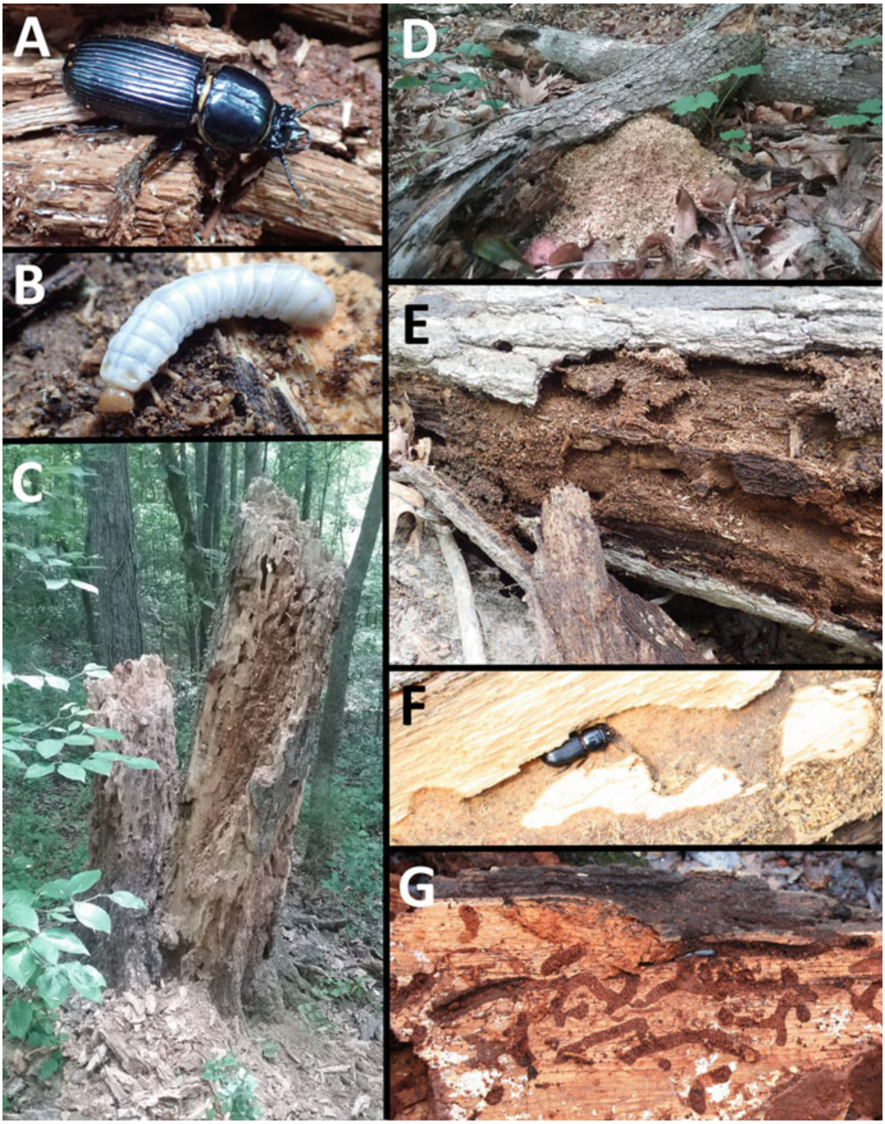

Fig. 3.2 *Odontotaenius disjunctus* in the southeastern United States: adult (**a**); third instar larvae (**b**); damage to standing trunk (**c**); pile of wood fragments near tunnel entrance (**d**); and galleries (**e**–**g**)

and a particularly interesting group of subsocial tenebrionids (*Phrenapates* spp.) which, as briefly discussed below, are in many ways similar to passalids (Nguyen et al. 2006). It is perhaps not surprising that a substrate as recalcitrant and nutritionally poor as wood would give rise to intraspecific cooperation in addition to the many examples of interspecific cooperation (e.g., endo- and ectosymbioses) documented among these insects. Just as N-fixing gut symbionts can greatly accelerate the development rates of their wood-feeding host insects (Ulyshen 2015), the parental care exhibited by passalids probably has similar benefits to the development of their offspring. Support for this comes from a study by Mori and Chiba (2009) who showed that a species of Asian lucanid, *Figulus binodulus* Waterhouse, develops more quickly when parents are present than when absent. The researchers concluded that improving food quality, e.g., by pulverizing wood, is the most likely mechanism by which *F. binodulus* parents improved juvenile growth. Moreover, passalids are known to develop more quickly than less social wood-feeding taxa. Whereas many lucanid species require one or more years to complete development, the larval period for passalids lasts for several months at the most (Mishima et al. 2016; Gray 1946; Castillo and Reyes-Castillo 2009). The passalid species with the shortest known larval period (approximately one month) is *Cylindrocaulus patalis* in Japan, a species that exhibits unusually high levels of parental care due to a parent/offspring ratio of 1:1 (Mishima et al. 2016).

The fact that passalids continue to feed on decomposing wood as adults, unlike most saproxylic scarabaeoids, may have set the stage for the development of subsocial behaviors by bringing adults and larvae into close contact (Schuster and Schuster 1997). Indeed, the wood-digesting gut symbionts passalid parents provide to their offspring in the form of frass appear to be of huge benefit to larval growth, and this may have selected for sociality. Evidence for the selective value of symbionts to larval wood-borer development comes from the existence of mycangia in female lucanids. These structures, which are absent in passalids and related groups, are thought to provide a mechanism (i.e., in the absence of gut symbionts since adult lucanids do not feed on wood) by which female lucanids can provide assistance to their larvae by inoculating oviposition sites with beneficial xylose-fermenting yeasts stored within their mycangia (Tanahashi et al. 2010). The subsocial behavior of another group of wood-boring beetles, Central and South American tenebrionids of the genus *Phrenapates*, is particularly informative given their similarity, in a number of respects, to passalids. *Phrenapates* not only look like passalids (so much so that they are often confused with them) but also live in subsocial groups within decomposing wood and have similar symbiotic relationships with xylose-fermenting yeasts (Nguyen et al. 2006). These similarities appear to reflect convergent solutions to the challenges facing wood-feeding insects, although it should be noted that sociality in *Phrenapates* remains poorly studied.

Other possible factors contributing to the emergence of sociality in passalids have received less attention, including the role adult passalids may play in protecting their offspring from predators as well as other passalids [i.e., adult passalids are known to cannibalize immature stages (Gray 1946)]. Alternative explanations for social behavior are worth further consideration given that some previous researchers have cast doubt on the idea that passalid larvae are closely attended to by their parents and adult siblings. Based on his observations in South America, for example, Heymons (1929) noted that parents and larvae are often widely separated within a gallery system, and the space between them is often clogged with wood fragments. The possibility that these piles of fragments may serve as fortifications against predators, similar to the fortifications termites construct using soil carried into logs, is deserving of investigation, as are the potential benefits parents provide in driving away predators. In North America, the tachinid *Zelia vertebrata* (Say), a generalist parasitoid of saproxylic beetle larvae, is one of the most important predators of *O. disjunctus*. It seems possible that walls of wood fragments, as well as the adults themselves, may provide a protective function against these and other natural enemies.

3.2.2 Endosymbionts

It has long been known that wood-feeding insects rely on a variety of symbiotic gut-dwelling microbes to aid in the digestion of wood and that many of them may gain more nourishment from these microbes than from the wood itself (Uvarov 1928). Although the gut-dwelling microbes of passalids have been studied for well over a century (Pearse et al. 1936; Leidy 1852; Lichtwardt et al. 1999), the biggest advances in understanding have been made in the past 10–20 years, and the findings from these more recent studies are briefly summarized here. It is clear that passalid guts house complex assemblages of microorganisms (including bacteria, Archaea, protists, nematodes, and various fungi) and that the composition of microbial communities varies among gut regions (Nardi et al. 2006). Ceja-Navarro et al. (2014), for example, reported significant compositional differences in bacteria and archaea communities among the four main gut regions (foregut, midgut, anterior hindgut, and posterior hindgut) of *O. disjunctus*, although the midgut and posterior hindgut communities did not differ from one another. Higher taxon richness was observed in the foregut and posterior hindgut than in the midgut or anterior hindgut. Moreover, aerobic bacteria were more abundant in the foregut and posterior hindguts, while anaerobic bacteria dominated the anterior hindgut and midgut. All gut regions contained an anaerobic core but also possessed radial gradients in oxygen concentration, indicating that aerobic and anaerobic metabolism occur within close proximity. Ceja-Navarro et al. (2014) also confirmed the presence of N-fixing prokaryotes (mainly *Bacteroidetes* spp., rather than the N-fixing spirochetes common in termites) in various gut regions of *O. disjunctus*, and these organisms are likely to contribute to the N economy of their hosts, as they do in so many other wood-feeding insects (Ulyshen 2015).

The first suspected endosymbionts reported from passalid guts were yeasts that Suh et al. (2003) found in consistent association with their hosts over a broad geographical area. Because some of the yeasts are known to ferment and assimilate xylose or hydrolyze xylan (major components of hemicellulose), they are suspected to play an important role in the digestion of wood within the passalid gut. More recently, Nguyen et al. (2006) showed that similar yeasts to those found in the guts of passalids can also be found in the guts of distantly related wood-boring beetles, such as *Phrenapates bennetti* Kirby, a tropical wood-feeding tenebrionid. Urbina et al. (2013) documented approximately 78 yeast species from 16 Guatemalan passalid species. Xylose- and cellobiose-fermenting yeasts belonging to *Scheffersomyces* and *Spathaspora* were the most abundant and consistently present clades reported in that study. In addition to their role in digesting wood, these yeasts have the potential to also benefit their hosts by providing certain essential amino acids, vitamins, and sterols or by detoxifying plant metabolites (Urbina et al. 2013). The importance of these and other gut-dwelling microbes to their hosts remains poorly understood, and the extent to which the growth of passalids is fueled by wood vs. microbial biomass remains an unanswered question. Mishima et al. (2016) recently argued that the Japanese passalid, *Cylindrocaulus patalis*, is primarily fungivorous because the activities of enzymes required to digest β-1,3-glucan (present in fungal cell walls) were much higher than those required to digest β-1,4-xylan (present in wood). Moreover, the researchers found much lower enzymatic activity in *C. patalis* larvae compared to adults.

3.2.3 Substrate Selection

Like many insects associated with wood at intermediate or late stages of decomposition, passalids are not very discriminating with respect to which wood species they utilize. The activities of most species are limited to angiosperms, however, with just a few known from pines or other conifers (Schuster 2008). In Puerto Rico, Galindo-Cardona et al. (2007) found *Spasalus crenatus* (MacLeay) in logs belonging to 18 (64%) of the 28 wood species sampled. Some wood species were less readily colonized than others, however, with the relatively soft wood of pioneer species being less preferred. Gray (1946) reported that *O. disjunctus* can be found using the logs or stumps of nearly all species of tree in North Carolina although only rarely pine and never cedar. Jackson et al. (2012) found the probability of *O. disjunctus* being present in logs to be higher for large logs compared to small logs as well as logs belonging to intermediate stages of decomposition and logs without heart rot. Moreover, *O. disjunctus* appears to strongly prefer white rot (Jackson et al. 2013). The extent to which these substrate associations hold true for other passalid species is not clear although many species exhibit preferences for particular microhabitats. For example, some species focus their activities beneath the bark, within the sapwood/heartwood or at the wood-soil interface (Kon and Johki 1987; Moreno-Fonseca and Amat-García 2016). Although the width/length ratio of passalid bodies is remarkably consistent across taxa (Fig. 3.1), species found primarily under bark tend to more dorsoventrally flattened than sapwood/heartwood feeders (Johki 1987; Lobo and Castillo 1997). Moreno-Fonseca and Amat-García (2016) also found differences in tibia morphology among different passalid guilds. Passalids are not limited to fallen logs but can also be found tunneling into standing deadwood (Fig. 3.2c). Working in Brazil at the end of the nineteenth century, Ohaus (1909) described the experience of witnessing a 20 m tall tree fall nearby. As it came crashing to the ground, it broke apart, revealing galleries extending along the entire length of the trunk and containing hundreds of passalids. Similarly, Schuster (1978) reported collecting a species of *Spasalus* at a height of 7 m in a standing trunk in Peru. *Odontotaenius disjunctus* has also been collected many meters above the ground (Schuster 1978) although Jackson et al. (2012) showed that the probability of standing deadwood being colonized by that species to be lower than that of downed wood.

Jackson et al. (2013) showed that the positive relationship observed between *O. disjunctus* density and log size (Jackson et al. 2012) is better explained by a preference for larger logs than by differences in habitat quality between large and small resources (i.e., beetle preference did not correspond with greater reproductive success). The possibility that large logs may result in higher lifetime fitness or allow for multiple generations by providing more stable habitats was not tested, however, and the researchers stopped short of suggesting that large-diameter logs have no special value to passalid conservation. Although little information has been published about the importance of large logs in providing long-term resources, Gray (1946) reported that an oak log approximately 1 m in diameter supported *O. disjunctus* for more than a decade in North Carolina. Jackson et al. (2013) also found that *O. disjunctus* preferred to colonize logs that already contained conspecifics (something they can detect from outside a log) even though this had short-term negative effects on reproductive success. Selecting logs that are already colonized may have benefits not measured in that study, however, including reduced search costs, increased mating opportunities, and reduced predation risk (Jackson et al. 2013). Although *O. disjunctus* is the only passalid species present throughout most of its range, it is not uncommon for multiple species to coexist within many tropical forests (Kattan et al. 2010) and as many as 5–10 species can be found residing within the same log (Castillo and Reyes-Castillo 2009; Luederwaldt 1931).

3.2.4 Succession

While relatively few studies have explored the succession of passalid species throughout the decomposition process, it is well established that species feeding beneath the bark are typically the first to colonize a dead log (often before the wood has begun to decompose). These species are characterized by rapid feeding and reproductive rates as well as strong dispersal abilities relative to those that feed on decomposing sapwood/heartwood (Castillo and Reyes-Castillo 2009). Castillo and Reyes-Castillo (2003) provide a table showing which species of passalids were present in logs belonging to four stages of decomposition in Mexico. While some species were found in all four decay classes, others showed a preference for those at early or late stages of decomposition.

3.2.5 Occupancy Rates

Early naturalists working in South America noted that dead tree trunks and branches are almost always occupied by passalids (Ohaus 1909). Only a few efforts have been made to carefully quantify this, however. In Chiapas, Mexico, passalids were found in 91% of logs examined by Morón et al. (1988). Galindo-Cardona et al. (2007) reported finding *Spasalus crenatus* (MacLeay) in 42% of sampled logs in Puerto Rico, with some wood species more likely to be occupied than others. Out of 248 decomposing logs examined in a primary Mexican rain forest, 64% were inhabited by one or more passalid species, with 13 species collected overall (Castillo and Reyes-Castillo 2009). A similar study carried out in a less pristine forest and pastureland in Brazil found 21.5% of all logs examined to have one or more passalid species, with a total of nine species detected overall (Castillo and Reyes-Castillo 2009). Castillo and Reyes-Castillo (2009) suggested that the differences in occupancy rates between these Mexican and Brazilian sites may indicate the negative effects of disturbance on passalid communities. In Colombia, Kattan et al. (2010) found passalids present within 36% of logs sampled in three forest types, but old-growth remnants appeared to have higher occupancy rates than Andean alder plantations or naturally regenerating forests. In Louisiana, Jackson et al. (2012) found 26% of hardwood logs ($\geq$5 cm in diameter and showing evidence of decay) were colonized by *O. disjunctus* and found the species in 73% and 95% of their 314 m^2 subplots and 1256 m^2 plots, respectively. In order of importance, Jackson et al. (2012) found the probability of occupancy in sampled log sections was higher when (1) logs were moderately decomposed, (2) logs were large, (3) the area did not experience flooding, (4) the surrounding 225 ha was more forested, (5) heartrot was absent, (6) ants were absent, (7) other wood borers were present, (8) there was less canopy cover, and (9) the piece of wood was downed and not standing.

3.2.6 Importance as Decomposers

Although passalids obviously play an important role in the physical degradation of wood (Morón 1985; Castillo and Reyes-Castillo 2003; Rodriguez and Zorrilla 1986) and are perhaps rivaled only by termites in their importance to wood decomposition in many tropical forests, their contributions to this process remain poorly quantified. With respect to insect-mediated decomposition, it is important to distinguish between the physical destruction (i.e., fragmentation or comminution) and chemical digestion of wood as these are two completely different processes. Only the latter qualifies as decomposition although comminution can indirectly accelerate decomposition by improving gas exchange and increasing the surface area of wood exposed to microbes (Ulyshen 2016). The extent to which wood-boring insects consume the wood they fragment varies greatly among species. Ambrosia beetles, for example, only fragment wood during the creation of the galleries within which they cultivate their symbiotic fungi. On the other end of the spectrum are wood-feeding termites which consume virtually all of the wood that they process and assimilate much of it with the help of endosymbionts. Passalids fall somewhere in between, fragmenting large amounts of wood and consuming some of it. Compared to the high assimilation efficiency exhibited by termites, wood passing through the gut of a passalid is not well digested. In fact, most of the chemical degradation of wood consumed by passalids occurs on the frass deposited by the beetles in their galleries [i.e., the external rumen as described by Mason and Odum (1969)]. The frass gets re-ingested multiple times and gets more digested and nutrient-enriched (Larroche and Grimaud 1988; Rodriguez and Zorrilla 1986) with each cycle. A full understanding of the role passalids play in wood decomposition will thus require information on how much wood is fragmented, how much of the fragmented wood is consumed, how thoroughly the consumed wood gets digested after multiple gut transits, etc. Another important question concerns how much faster (or slower) wood fragments created but not consumed by passalids decompose relative to intact wood.

The most straightforward way to assess the net effect of insects on wood decomposition is to compare differences in dry wood mass loss between logs from which the insects of interest have or have not been excluded [preferably under field conditions, as discussed below and described by Ulyshen et al. (2016)]. However, most past efforts to assess the role of passalids in wood decomposition have focused on measuring the amount of debris (including fragments and frass) produced per individual over a given unit of time. While such information provides a sense of how much wood is transformed by these insects, it is technically a measure of physical breakdown and should not be confused with decomposition. One of the earliest efforts to quantify the role of passalids as decomposers was a laboratory study by Preiss and Catts (1968). Although wood mass loss was not calculated in that study, the researchers found an oak log to be almost completely fragmented by seven adult *O. disjunctus* after a 30-week period. In another laboratory study, Rodriguez and Zorrilla (1986) similarly found *Passalus interstitialis* (Eschscholtz) fragmented 3–33% of wood weight within one month, with some wood species experiencing higher rates of fragmentation than others.

A study by Castillo and Morón (1992) yielded some of the best existing information about the importance of passalids to both the physical and chemical breakdown of wood. They investigated the rate at which ten species of passalids native to Mexico processed wood under laboratory conditions. Overall, the 110 beetles used in the study processed 43.6% of the dry wood weight provided. More than half (54.7%) of the processed wood (or 23.8% of the total wood provided) was converted to detritus. Although not explicitly stated in the article, the remaining 45.3% (or 19.8% of the total wood provided) was presumably respired or assimilated by the beetles (it is not possible to determine what fraction of this weight was due to decay fungi active in the wood vs. due to the passalids themselves, however). Overall, passalids in that study processed about 4.5 times their total body weight in wood although the relative rate of consumption (i.e., rate of immobilization/assimilation after correcting for differences in body mass) varied greatly among the ten passalid species studied. The relative rate of consumption decreased with increasing body weight and was highest for *P. interstitialis*, a species that feeds on the relatively nutritious (and perhaps more readily assimilated) wood just beneath the bark. Species that feed under the bark are also characterized by rapid population growth in order to make use of an ephemeral resource (Castillo and Reyes-Castillo 2009), and this might also explain their higher relative consumption rate. The researchers also observed strong differences in the amount of wood processed (fragmented) by the different passalid species and attributed these to differences in body size (i.e., large species create larger tunnel systems) as well as to uneven levels of acceptance among the species for the type of wood used in the experiment.

Most recently, Fonseca (2014) used similar methods to investigate the amount of wood processed by six species of Colombian passalids held under laboratory conditions. Closely matching the findings of Castillo and Morón (1992), detritus accounted for about 58%, on average (with a range of about 33–79% among the six species studied), of wood mass loss. As with the study by Castillo and Morón (1992), however, it is not possible to determine how much of the remaining wood loss was due to the activities of wood-rotting fungi vs. the beetles. Future studies addressing this question would benefit from the addition of a reference treatment as this would provide information on how much mass loss occurs in the absence of passalids. Inconsistent with the pattern reported by Castillo and Morón (1992), Fonseca (2014) found sapwood/heartwood feeders and generalists to exhibit higher relative consumption rates than species belonging to the under-bark feeding guild. It is clear from these and other studies that the degree to which passalids accelerate wood decomposition will ultimately depend on the species of passalid(s) present; wood characteristics such as density, nutritional content and other factors that vary among tree species; and abiotic conditions (Cano and Schuster 2012).

To my knowledge, no effort has been made to experimentally quantify the contributions of passalids to wood decomposition under natural conditions in the field. Such work would be of great value considering that laboratory studies are typically done under unnatural conditions including forced colonization by beetles (after removing them from active colonies located elsewhere), an absence of inter-specific interactions with other insects known to coexist with passalids in decomposing logs, and disturbed or unrealistic fungal communities. One of the biggest challenges to overcome in field-based insect exclusion studies is to avoid differences in microclimate (and therefore microbial activity) between treatments (Ulyshen and Wagner 2013; Kampichler and Bruckner 2009). Among several methods tested in Mississippi over a 10-year period, Ulyshen et al. (2016) found that pans with screened bottoms and open tops showed the most promise with respect to excluding termites without resulting in differences in microclimate between experimental logs protected or unprotected from termites. Although passalids were not included in that study, future studies could include holes along the sides of the pans to permit the natural colonization of “unprotected logs” by walking passalids. Pans without holes could serve as the “protected” treatment.

3.2.7 Interspecific Interactions

Many animals have been shown to opportunistically use the galleries created by passalids. Gray (1946), for example, reported a long list of invertebrates (including nematodes and earthworms) as well as various reptiles and amphibians found within *O. disjunctus* tunnels in North America. Some species appear to be strongly, if not entirely, dependent on passalids for food, shelter, or transportation. Examples include cockroaches (e.g., *Panchlora* in Mexico) that feed on detritus within passalid galleries in Central and South America (Castillo and Reyes-Castillo 2009; Ohaus 1909), ceratocanthids associated with passalid galleries in Southeast Asia and the Americas (Ballerio and Maruyama 2010; Ohaus 1909; Woodruff 1973), a scarab in West Africa (*Paraphytus aphodioides* Boucomont) that forms brood balls from a mixture of passalid frass and wood fragments (Cambefort and Walter 1985), and many species of mostly phoretic mites and pseudoscorpions (Ohaus 1909). Hunter (1993) reported 21 families, 68 genera, and over 200 species of mites known from passalid beetles, including 6 families found only in association with these insects. Although a few mite species associated with passalids are believed to be parasitic, most are believed to be commensal and phoretic, using their hosts as transportation to new habitats. Different phoretic mite species attach to different parts of the passalid body. The 16 mite species associated with *O. disjunctus* in North America, for example, can be distinguished between those that ride on external surfaces (e.g., gular region, frons, near the front coxae) vs. those that ride in protected body niches (e.g., antennal and maxillary sulci, between the pro- and mesothorax, under the elytra) (Hunter 1993). By contrast to that of *O. disjunctus*, the phoretic arthropod community associated with most passalid species remain mostly, if not entirely, unknown. This includes even some of the largest mites, as evidenced by the recent description of a giant (>5 mm) mesostigmatan mite from an Australian passalid (Seeman 2017). Moreover, only a few studies have investigated the habits of mites within passalid galleries (e.g., Butler and Hunter 1968).

Passalids commonly share logs with termites and ants throughout the tropics. In the Brazilian Amazon, for example, Fonseca (1988, see Table 2) reported that ants and/or termites were present in 86% of the logs containing passalids, with 54% of the logs containing all three taxa. Morón (1985) suggested there is intense competition for decomposing logs among termites, ants, and passalids in Mexican forests below 1000 m elevation and that the social insects tend to displace the beetles. Ants, in particular, are major predators of insects within deadwood and no doubt pose a serious threat to larval passalids. In Chiapas, Mexico, Morón et al. (1988) observed that ants commonly (in about 50% of the logs examined) colonize galleries excavated by passalids and other wood-boring beetles. They further noted that any larval or adult beetles present within these galleries were either killed by the ants or forced to leave. Consistent with this, Jackson et al. (2012) found the probability of a log section being occupied by *O. disjunctus* to be lower when ant colonies were present. The presence of subterranean termites (*Reticulitermes* spp.) was not important, however, Gray (1946) reported that adult *O. disjunctus* sometimes bite into

Reticulitermes galleries and will sometimes even eat termites they encounter but that *Reticulitermes* are only occasional and accidental inhabitants of passalid galleries.

Documented insect predators of passalid larvae include opportunistic predatory families like Reduviidae and generalist parasitoids like certain members of the fly family Tachinidae (Castillo and Reyes-Castillo 2003). In North America, Gray (1946) found *O. disjunctus* larvae to sometimes be parasitized at very high rates (up to 60% of third instar larvae, for example) by the tachinid *Zelia vertebrata*. It is possible that adult passalids can drive many potential predators out of their tunnels given the aggressive behaviors (e.g., biting and pushing) they exhibit toward conspecific intruders (Castillo and Reyes-Castillo 2009). According to Castillo and Reyes-Castillo (2009), predation of passalids by vertebrates is rarely seen but can include lizards and woodpeckers. Documented vertebrate predators of *O. disjunctus* include lizards, opossums, and bears (Brown 2004; Reynolds 1945; Vitt and Cooper 1985).

3.3 Conservation

3.3.1 Threatened Species

Many passalid species are inherently at risk due to small distributions, dependence on particular habitats, or an inability to fly, and this appears to be the case throughout the world, e.g., flightless species are known from all subfamilies (Hinks 1933). Restricted to the Americas and containing roughly 19 genera (Boucher 2005), the tribe Proculini (subfamily Passalinae) exhibits particularly high levels of endemism and flightlessness. This is especially true for species limited to cloud forests, including the genus *Proculus* which contain some of the largest passalid species in the world (Fig. 3.1). Schuster et al. (2003) concluded their revision of the genus with this warning: “In general *Proculus*, as well as other montane species of passalids, is probably in danger of extinction throughout its range due to the elimination of most of the forest where it occurs.” *Odontotaenius* also exhibits high levels of endemism. For example, Schuster (1994) described a second species of North American *Odontotaenius*, *O. floridanus* Schuster, that is restricted to sandy ridges in Florida that were once islands separated from the mainland. The limited distribution of this species makes it potentially at risk from future landscape changes.

3.3.2 Sensitivity to Disturbance

Castillo and Lobo (2004) compared passalid diversity and community structure between primary and secondary (i.e., dominated by pioneer tree species) tropical forests in Mexico. There were no strong differences in the abundance or richness of passalids collected in the two forest types. Only one species, *Verres cavicollis* Bates, differed in abundance per log between forest types, being more abundant in the secondary forest. Two of the least common species were only captured in old-growth forests, however. Although these findings suggest that passalids are not very sensitive to forest disturbance, not enough information was provided about the secondary forest to fully interpret these results. It is not clear if the logs sampled in the secondary forest originated from that or the previous forest, for example. More recently, Kattan et al. (2010) compared passalid communities among native Andean alder (*Alnus acuminata* Kunth) plantations planted as part of a restoration effort, naturally regenerating forests and old-growth forests in the Colombian Andes. The two secondary forest types were planted approximately 40 years before sampling took place on land formerly used for cattle ranching. The old-growth and naturally regenerating forests had more than twice the wood volume as the alder plantations and old-growth forests had more passalid individuals overall and per cubic meter of wood sampled than the other two forest types. Of the six species collected, one was found only in the regenerating forest, and two were only found in the old-growth forest. In India, Sarasija et al. (2012) reported that passalids were more common in natural forests containing moist logs at advanced stages of decay than in teak plantations.

Jackson et al. (2009) found walking *O. disjunctus* to be reluctant to venture into open habitats in Louisiana, suggesting a low likelihood of movement among forest fragments. Because *O. disjunctus* is abundant throughout much of its range and is often present within isolated forest fragments, the researchers predicted that the species may fly, rather than walk, between patches of forests. Although *O. disjunctus* is typically observed walking (Jackson et al. 2009), so much so that Gray (1946) suggested the species was incapable of flight, the observation of 12–15 individuals flying approximately 30 m from the nearest forest edge at dusk in Mississippi (MacGown and MacGown 1996) supports the idea that occasional flight events may be important to the dispersal of the species. Other species of passalids are truly flightless, however, and may benefit from wooded corridors connecting separate patches of forest.

3.3.3 Utility as Indicator Taxa

Because they are relatively well described compared to many other tropical insect taxa, exhibit high levels of endemism, and can be sampled quickly at any time of the year, passalids have been used in prioritizing areas for conservation in some countries. In Guatemala, for example, passalids were used as indicator organisms to justify the creation of the Sierra de las Minas Biosphere Reserve (Schuster et al. 2000). Schuster et al. (2000) developed a method to identify Guatemalan cloud forests in the greatest need for protection based on data collected for 66 species of passalids (e.g., richness, endemism, similarity among guilds) and forest conditions. Support for the use of passalids as indicator taxa in Guatemala comes from the fact that their endemism patterns are similar to those of other animals, e.g., scarab beetles, salamanders, and small mammals (Cano and Schuster 2009).

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Chapter 4
Diversity and Ecology of Stag Beetles (Lucanidae)

Ta-I Huang

Abstract The beetle family Lucanidae contains over 1200 described species worldwide, with the highest diversity found in Southeast Asia. Most species are saproxylic, with larvae feeding on deadwood at various stages of decomposition and contributing to the breakdown of this material. Female lucanids usually oviposit eggs either directly within decaying wood, at the soil-wood interface beneath logs, or in the soil. Larvae of lucanid beetles spend the majority of their life span living in decaying wood or other decomposing substrates, where they feed on materials rich in fungal biomass. In addition, adults of many lucanid beetles are highly dependent on living trees where either they can find sap as a food source or locate partners for mating. Relatively little is known about the biology, life history, or substrate associations of saproxylic stag beetles despite their striking morphology and popularity among entomologists and amateur insect collectors. In this chapter I discuss ecological niche partitioning among lucanid beetles, with a focus on the relatively well-studied fauna of Taiwan as a case study. I also review the importance of fungal associations to lucanid beetles and the role these insects play in wood decomposition.

4.1 Diversity and Ecology of Stag Beetles

Lucanid beetles are among the largest and most charismatic groups of insects associated with decomposing wood and can serve as important bioindicators of forest integrity. Within a given region, forests with the highest lucanid diversity are generally characterized by lower levels of disturbance and larger amounts of deadwood (Wang 1990; Chang 2006). In Europe, for example, Lachat et al. (2012) reported that lucanids were among the species most sensitive to deadwood amount and temperature among 69 families of saproxylic beetles examined in that study.

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Although most lucanid adults are thought to feed on sap flows and breed in decomposing logs or stumps (Blatchley 1910; Kojima 1996), information about their basic ecology, including host plant associations, is limited. The European giant stag beetle, *Lucanus cervus* (L.), is probably the most well-studied lucanid beetle worldwide, and most studies have focused on its distribution (Thomaes et al. 2008; Harvey et al. 2011a), monitoring and sampling (Harvey et al. 2011b; Chiari et al. 2014; Bardiani et al. 2017), and morphological variation (Clark 1977; Harvey and Gange 2006). Recently, Ulyshen et al. (2017) reported on the basic ecology, genetics, and geographic distribution of the giant stag beetle, *L. elaphus*, in the USA. Tropical and subtropical mature forests in East and Southeast Asia host the highest diversity of lucanid species (Krajcik 2001; Smith 2006), with most published information focusing on new species description and taxonomy (Araya et al. 1998; Han et al. 2010; Zilioli 2012) as well as conservation (Lin et al. 2009; Huang 2014).

4.1.1 Breeding Substrates and Behavior

Most lucanid beetles inhabiting decaying wood feed on cellulosic material highly colonized by fungi and other microorganisms. Although some adult lucanids show strong preferences for the sap of particular host plants, most female lucanids are less discriminating about their selection of breeding substrates (Araya 1993a; Chang 2006). When lucanid females find an appropriate log for oviposition, they will decide how many eggs to lay according to the size and quality of the substrate (Chang 2006). In general, as long as logs are rotten and soft, with adequate humidity and without many termites or other insects, they can provide potentially suitable habitat for oviposition, regardless of whether the log is in contact with the soil or still standing (Chang 2006). Relationship between the decay types (white, brown, and soft rot) in decaying wood and occurrence of lucanid beetles was studied in Japan by Araya (1993a) who found that some lucanid species such as *Ceruchus lignarius* (Lewis) and *Aesalus asiaticus* (Lewis) prefer brown rot and *Platycerus acuticollis* (Kurosawa) is associated with soft rot. However, *P. delicatulus* (Lewis) and other lucanids such as *Prismognathus angularis* (Waterhouse), *Macrodorcas striatipennis* (Motschulsky), *Dorcus montivagus* (Lewis), *D. rubrofemoratus* (Vollenhoven) showed no clear patterns of decay type use. Araya (1993b) further reported that *C. lignarius* occurred exclusively in highly decayed brown rot (brown rot specialist), whereas the occurrence of *P. angularis* was not as clearly associated with either decay type or its stage (decay type generalist).

In Taiwan, females of only a few lucanid species show specificity for particular kinds of decomposing logs for oviposition. For example, *Aegus jengi* is distributed in the northern hills around Taipei City, with adults and larvae being only associated with large pine logs (Huang and Chen 2016). About 10 years ago, with the devastating infection of *Bursaphelenchus xylophilus* (Steiner and Buhrer) vectored by *Monochamus alternatus* (Hope), most pine trees in northern Taiwan were chopped and removed. Although the population and abundance of *A. jengi* has not been officially investigated, such anthropogenic disturbances have the potential to extirpate populations of specialist species.

4.1.2 Larval Ecology and Development

All the known lucanid larvae in Taiwan go through three instars, with the 1st and 2nd instars being relatively brief, usually 2–4 weeks (Chang 2006). The 3rd instar is usually the longest in duration, with most species remaining in this stage for more than half a year and as long as 2 years at cooler elevations. Due to this age structure, most larvae encountered in logs or soil are 3rd instars. Due to the relatively large size of 3rd instar larvae, they typically receive more attention from researchers. However, lack of information about 1st and 2nd instars in the wild results in incomplete knowledge about the development of these species and their importance to decomposition.

Larvae of *Odontolabis siva parryi* (Boileau) and most species in the genus of *Neolucanus* do feed on decaying woody fibrous tissue, but most of the time inhabit in the decomposed soil underneath dead trees. Therefore, adult females often choose rotten roots underneath decaying trees or the undersides of large logs adjacent to the ground for oviposition spots. *Aegus laevicollis formosae* and most *Lucanus* larvae inhabit shallow soil depths where they feed on rich fibrous rotten substrates (Yang 2007). Thus when females of these lucanids find a suitable environment, they will dig into the soil and crawl around to lay eggs. Several genera mentioned above share the same habitat in a specific forest belt, partitioning different niches among logs and the underlying soil to ensure their survivorship and sustainability.

In Australia, different lucanid beetles are reported to utilize white rot, brown rot, drier substrates, sapwood, lower elevation, etc. (Wood et al. 1996). The rainbow stag beetle, *Phalacrognathus muelleri* (Macleay), only breeds in rotting wood in the rainforests of northern Queensland where larvae have been extracted from the wood of 27 tree species in 13 families, all logs experiencing white rot (Wood et al. 1996). In the USA, *Lucanus elaphus* was found in association with a wide range of rot types without any noticeable preference, including white rot, brown rot, and even within veins of relatively intact wood surrounded by rot (Ulyshen et al. 2017).

4.1.3 Fungivory and Symbiotic Microbes

Fungivory is widely observed in insects (Kukor and Martin 1987). Some social insects such as leaf-cutting ants (Hymenoptera) and macrotermitine termites (Blattodea) culture specific fungi in their nests and feed directly on the fungal tissues (Chapela et al. 1994; Wood and Thomas 1989). Some wood-inhabiting insects have endosymbiotic microbes within their guts that help digestion of wood. For example, lower termites and wood-feeding cockroaches have protozoa or bacteria in their digestive organs which produce cellulolytic enzymes (Cleveland 1924; Slaytor 1992; Breznak and Brune 1994). Ambrosia beetles culture and consume ambrosia fungi growing within their galleries in wood (Batra 1963; Beaver 1989). Fungivory is evidently clear for these insect groups. However, for insects that feed on substrates containing fungi, it is difficult to determine if the fungi are used for nutrients or merely consumed along with the substrate. Lucanids, some cerambycid and buprestid beetles, and higher termites inhabit and feed on wood decayed by wood-rotting fungi (Araya 1993a, b; Saint-Germain et al. 2007; Abe et al. 2000). Passalid and cerambycid beetles are associated with xylose-fermenting yeasts that may help in the digestion of wood hemicelluloses (Suh et al. 2003, 2006).

Little is known about what kinds of microbes are associated with stag beetles, although Kuranouchi et al. (2006) indicated the presence of nitrogen-fixing microbes within *Dorcus rectus* (Motschulsky) larvae. Despite their close connection with decomposing wood and associated microbial activity, it remains poorly understood how lucanids interact with fungi and other microorganisms. Wood is composed mostly of cellulose as well as lignin and hemicellulose which together comprise about 90% of the total volume (Parkin 1940). These compounds are difficult to digest and contain low contents of nitrogen, sugars, and starch (Haack and Slansky 1987); such nutrient conditions make wood a poor food resource for insects. Hanula (1996) pointed out five possible advantages of fungal-infested wood over fresh wood as food for insects:

1. Increased concentrations of nitrogen and other elements in fungal mycelia.
2. Increased ingestion and digestion of wood made fragile by wood-rotting fungi.
3. Increased moisture content of wood.
4. Increased digestion of woody tissue by enzymes originating from fungi.
5. Detoxification of toxic or repellent allelochemicals in wood.

Tanahashi et al. (2009) suggested that direct nutrient acquisition from the fungal mycelia may be particularly important. *Dorcus rectus* represents one of the most common and widely distributed stag beetles in Japan (Kurosawa 1985). Tanahashi et al. (2009) reported that adult females of *D. rectus* locate decaying wood of broad-leaved trees affected by white-rot fungi, and it was found that the larvae were able to develop on fungal mycelia without wood; thus, they can be considered fungivorous. This is the first demonstration of fungivory in stag beetles but may be the case for other species as well.

Some fungivorous insects possess a mycangium (pl. mycangia), a special structure on the body in which symbiotic fungi (usually in spore form) are transported to new locations (Beaver 1989). Mycangia have evolved in a number of beetle lineages including multiple times in Scolytinae (Curculionidae) and lymexylids. In some cases, as in ambrosia beetles, the fungi are cultivated for food on the gallery walls. In other cases, such as the southern pine beetle, *Dendroctonus frontalis* Zimmermann, phloem is the main food, and fungi weaken the defense response from host plant (Six and Wingfield 2011).

Tanahashi et al. (2010) further reported the first evidence of a mycangium in lucanids which is located near the dorsal side of the rectum in the abdomen.

Interestingly, there was no mycangium near the rectums of any male lucanid or of either sex in the sampled passalid, geotrupid, and scarabaeid species, which are families of beetles closely related to Lucanidae (Smith et al. 2006). Yeastlike microbes, closely related to the xylose-fermenting yeasts *Pichia stipitis* Pignal, *P. segobiensis* Santa María and García Aser, or *P.* sp., were isolated from the mycangium of five lucanid species (Tanahashi et al. 2010). The larvae of the five lucanid species from which xylose-fermenting yeasts were isolated in that study exclusively feed on wood colonized by white-rot fungi. *Dorcus rectus* and *D. striatipennis* (Motschulsky) are white-rot specialists, and three other species, *D. titanus sakishimanus* (Nomura), *Prosopocoilus pseudodissimilis* (Kurosawa), and *Prismognathus angularis* (Waterhouse), are somewhat less specialized. Although not confirmed, Tanahashi and Fremlin (2013) proposed that ovipositing female stag beetles may inoculate the substrate with their mycangium yeasts. If so, this is potentially another example of parental care behavior. The absence of mycangia in passalids may be explained by the subsocial behavior of this group, where adults help prepare food for developing larvae (Tanahashi et al. 2010). Moreover, whereas passalid adults and larvae both feed on decomposing wood, lucanid adults are primarily sap feeders and may thus lack the gut microbes needed in the larval stage to digest wood (Tanahashi et al. 2010). Inoculating oviposition sites with xylose-fermenting yeasts from mycangia may thus be a way for female lucanids to help their offspring digest wood. More research is needed to explore these possibilities.

4.1.4 Parental Care

Parental care is thought to be one of the key factors in the evolution of social behavior and is favored in situations characterized by ephemeral resources (Bartlett and Ashworth 1988), nesting systems relatively safe from predators (Scott 1990), or situations where finding and establishing a new nesting system may be difficult and dangerous (Kirkendall et al. 1997). In Japan, it was found that the initial growth rate of 3rd instar *Figulus binodulus* (Waterhouse) was significantly higher when the larvae were in a nest with adults compared to those in a nest without adults (Mori and Chiba 2009). Their results suggest that *F. binodulus* has a level of sociality and nest mate recognition that is very rare in stag beetles (Mori and Chiba 2009). In Taiwan, females of all species of *Figulus*, several species of *Aegus*, and *Nigidionus parryi* (Bates) usually burrow into the log using their mandibles and stay inside the log laying eggs in the rotten substrates until they die. *Nigidionus parryi* especially shows "parental care" as most larvae found in the decaying logs coexist with adults (Chang 2006).

4.2 Niche Partitioning of Lucanids in Taiwan

4.2.1 Diversity and Environment of the Taiwan Island

Taiwan is unique among all subtropical regions because it is the only sizeable island located immediately north or south of the tropical zone between the 23rd parallels (Huang and Lin 2010). The island is unique for its complex terrain, from low altitude coastal plains to a Central Mountain Range (CMR) containing more than 200 peaks exceeding 3000 m elevation (Huang et al. 2006). Forests in Taiwan can be categorized as the tropical monsoon forest, the subtropical forest, and the temperate grassland. Su (1992) categorized seven forest belts based on the seven different climate zones with their corresponding elevation (Table 4.1). The island contains more than 4000 native plant species, and a quarter (1054 species) of them are endemic (Su 1984). The number of insect species recorded in Taiwan is about 2% of the world's total, but the total land area of the island accounts for only 0.25% of the global total. There are nearly 5000 kinds of beetles in Taiwan, including at least 55 described species of Lucanidae (Chang 2006; Huang and Chen 2015, 2016) (Table 4.2). Taiwan thus contains nearly one twentieth of the 1200 lucanid species known globally. By contrast, the neighboring country of Japan, which has more than a tenfold larger land area, has just 40 species of lucanids. On the other side of the Pacific Ocean, North America harbors only 24 lucanid species, but the total area is near 700 times larger than the Taiwan Island. The lucanid fauna of Taiwan is not only diverse but also relatively well-studied, providing an excellent opportunity to gain insights into the ecology of this group of insects.

Among the 55 lucanid species in Taiwan (Fig. 4.1), all of them are found from tropical to temperate zones below 2800 m in elevation, and most species are restricted to a specific vegetation zone (Chang 2006). The absence of species above 3000 m is presumably due to the low temperatures and low floral diversity associated with the cool temperate to subarctic zones. Except for some species of *Lucanus* that are speculated to feed on grass roots, most lucanids in Taiwan are considered saproxylic as the larvae feed directly on decomposing woody substrates or rotten soil that contains highly decomposed wood such as the genus *Neolucanus* (Table 4.2). Ecological niches among lucanids in Taiwan are discussed mainly based on forest belt (climate niche) and host plants (food niche).

Table 4.1 Taiwan flora category with the corresponding climate zone and elevation

Climate zone	Flora belt	Elevation (m)
Subarctic zone	Alpine vegetation	>3600
Cold temperate zone	*Abies* zone	3100–3600
Cool temperate zone	*Tsuga-Picea* zone	2500–3100
Temperate zone	*Quercus* zone (upper)	2000–2500
Warm temperate zone	*Quercus* zone (lower)	1500–2000
Subtropical zone	*Machilus-Castanopsis* zone	500–1500
Tropical zone	*Ficus-Machilus* zone	<500

Table 4.2 Lucanid species known from Taiwan and their substrate associations

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Aegus			
Aegus laevicollis formosae Bates	*Machilus-Castanopsis*–*Quercus* (lower)	Decomposed soil	Brown rot
Aegus jengi (Huang and Chen)	*Machilus-Castanopsis*	Decomposed pine	Brown rot
Aegus kurosawai Okajima and Ichikawa	*Quercus* (upper and lower)	Decomposed pine mud	Brown rot
Aegus chelifer Macleay	*Ficus-Machilus*	Decomposed wood	Brown rot
Aesalus			
Aesalus imanishii Inahara and Ratti	*Quercus* (upper and lower)	Decomposed conifer	Brown rot
Cyclommatus			
Cyclommatus scutellaris Mollenkamp	*Ficus-Machilus*–*Machilus-Castanopsis*	Decaying hardwood	White rot
Cyclommatus asahinai Kurosawa	*Machilus-Castanopsis*–*Quercus* (lower)	Decaying hardwood	White rot
Cyclommatus mniszechi Thomson	*Ficus-Machilus*–*Machilus-Castanopsis*	Decaying hardwood	White rot
Dorcus			
Dorcus grandis formosanus Miwa	*Ficus-Machilus*–*Machilus-Castanopsis*	Decaying hardwood	White rot
Dorcus schenkingi Mollenkamp	*Machilus-Castanopsis*–*Quercus* (lower)	Decaying hardwood	White rot
Dorcus miwai Benesh	*Machilus-Castanopsis*–*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus yamadai Miwa	*Machilus-Castanopsis*–*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus titanus sika Kriesche	*Ficus-Machilus*–*Machilus-Castanopsis*	Decaying hardwood	Generalist
Dorcus kyanrauensis Miwa	*Ficus-Machilus*–*Quercus* (lower)	Decaying hardwood	Generalist
Dorcus parvulus Hope and Westwood	*Ficus-Machilus*	Decaying hardwood	Generalist
Dorcus reichei clypeatus Benesh	*Machilus-Castanopsis*–*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus gracilicornis Benesh	*Machilus-Castanopsis*–*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus mochizukii Miwa	*Machilus-Castanopsis*–*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus rectus Motschulsky	*Machilus-Castanopsis*–*Quercus* (lower)	Decaying hardwood	White rot
Dorcus striatipennis yushiroi Sakaino	*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus taiwanicus Nakane and Makino	*Machilus-Castanopsis*–*Quercus* (lower)	Decaying hardwood	White rot

(continued)

Table 4.2 (continued)

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Dorcus carinulatus Nagel	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Echinoaesalus			
Echinoaesalus chungi Huang and Chen	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus			
Figulus binodulus Waterhouse	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Figulus punctatus Waterhouse	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus curvicornis Benesh	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus fissicollis Fairmaire	*Ficus-Machilus*	Decaying hardwood	Unknown
Lucanus			
Lucanus formosanus Planet	*Machilus-Castanopsis*	Decomposed soil	Brown rot
Lucanus maculifemoratus taiwanus Miwa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus swinhoei Parry	*Ficus-Machilus–Quercus* (upper)	Decomposed soil	Unknown
Lucanus datunensis Hashimoto	*Machilus-Castanopsis*	Decomposed soil in bottom grassland	Unknown
Lucanus kanoi Kurosawa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus kurosawai Sakaino	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus miwai Kurosawa	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus ogakii Imanishi	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Neolucanus			
Neolucanus swinhoei Bates	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Brown rot
Neolucanus maximus vendli Dudich	*Machilus-Castanopsis–Quercus* (lower)	Decomposed soil	Brown rot
Neolucanus eugeniae Bomans	*Machilus-Castanopsis*	Decomposed soil	Unknown
Neolucanus doro Mizunuma	*Machilus-Castanopsis–Quercus* (lower)	Decomposed soil	Brown rot
Neolucanus sinicus formosanus Mizunuma	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Unknown
Nigidionus			
Nigidionus parryi Bates	*Machilus-Castanopsis*	Decaying hardwood	White rot

(continued)

Table 4.2 (continued)

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Nigidius			
Nigidius acutangulus Heller	*Machilus-Castanopsis*	Decaying hardwood	Unknown
Nigidius baeri Boileau	*Ficus-Machilus*	Decaying hardwood	Brown rot
Nigidius formosanus Bates	*Ficus-Machilus*	Decaying hardwood	White rot
Nigidius lewisi Boileau	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	Unknown
Odontolabis			
Odontolabis siva parryi Boileau	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Brown rot
Prismognathus			
Prismognathus formosanus Nagel	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prismognathus piluensis Sakaino	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prismognathus davidis Bomans and Ratti	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prosopocoilus			
Prosopocoilus astacoides blanchardi Parry	*Ficus-Machilus–Quercus* (lower)	Unknown	Unknown
Prosopocoilus forficula austerus DeLisle	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Prosopocoilus motschulskii Waterhouse	*Ficus-Machilus*	Decomposed soil	Unknown
Prosopocoilus formosanus Miwa	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Pseudorhaetus			
Pseudorhaetus sinicus concolor Benesh	*Machilus-Castanopsis*	Decaying hardwood	White rot
Rhaetulus			
Rhaetulus crenatus Westwood	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	Generalist

4.2.2 *Lucanus*

The lower and upper *Quercus* zones, together ranging from 1500 to 2500 m, contain the most well-protected forest habitats for lucanid beetles in Taiwan. These *Quercus* forests are generally given protected status by the government as national parks or preserves, thus providing relatively less disturbed conditions for a diverse lucanid assemblage. *Lucanus* is the typical genus of lucanids living in this temperate *Quercus* zone. In the upper *Quercus* forest, the distributions of *Lucanus maculifemoratus taiwanus* Miwa, *L. swinhoei* Parry, *L. kanoi* Kurosawa,

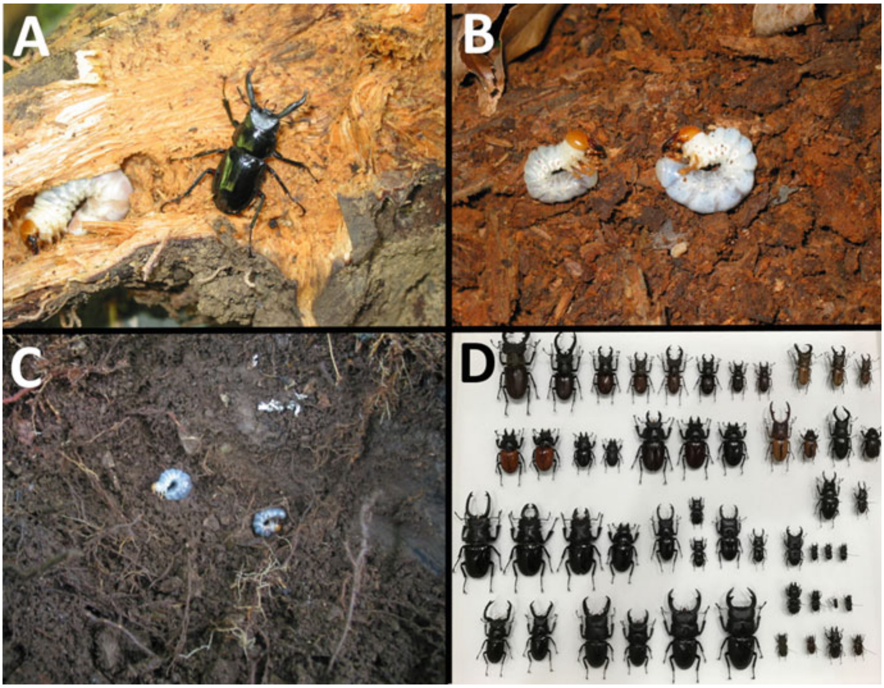

Fig. 4.1 Lucanid beetle larvae and associated feeding environment: (**a**) adult and 3rd instar larva of *Pseudorhaetus sinicus* associated with white rot; (**b**) larvae of *Neolucanus maximus vendli* associated with brown rot; (**c**) 3rd instar larvae of *Lucanus kurosawai* associated with decomposed soil; (**d**) lucanid diversity in Taiwan

L. kurosawai Sakaino, and *L. miwai* Kurosawa could overlap in certain areas (elevation, 1800–2300 m) of the Central Mountain Range (Chang 2006). These lucanids can be found together in mature forests with one species more numerous than the others, depending on the location. It is believed that these lucanid species share the same habitat and utilize similar food sources in the larval stage, all feeding on decaying rotten wood or soil substrates. The degree of rottenness might be an important factor in determining where females choose to oviposit. In artificial rearing chambers, most *Lucanus* females will lay eggs in fermented rotten soil made from saw dust of *Quercus* trees (Lai 2001). However, more eggs can be found between soil surface and decayed wood when given additional material (e.g., piece of decayed maple wood) for oviposition (Lai 2001). Interestingly, these *Lucanus* larvae were never found in living trees or dead dry logs without any moisture in the wild. This may explain that these *Lucanus* can feed on decaying *Quercus* wood in general, but the degree of decaying might be the key for females to determine where to lay eggs. In the USA, Ulyshen et al. (2017) reported the substrates within which *L. elaphus* (Fabricius) were found feeding were always damp and sometimes thoroughly saturated. Drier wood, as sampled at upland sites or in logs with limited ground contact, never yielded *L. elaphus* (Ulyshen et al. 2017).

Niche partitioning among lucanid larvae remains far from understood which requires more research to explore the ecology of oviposition behavior.

Some lucanid species can be found in several vegetation zones, suggesting a high degree of flexibility with respect to both adult and larval plant associations. *Lucanus swinhoei*, for example, can be found in subtropical and warm temperate (i.e., lower *Quercus*) zones and appears to behave differently in the different areas. Within the lower *Quercus* zone, for example, adults of *L. swinhoei* associate strongly with *Quercus variabilis* (Blume), commonly feeding on sap flows during the daytime and rarely coming to lights at night. *Lucanus swinhoei* also occurs within the *Ficus-Machilus* zone (<200 m in the northern coastal hills), where *Q. variabilis* does not occur; instead, the dominant plants are *Acacia confusa* Merr., *Sapium sebiferum* (L.) Roxb., and Lauraceae. In addition, adults of *L. swinhoei* in this region are strongly attracted to lights at night. How *L. swinhoei* has adapted to these highly dissimilar climates and plant communities remains a question for enthusiasts or ecologists to answer. On the other hand, a related species, *L. maculifemoratus taiwanus*, inhabits the same *Quercus* zone in CMR but never occurs down to *Ficus-Machilus* zone in northern coastal hills (Chang 2006).

Another classic example is the endemic lucanid *L. formosanus* Planet. Adults of *L. formosanus* exhibit a strong association with *Cyclobalanopsis glauca* (Thunb) distributed in *Machilus-Castanopsis* zone. Adults of *L. formosanus* often rest in the canopy of *C. glauca* where there is an availability of sap flow on trunks and branches. A clear preference for the canopy layer of *L. formosanus* is similar to *L. cervus* and *L. elaphus*, the two large *Lucanus* species occurring in Europe and the USA, respectively (Bardiani et al. 2017; Ulyshen et al. 2017). Larvae of *L. formosanus* can also be found feeding on rotten soil substrate beneath logs similar to other members of *Lucanus*. Ulyshen et al. (2017) also indicated larvae of *L. elaphus* were found either tunneling inside logs or feeding beneath logs at the soil-wood interface.

One that exhibits a completely different ecology from other *Lucanus* is *L. datunensis* (Hashimoto). Its distribution is limited to the hilltop area of Daiton Mountain (elevation 800–1100 m) located in Yangmingshan National Park in Taipei City (Lin et al. 2009). Interestingly, although this area is within *Machilus-Castanopsis* zone, there is no hardwood forest locally due to severe winter and northeast monsoon. Instead, only two grasses dominate this habitat, dwarf bamboo [*Pseudosasa usawai* (Hayata.) Makino & Nemoto.] and Japanese silver grass [*Miscanthus floridulus* (Labill.) Warb. ex K. Schum. & Lauterb.], with some Azaleas and *Eupatorium shimadae* (Kitam.) growing along the roadside. Males of *L. datunensis* often fly in the daytime around the grassland hovering up and down among grasses seeking mates; females are rarely found and probably spend most of the time near their breeding substrates at the bases of grasses. Lin et al. (2009) hypothesize that diurnal mate searching and the small size of *L. datunensis* are both adaptations in response to a habitat shift from forests to grasslands. Although there have been no field observations of larval *L. datunensis*, it is speculated that *L. datunensis* feed on the rotten soil under the two grass species (Chang 2006). Due to the extremely limited distribution, Lin et al. (2009) proposed that protection and restoration of the grassland habitat consisting of the dwarf bamboo and Japanese silver grass in Yangmingshan National Park should be a top priority for developing a conservation strategy for the threatened *L. datunensis*.

Another daytime-active *Lucanus* is *L. miwai*; it inhabits in the *Quercus* zone in CMR overlapping with *L. maculifemoratus taiwanus*, *L. swinhoei*, *L. kanoi*, and *L. kurosawai*. Males of *L. miwai* hover up and down along the edge of forests or grassy areas on warm spring (April–May) days looking for mates (Wang 1990; Huang 2014), a flying behavior similar to *L. datunensis*. It is noteworthy that both *L. miwai* and *L. datunensis* are only active in the daytime and are never attracted to lights at night, contrasting with the nocturnal habits of the other four *Lucanus* species found in the same habitat. Males of many lucanid species possess curving and greatly enlarged mandibles that often are used in male-male competition for access to females (Clark 1977; Kawano 1992). The active diurnal mate searching flight in open fields in these two species may result in a better strategy over a more widespread behavior of intra-sex competition for resources and mating found in most forest-dwelling lucanids (Harvey and Gange 2006; Rink and Sinsch 2007; Lin et al. 2009). Diurnal activity has also been observed in other lucanids. In Brazil, all members of the genus *Leptinopterus* have diurnal habits and have been collected flying or feeding at sap flows of trees and shrubs (Grossi 2009).

Spatial niche is also partitioned among these *Lucanus* species. Although they are present within the same vegetation zone, the distributions of the various *Lucanus* species differ slightly in terms of altitude. In general, *L. kurosawai* occurs at the highest elevations, followed by *L. miwai*, *L. kanoi*, *L. maculifemoratus taiwanus*, and *L. swinhoei* in the Central Mountain Range. While some species can be found at a wide range of elevations (*L. maculifemoratus taiwanus* and *L. swinhoei*), the altitudinal distributions of other species are more restricted (*L. kurosawai*, *L. miwai* and *L. kanoi*) (Chang 2006; Yang 2007).

4.2.3 *Aegus*

Niche partitioning is well documented among the four species of *Aegus* found in Taiwan. *Aegus laevicollis formosae* (Bates) occurs across a broad range of elevation from 500 to 2000 m in Taiwan. Adults of *A. laevicollis formosae* are often seen feeding on tree flows of *Acacia confusa* (Merr.) and *C. glauca*. Larvae of *A. laevicollis formosae* were found in rotten substrates under *Miscanthus* or *Fargesia* logs. *Aegus jengi* (Huang and Chen) occurs in the *Machilus-Castanopsis* zone of northern Taiwan, with larvae often found in reddish rotten pine wood, especially *Pinus taiwanensis* (Hayata) (Chang 2006). Adults are seldom observed outside away from breeding substrates. *Aegus kurosawai* (Okajima and Ichikawa) also utilizes highly decomposed pine wood that is often mud-like in consistency but occurs at higher elevations in the *Quercus* zone (1600–2600 m). *Aegus chelifer* (Macleay) is the only *Aegus* species not living in mountain ranges; instead, they are only found in deadwood in coastal areas where they are attracted to lights. It is believed that *A. chelifer* was introduced to Taiwan through the movement of wood from South Asia, and populations of the species have since become well established in certain coastal areas.

4.2.4 Neolucanus

Species of the genus *Neolucanus* prefer to feed on completely decomposed rotten soil substrates, e.g., under logs in broadleaf forests. *Neolucanus swinhoei* (Bates) is diurnally active and is commonly found walking on roadsides or hanging on trees in the *Ficus-Machilus* and *Machilus-Castanopsis* zones. *Neolucanus doro* (Mizunuma) occurs at relatively higher elevations from the *Machilus-Castanopsis* to lower *Quercus* zones and is also diurnal, often seen walking on trails or roads similar to *N. swinhoei* (Chang 2006). *Neolucanus maximus vendli* (Dudich) also occurs within the same forest belt between the *Machilus-Castanopsis* and lower *Quercus* zones but is active at night, and adults can be attracted to lights after 10 pm. However, *N. maximus vendli* can also be found in the daytime feeding on tree flows in the forest canopy (Chang 2006). Larvae of *N. maximus vendli* are found in red rotten soil underneath big decaying trunks or dead roots. Temporal and spatial niche partitioning is demonstrated between *N. doro* and *N. maximus vendli*, presumably a strategy for these species to avoid interspecific competition while sharing the same habitat.

4.3 Threats to Lucanid Diversity and Future Recommendation

In Japan, the wild populations of native stag beetles are rapidly decreasing because of artificial disturbance of habitats, and some species are already close to endangered (Kojima 2003). It has been reported that Southeast Asia has the highest relative rate of deforestation of any major tropical region and could lose three quarters of its original forests by 2100 and up to 42% of its biodiversity (Sodhi et al. 2004). Recent research has highlighted the sensitivity of saproxylic insects to forest management, with managed or secondary forests generally supporting fewer individuals, fewer species, and different assemblages compared to old-growth or primary forests (Grove 2002). Habitat loss in recent years has been an unsolved issue that will ultimately lead to extinction of species, including lucanid beetles that are highly dependent on forest and logs. Meanwhile, biological invasions by exotic stag beetles may also pose a threat to native lucanid populations (Goka et al. 2004). It is believed that the first impact will be competition for food and habitat, the second, genetic introgression as a consequence of hybridization between exotic and native species, and the third, invasion of imported parasites (Goka et al. 2004). In Japan, Kanzaki et al. (2011) reported that eight species of nematodes were cultured from eight species of lucanid beetles, including four phoretic nematodes considered to predominate. The nematodes exhibited low host specificity and were widely distributed. Global trading of lucanids among hobbyists thus risks the introduction of exotic nematodes in Japan and elsewhere, with the potential to be then passed on to native lucanid populations where they can potentially hybridize or otherwise disrupt native nematode populations (Kanzaki et al. 2011).

Due to their relatively large size and to the greatly exaggerated mandibles of many species, stag beetles are among the most enthusiastically collected insect groups by amateur collectors and insect vendors (Goka et al. 2004). The market size of the stag beetle commerce is considered to be over 10 billion Japanese yen (USD100 million) (Goka et al. 2004), involving 700 lucanid species from all over the world with over 15 million specimens imported to Japan each year (Tournant et al. 2012). Mass capturing for commercial purposes, exotic invasion from global trading, and destruction of suitable habitats by human activities inevitably threaten stag beetle populations and their long-term survival (Speight 1989; Berg et al. 1994).

Since 2015, the Taiwanese government implemented a comprehensive replacement of street lights from mercury light bulbs to LED lights throughout the island to save energy. This action incidentally saved millions of lucanids and other nocturnal beetles attracted to mercury street lights at night and killed by vehicles, especially in mountainous areas. Ultimately, in order to protect saproxylic insects like lucanid beetles, efforts to preserve their original habitats are no doubt the best practice. Minimizing anthropogenic exploitation, prohibiting or limiting logging activities, and preserving natural habitats will together promote the long-term conservation of lucanid beetles.

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Chapter 5
Saproxylic Diptera

Michael D. Ulyshen

Abstract Diptera rivals Coleoptera as perhaps the most abundant and diverse order of saproxylic insects, with saproxylic habits known from at least 75 (48%) of the 157 fly families recognized globally. Some fly families are mostly if not entirely saproxylic including Aulacigastridae, Axymyiidae, Canthyloscelidae, Clusiidae, Pachyneuridae, Pantophthalmidae, Periscelididae, Xylomyidae, and Xylophagidae. Saproxylic flies are common inhabitants of virtually all moist to wet microhabitats including sap flows, under bark, in rotting wood, tree hollows, and fungal fruiting bodies. Most species are saprophagous or fungivorous although many predatory species exist as well, including some of the most important natural enemies of bark beetles. Although very poorly studied compared to beetles, it is clear that many saproxylic fly species are declining due to forest loss or degradation, and some taxa (e.g., mycetophilids) are good indicators of forest continuity. The dependence of flies on wet or even saturated substrates suggests they need special consideration when developing conservation strategies. Studies addressing their sensitivity to various management interventions are urgently needed.

5.1 Introduction

Originating approximately 270–251 million years ago (Bertone and Wiegmann 2009), flies belong to one of the four most taxonomically diverse insect orders, Diptera, with approximately 157 extant families and over 160,000 named species (Marshall 2012). They are also the most ecologically diverse, occurring in virtually all terrestrial and freshwater habitats where they exploit an unmatched variety of food resources. Although sometimes overshadowed by beetles and other groups, flies are ubiquitous and are often among the most numerous insects encountered in saproxylic habitats (Swift et al. 1984; Krivosheina 2006; Teskey 1976; Derksen

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1941; Vanderwel et al. 2006; Schiegg 2001). Hövemeyer and Schauermann (2003) collected nearly 12,000 flies from 37 families and 163 species from decomposing beech logs in Germany, for example, and flies accounted for over 90% of insects emerging from decaying wood in a Canadian study (Vanderwel et al. 2006). As members of the saproxylic insect community, flies are second only to beetles in functional and taxonomic diversity (Figs. 5.1 and 5.2) and may prove to be even more species rich than beetles in some regions [e.g., Nordic countries, see Stokland et al. (2012)]. The diversity of saproxylic flies is generally underappreciated due to

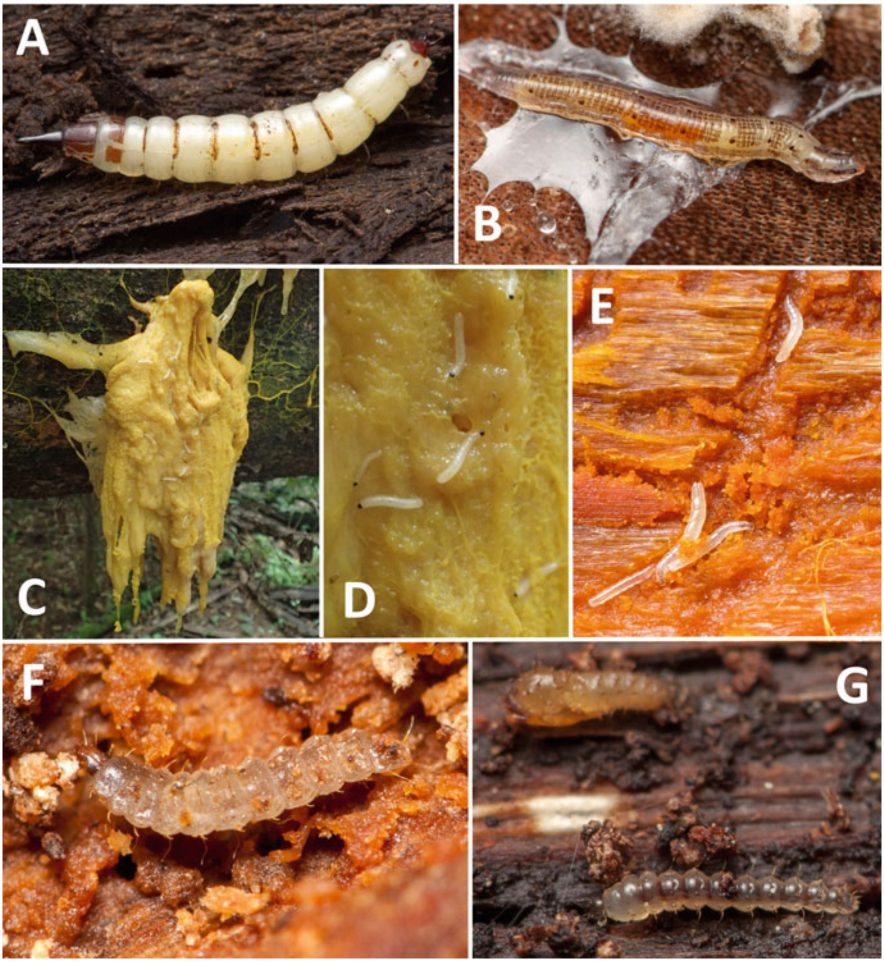

Fig. 5.1 Examples of larval saproxylic flies. (**a**) *Xylophagus lugens* Loew (Xylophagidae) in rotting wood, North Carolina; (**b**) Keroplatidae on a polypore, North Carolina; (**c**) Sciaroidea on the plasmodium of a slime mold (*Physarum*) atop the rotting fruiting bodies of *Pleurotus*, South Carolina; (**d**) close-up view of the same larvae shown in the previous image; (**e**) *Medetera* (Dolichopodidae) in bark beetle galleries, Florida; (**f**) Stratiomyidae under bark, North Carolina; (**g**) Forcipomyiinae ceratopogonids (pupa and larva) under bark, North Carolina. Images (**a**), (**b**), and (**e**–**g**) by Matthew Bertone and images (**c**) and (**d**) by Michael Ulyshen

their small size and the difficulty of identifying many families to species. Efforts to study the most challenging families have revealed an incredible diversity of species associated with dead wood, however. In Canada, for instance, Selby (2005) collected 323 cecidomyiid species or morphospecies from rotting logs in an old-growth forest.

Flies are typically saproxylic only as larvae (Fig. 5.1), whereas adults (Fig. 5.2) usually function away from dead wood as nectar feeders, predators, etc. Certain

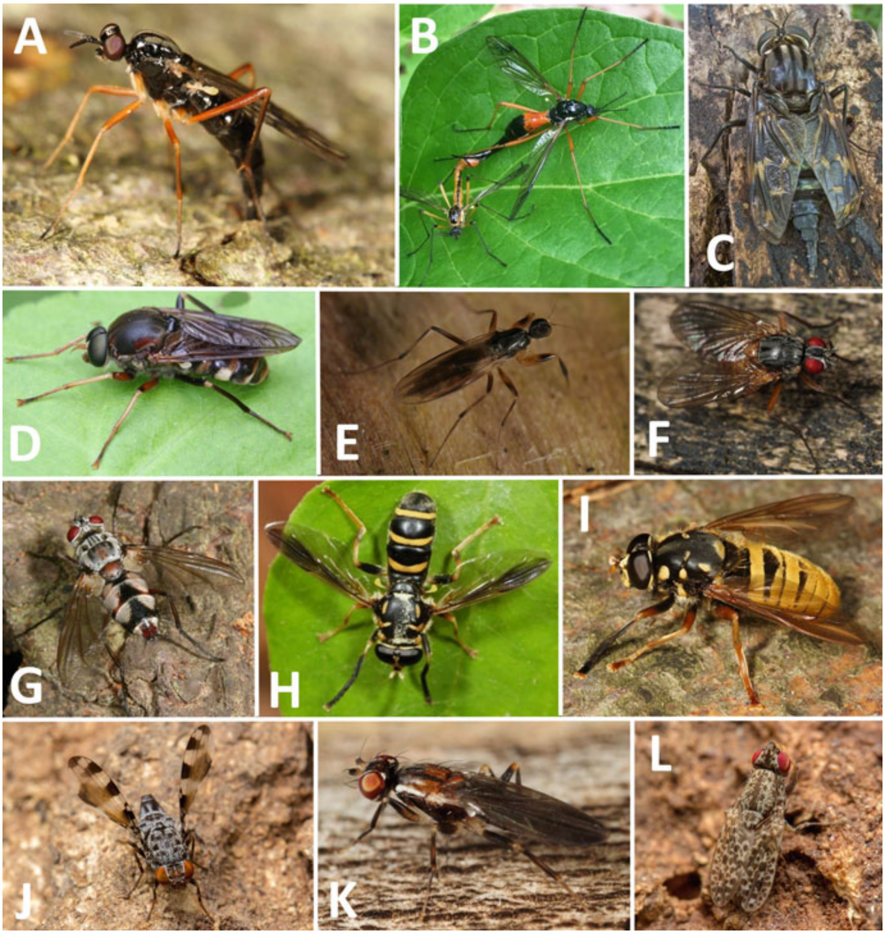

Fig. 5.2 Examples of adult saproxylic flies. (**a**) *Xylophagus compeditus* Meigen (Xylophagidae), Germany; (**b**) *Tanyptera dorsalis* (Walker) (Tipulidae), New York; (**c**) *Pantophthalmus bellardii* (Bigot) (Pantophthalmidae), Costa Rica; (**d**) *Coenomyia ferruginea* (Scopoli) (Xylophagidae), Illinois; (**e**) *Tachypeza* sp. (Hybotidae), Germany; (**f**) *Phaonia rufiventris* (Scopoli) (Muscidae), Germany; (**g**) *Zelia vertebrata* (Say) (Tachinidae), North Carolina; (**h**) *Temnostoma balyras* (Walker) (Syrphidae), North Carolina; (**i**) *Temnostoma vespiforme* (L.) (Syrphidae), Germany; (**j**) *Pseudotephritis vau* (Say) (Ulidiidae), North Carolina; (**k**) *Clusiodes albimanus* (Meigen) (Clusiidae), Germany; (**l**) *Traginops irroratus* Coquillett (Odiniidae), North Carolina. Images (**a**), (**e**), (**f**), (**i**), and (**k**) by Frithjof Kohl; (**b**) by Brandon Woo; (**c**) by Piotr Naskrecki; (**j**) and (**l**) by Matthew Bertone; (**d**) by Thomas Bentley; and (**g**) and (**h**) by Patrick Coin

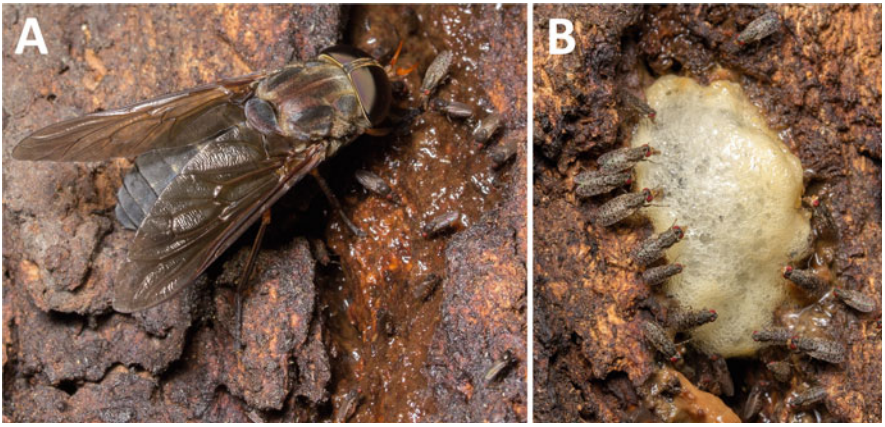

Fig. 5.3 Flies on slime flux in North Carolina, USA. Members of Aulacigastridae, Drosophilidae, Odiniidae, and Tabanidae are shown in image (**a**), and Odiniidae (*Traginops*) and Drosophilidae are shown in image (**b**). Images by Matthew Bertone

syrphids and other species that feed exclusively on sap runs (Fig. 5.3) are some of the few taxa that are saproxylic as adults (Speight 1989). As with other insect orders, many non-saproxylic fly taxa also benefit from the conditions and resources provided by dead wood. In Germany, for instance, Hövemeyer and Schauermann (2003) found that many fly species benefit from the moss layer that sometimes forms on rotting logs, with moss coverage being one of the two strongest determinants (the other being water content) of fly diversity associated with dead wood. A number of non-saproxylic predatory fly taxa also benefit from dead wood. One example, *Pherbellia annulipes* (Zetterstedt), is a specialist predator of snails in Europe that is rarely found away from rotting logs due to the high numbers of snails to be found there (Speight 1989).

Compared to beetles, the habits of saproxylic flies remain poorly studied. Many species are presumed to be saproxylic due to their close association with dead wood (Roháček and Marshall 2017), but little or nothing is known about their larval habits or requirements. The threatened status of saproxylic flies is thus likely to be underestimated (Jonsell et al. 1998). Unlike beetles and other groups, saproxylic flies typically prefer moist to wet microhabitats and often dominate assemblages in saturated or submerged wood (Hövemeyer and Schauermann 2003; Braccia and Batzer 2008). Many saproxylic fly species develop within fermenting sap, either flowing from wounds on trees or under the bark, where they function as microbial grazers or predators of other insects (Marshall 2012). Many other species feed within wet or saturated wood at various stages of decomposition and can best be described as saprophagous, benefiting more from the microbes associated with rotting wood than from the wood itself. Species that are restricted to water-filled tree holes, including many mosquito taxa, are also saproxylic. Saproxylic flies associated with the wettest environments commonly have special morphological structures to aid in respiration. Axymyiid larvae, for example, have tail-like respiratory syphons ending in a pair of spiracles that allow them to maintain contact with the surface of wood partially submerged in streams (Marshall 2012) (see Fig. 22.3e, this volume). Larval sap flies belonging to the family Aulacigastridae also breathe through long respiratory tubes as do many syrphid larvae (Marshall 2012).

There is some disagreement over family-level divisions among flies, creating uncertainty about the total number of fly families. Whereas crane flies are typically divided into four families in Europe (Tipulidae, Limoniidae, Cylindrotomidae, and Pediciidae), for example, others give these groups subfamily status within Tipulidae (Petersen et al. 2010). Here I follow the classification system used by Marshall who listed 157 extant fly families. As summarized in Table 5.1, saproxylic habits are known from at least 75 (48%) of these families although this probably underestimates the true number given that the habits of many species, genera, and even families (e.g., Lygistorrhinidae, Rangomaramidae, Syringogastridae, etc.) remain entirely unknown. While many of the families listed in Table 5.1 contain relatively few saproxylic species, other families are mostly if not entirely saproxylic. Examples of the latter include Aulacigastridae, Axymyiidae, Canthyloscelidae, Clusiidae, Pachyneuridae, Pantophthalmidae, Periscelididae, Xylomyidae, and Xylophagidae. The most well-studied group of saproxylic flies are those belonging to the family Syrphidae. Although only a small proportion of syrphid species are saproxylic [e.g., ~14% of European species (Reemer 2005)], this still amounts to many hundreds of species including most members of the largest subfamily, Eristalinae. Fungus gnats belonging to a variety of families are perhaps the most diverse members of the saproxylic community. They are also among the least understood, with most species awaiting discovery and description. In the Neotropics, for example, the ratio of undescribed to known species of mycetophilids is thought to exceed 10:1 (Amorim 2009).

This chapter aims to promote the appreciation for and conservation of saproxylic flies. My main objectives are to (1) summarize the family-level diversity of saproxylic flies globally (Table 5.1), (2) describe the main resources utilized by saproxylic flies, and (3) discuss the conservation status of these insects and how best to protect them in managed forests.

5.2 Feeding Groups and Microhabitats

Most saproxylic flies are either saprophagous, fungivorous, or predatory as larvae. The saprophagous species feed on a variety of decomposing substrates including fermenting sap near tree wounds or under bark, rotting wood and the frass or nest material of saproxylic insects. Fungivorous species are commonly associated with the fruiting bodies of wood-rotting fungi. Predatory taxa, including parasitoids, can be found in all of these microhabitats and attack a wide range of species including other fly species, wood-boring beetles, termites, etc. According to Krivosheina (2006), predatory habits are much more widespread among brachyceran (especially Orthorhapha) saproxylic flies than among the lower families of Diptera. Some fly

Table 5.1 Alphabetical list of fly families of the world known to include saproxylic species, their habits, and distribution

Family	Habits of saproxylic members
Acartophthalmidae	Rotting wood, presumably saprophagous (Marshall 2012) (Holarctic)
Anisopodidae	Saprophagous in decaying wood, roots, wet tree holes, beetle galleries, or sap flows (e.g., *Mycetobia*) on wounded trees (Marshall 2012; Teskey 1976) (widespread)
Anthomyiidae	Saprophagous in rotting wood or under bark and predators of cavity nesting bees and wasps (e.g., *Eustalomyia*) (Teskey 1976; Speight 1989; Marshall 2012) (widespread but mostly Holarctic)
Asilidae	Predatory in rotting wood (especially Laphriinae) including within beetle burrows, often in light gaps (Speight 1989; Rotheray et al. 2001; Teskey 1976) (widespread)
Asteiidae	Saprophagous in tree hollows, fungi, etc. (Marshall 2012) (widespread)
Aulacigastridae	Saprophagous on sap flows (*Aulacigaster*) (Rotheray et al. 2001; Teskey 1976) (widespread but concentrated in Neotropics)
Axymyiidae	Develop only in partially submerged rotting wood in small forest streams (Wihlm and Courtney 2011) (northern hemisphere, temperate)
Bibionidae	Saprophagous in rotting wood (e.g., Hesperiinae) (Marshall 2012) (widespread)
Bolitophilidae	Fungivorous, some monophagous on wood-rotting fungi [e.g., *Bolitophila (C.) retangulata* Lundström on *Laetiporus sulphureus* (bull.) Murrill.] (Ševčík 2010) (Holarctic and Taiwan)
Braulidae	Inquiline of honey bee hives (widespread)
Calliphoridae	Saprophagous or predatory within termite nests (e.g., Bengaliinae and Prosthetosomatinae) (Marshall 2012). Also reported under bark (Rotheray et al. 2001) (widespread)
Canthyloscelidae	Saprophagous in wet decaying wood (e.g., *Synneuron*), especially in "ancient" forests (Teskey 1976; Marshall 2012) (Holarctic, South America and New Zealand)
Cecidomyiidae	Saprophagous, fungivorous, or predatory in rotting wood, under bark (e.g., *Miastor*), fungal fruiting bodies, beetle galleries, or termite nests (Økland 1995a; Ševčík 2010; Marshall 2012; Teskey 1976; Selby 2005) (widespread)
Ceratopogonidae	Saprophagous or predatory, in tree holes (e.g., *Dasyhelea*), under bark, and rotting wood (Marshall 2012; Teskey 1976; Kitching 1971). Other species are fungivorous (Ševčík 2010) (widespread)
Chaoboridae	Predators in tree holes (e.g., *Corethrella*) (Yanoviak 2001)
Chironomidae	Saprophagous in soggy or submerged rotting wood (Braccia and Batzer 2008; Teskey 1976) or water-filled tree holes (e.g., *Metriocnemus*) (Kitching 1971) and a few terrestrial species are fungivorous (e.g., *Bryophaenocladius*) (Ševčík 2010) (widespread)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Chloropidae	Saprophagous or rarely predatory in rotting wood and tree holes; some species fungivorous on fungal fruiting bodies (Ševčík 2010; Teskey 1976) (widespread)
Chyromyidae	Saprophagous in tree holes (Teskey 1976) (widespread)
Clusiidae	Predatory in rotting wood, under bark, and beetle galleries (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Corethrellidae	Predatory in water-filled tree holes (Marshall 2012) (widespread but mostly tropical)
Culicidae	Saprophagous or predatory (e.g., *Toxorhynchites*) in water-filled tree holes (Teskey 1976) (widespread)
Cypselosomatidae	Under bark (Krivosheina 1979) (widespread)
Diadocidiidae	Fungivorous in decaying wood (Jakovlev 2011) (widespread)
Ditomyiidae	Fungivorous (e.g., *Ditomyia*) on bracket fungi or saprophagous in relatively hard (e.g., *Symmerus*) or rotting wood (Ševčík 2010; Krivosheina 2006) (widespread but concentrated in Australasia and South America)
Dolichopodidae	Predatory (or necrophagous) in rotting wood, sap flows, tree holes (e.g., *Systenus*), under bark, and in beetle burrows (e.g., *Medetera*) (Rotheray et al. 2001; Teskey 1976; Marshall 2012; Kishi 1969) (widespread)
Drosophilidae	Saprophagous in rotting wood, under/in bark, wet tree holes, sap flows, and in the tunnels of ambrosia beetles (*Amiota*) (Rotheray et al. 2001; Teskey 1976; Krivosheina 2006); other species are fungivorous (Ševčík 2010; Jonsell et al. 1999) (widespread)
Empididae	Saprophagous in rotting wood (e.g., *Rhamphomyia*, *Drapetis*, and *Platypalpus*) and under bark (Rotheray et al. 2001); other species are predatory (Hövemeyer and Schauermann 2003) (widespread)
Fanniidae	Fungivorous in fungal fruiting bodies (Ševčík 2010) or saprophagous in rotting wood or in tree holes (e.g., *Fannia*) (Hövemeyer and Schauermann 2003) (widespread)
Heleomyzidae	Fungal fruiting bodies and in wood-boring beetle tunnels (e.g., the Australian *Cairnsimyia*) (Marshall 2012) (widespread)
Hybotidae	Predators in rotting wood, under bark, and rarely in fungi (Rotheray et al. 2001; Ševčík 2010) (widespread)
Keroplatidae	Fungivorous or predatory on bracket fungi, under bark, or in rotting wood (Speight 1989; Marshall 2012; Ševčík 2010) (widespread)
Lauxaniidae	Saprophagous or fungivorous in rotting wood (e.g., *Lyciella*) (Rotheray et al. 2001) (widespread)
Lonchaeidae	Saprophagous or predatory in rotting wood, under bark, and in beetle galleries (Rotheray et al. 2001; Wegensteiner et al. 2015). *Lonchaea* is particularly common in dead or dying wood (Marshall 2012) (widespread but most diverse in north temperate region)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Lonchopteridae	Saprophagous "surface scrapers" on rotting wood (Hövemeyer and Schauermann 2003)
Megamerinidae	Predatory under bark (Marshall 2012) (Palearctic and oriental)
Micropezidae	Saprophagous in rotting wood and under bark (especially Taeniapterinae) (Teskey 1976) (widespread)
Milichiidae	Saprophagous? In tree holes (e.g., *Stomosis*) and under bark (Teskey 1976; Krivosheina 2006) (widespread)
Muscidae	Predatory of saprophagous or predatory in rotting wood (e.g., *Phaonia*), tree holes, or at sap flows (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Teskey 1976) (widespread)
Mycetophilidae	Fungivorous or predatory in rotting wood, tree holes, under bark, and in fungal fruiting bodies (Ševčík 2010; Marshall 2012; Jakovlev 2011) (widespread)
Mydidae	Predatory in rotting wood (e.g., *Mydas*) (Teskey 1976) (widespread)
Neriidae	Rotting wood and sap flows (Marshall 2012) (widespread but mostly tropical)
Odiniidae	Saprophagous or predatory in sappy wood, beetle and Lepidoptera galleries, and fungus (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Opetiidae	Rotting wood (Marshall 2012) (Palearctic only)
Pachyneuridae	Saprophagous or fungivorous in rotting wood (Marshall 2012; Krivosheina 2006) (Holarctic)
Pallopteridae	Predatory under bark (*Palloptera*) (Rotheray et al. 2001; Teskey 1976) (mostly Holarctic)
Pantophthalmidae	Saprophagous on fermenting sap within their galleries (Neotropical)
Periscelididae	Saprophagous in sap flows (e.g., *Periscelis*), (Teskey 1976) (widespread)
Phoridae	Saprophagous in rotting wood and under bark; fungivorous (e.g., *Megaselia*) and parasitoids or inquilines of termites (Marshall 2012; Ševčík 2010; Matthewman and Pielou 1971) (widespread)
Pipunculidae	Predatory in rotting wood (e.g., *Chalarus*) (Hövemeyer and Schauermann 2003)
Platypezidae	Fungivorous in rotting logs, under bark (*Callomyia*), and on fungal fruiting bodies (e.g., *Agathomyia*, *Bertamyia*, and *Polyporivora*) (Marshall 2012; Krivosheina 2006) (widespread)
Platystomatidae	Saprophagous in rotting wood and root-feeders (Marshall 2012) (mostly Australasian, oriental, and Afrotropical but also in new world)
Pseudopomyzidae	Under bark (Marshall 2012) (widespread except for the Afrotropics)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Psilidae	Under bark or in sappy wood (e.g., *Chyliza*) (Teskey 1976) (mostly Holarctic and Afrotropical)
Psychodidae	Saprophagous in rotting wood (e.g., Trichomyiinae), tree holes (e.g., *Telmatoscopus*, *Brunettia*, and *Psychoda*), sap flows, and decaying fungal fruiting bodies (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Teskey 1976) (widespread)
Rhagionidae	Rotting wood (Rotheray et al. 2001) (widespread)
Richardiidae	Saprophagous, wet dead wood (e.g., *Omomyia*) (Marshall 2012) (new world only, especially Neotropics)
Ropalomeridae	Rotting wood and tree wounds (Marshall 2012) (Neotropics)
Sarcophagidae	Predatory on termites, honey bees, etc. (Marshall 2012; Hövemeyer and Schauermann 2003) (widespread)
Scatopsidae	Saprophagous in rotten wood (e.g., *Ectaetia*), tree holes, under bark (e.g., *Rhexoza*), or decaying fungi (Rotheray et al. 2001; Ševčík 2010; Marshall 2012) (widespread)
Scenopinidae	Predatory in rotting wood, wood-boring insect galleries, under bark, and termite nests (Marshall 2012; Teskey 1976) (widespread)
Sciaridae	Saprophagous in rotting wood, under bark, at sap runs, or fungivorous (Ševčík 2010; Sokoloff 1964) (widespread)
Sphaeroceridae	Fungivorous on fungal fruiting bodies (Ševčík 2010) or saprophagous in rotting wood (Roháček and Marshall 2017) (widespread)
Stratiomyidae	Saprophagous or predatory (or necrophagous) under bark (e.g., Pachygastrinae), rotting wood, tree holes (Rotheray et al. 2001; Marshall 2012; Krivosheina 2006). Occasionally fungivorous (*Beris*) (Krivosheina 2006) (widespread)
Strongylophthalmyiidae	Under bark (Rotheray et al. 2001) (mostly old world but also North America)
Syrphidae	Saprophagous in rotting wood, under bark (*Hammerschmidtia)*, in tree holes (*Blera*, *Callicera*, *Ceriana*, *Eristalis*, *Mallota*, *Myathropa*, *Spilomyia*, *Pocota*, etc.), sap runs (*Brachyopa*), or insect tunnels (*Brachyopa*) (Rotheray et al. 2001; Reemer 2005; Krivosheina 2006). Most members of Eristalinae are saproxylic (Marshall 2012) (widespread)
Tabanidae	Predatory in tree holes and rotting wood (e.g., *Leucotabanus*) (Teskey 1976) (widespread)
Tachinidae	Predatory in rotting wood or in fungal fruiting bodies (e.g., *Elodea* and *Phytomyptera*) (Jonsell et al. 2001) (widespread)
Tanyderidae	Saprophagous in submerged wood (Marshall 2012) (widespread)
Tephritidae	Saprophagous in rotting wood (e.g., Phytalmiinae) or under bark (*Lenitovena*), predatory in termite nests (Marshall 2012; Krivosheina 2006) (widespread)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Therevidae	Predatory in rotting wood (e.g., *Psilocephala* and *Thereva*) or tree hollows (e.g., *Pandivirilia*, *Thereva*) (Marshall 2012; Stokland et al. 2012) (widespread)
Tipulidae (including Tipulinae, Limoniinae, Cylindrotominae, and Pediciinae)	Saprophagous, predatory, or fungivorous in rotting wood (e.g., *Ctenophora*), under bark (e.g., *Gnophomyia*), in tree holes (e.g., *Sigmatomera, Ctenophora*), or fungal fruiting bodies (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Yanoviak 2001) (widespread)
Trichoceridae	Saprophagous in rotting wood and sometimes fungivorous in fruiting bodies (Ševčík 2010) (widespread)
Ulidiidae	Saprophagous in rotting wood or under bark, including the frass of wood-boring beetles (e.g., *Callopistromyia*) (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Xylomyidae	Saprophagous or predacious (or necrophagous) under bark (e.g., *Solva*) and in tree holes (e.g., *Xylomya*) (Krivosheina 2006; Teskey 1976) (widespread)
Xylophagidae	Predatory under bark and in rotting wood (e.g., *Xylophagus, Rachicerus*, and *Coenomyia*) (Teskey 1976) (widespread)

species appear to function primarily as necrophages, feeding on dead rather than living insects, including various xylomyids, stratiomyids, and dolichopodids (Krivosheina 2006; Kishi 1969). Other flies are inquilines of saproxylic termites and bees, and there are aquatic species that require water-filled tree holes. Major microhabitats utilized by saproxylic flies are summarized below.

5.2.1 Sap Runs

Trees wounded by insects [e.g., cossids; see Yoshimoto and Nishida (2007)], vertebrates, or other factors typically ooze sap, sometimes chronically, and this sugary substance is quickly colonized by bacteria and yeasts. The term “slime flux” is often used to refer to sap overgrown with microbes (Fig. 5.3). Sap runs (also referred to as flows or exudations) attract a wide range of insects, including species that breed in fermenting sap and those that opportunistically feed on this material as adults or prey upon other insects (Speight 1989). Diptera are typically by far the most abundant and diverse insects associated with these habitats (Wilson and Hort 1926; Yoshimoto et al. 2005) (Fig. 5.3). Wilson and Hort (1926) reported 10 families and at least 20 species from sap runs in Britain, with anthomyiids and muscids being present in the highest numbers. Sokoloff (1964) similarly reported 12 families and 21 species from sap runs in California, including 6 families and at least 8 species that were present as larvae. Some families of flies are mostly or entirely restricted to sap runs such as Aulacigastridae, Odiniidae, and Periscelididae, and many other families (e.g., Anisopodidae, Cecidomyiidae, Ceratopogonidae, Dolichopodidae, Drosophilidae, Syrphidae) include species known only from this microhabitat. Sap-feeding flies are essentially saprophagous, grazing on the microbes present in this material.

5.2.2 Subcortical Zone

The zone between the bark and wood provides a variety of resources for saproxylic flies. Many researchers have reported flies from fermenting sap beneath bark, and this was one of the most productive habitats reported by Rotheray et al. (2001) in their search for saproxylic flies in Scotland. This resource appears to support a number of species also found breeding in sap runs, such as *Hammerschmidtia ferruginea* (Fallén), an endangered syrphid in Europe (Rotheray et al. 2009). Krivosheina (2006) listed a number of fly taxa associated with the phloem layer in Russia, including various tipulids (*Libnotes*, *Gnophomyia*), Scatopsidae, syrphids (*Graptomyza*), tephritids (*Lenitovena*), and ulidiids (*Pseudoseioptera*). Most of these species are associated with decomposing phloem and are presumably saprophagous although several cecidomyiids primarily occur beneath the bark of dying trees. Other families found under bark include Pseudopomyzidae, Strongylophthalmyiidae, and Megamerinidae, but the habits of these taxa remain mostly unresolved (Krivosheina 2006). Some of the fly taxa found under bark (e.g., tipulids of the genera *Discobola* and *Ula*) appear to be largely fungivorous, feeding primarily on growths of mycelia.

In addition to the many saprophagous and fungivorous species, a number of predatory fly taxa occur under bark, and they often exceed other subcortical predators in both number and importance (Wegensteiner et al. 2015). Among these are important natural enemies of bark beetles including genera like *Phaonia* (Muscidae) (Fig. 5.2f), *Lonchaea* (Lonchaeidae), *Palloptera* (Pallopteridae), and *Medetera* (Dolichopodidae) (Fig. 5.1e) (Krivosheina 2006). Species of *Medetera* in particular are widely considered to be among the most valuable natural enemies of bark beetles in many areas (Wegensteiner et al. 2015). Other zoophagous species occurring beneath bark are thought to be primarily necrophagous, including various stratiomyids (*Neopachygaster*, *Pachygaster*, *Zabrachia*) (Fig. 5.1f), xylomyids, and dolichopodids (Kishi 1969; Krivosheina 2006). Some scavenging flies function as saprophagous detritivores, feeding on the mixture of rotting wood particles, fungi, bacteria, insect frass, and dead body parts that accumulates under bark and in insect tunnels. This group includes various species of Scatopsidae, Psychodidae, Tipulidae, etc. (Krivosheina 2006).

5.2.3 Wood

Members of many fly families tunnel through wood but are generally more saprophagous than xylophagous, benefiting primarily from the microbial biomass within wood rather than from the plant matter itself. One of the few exceptions is the phytophagous family Agromyzidae which includes species that feed on the cambium of living trees (Teskey 1976). Because they feed on healthy tissues, however, agromyzids are not truly saproxylic and are therefore not listed in Table 5.1. Certain cecidomyiids also feed on living wood tissue, but this family also includes many saproxylic species found under bark, in beetle galleries, or in rotting wood (Teskey 1976; Krivosheina 2006). Famous for their large size (20–55 mm in length), timber flies of the Neotropical family Pantophthalmidae (Fig. 5.2c) bore through the sound wood of dying or recently dead trees and are sometimes considered pests of living trees (e.g., *Casuarina* introduced into Central America) (Zumbado 2006). Rather than being xylophagous, the larvae of these flies feed primarily on fermenting sap within their galleries and are thus saprophagous. According to Zumbado (2006), pantophthalmids typically attack trees that produce latex or mucilaginous sap such as *Ficus* or *Ceiba pentandra* (L.) in Central America. Tipulidae is among the most significant families of wood-borers and can be found in all stages of decomposition. Swift et al. (1984) reported that *Tipula flavolineata* Meigen was the most common invertebrate present in branches from the forest floor in England, with evidence of the species in 39% of the sampled branches. The largest and most colorful tipulid genera (e.g., *Ctenophora*, *Dictenidia*, *Phoroctenia*, *Tanyptera*, and *Pselliophora*), belonging to the subfamily Tipulinae (or Ctenophorinae, depending on the classification system), all develop in dead wood, and many have become rare (Oosterbroek et al. 2006). Although some tipulid genera are capable of penetrating hardwood (e.g., *Ctenophora* and *Epiphragma*), many others (e.g., *Austrolimnophila*, *Elephantomyia*, *Limonia*) feed primarily in rotting logs and, in some cases (e.g., *Lipsothrix*), in saturated rotten logs (Teskey 1976; Dudley and Anderson 1987; Krivosheina 2006). Members of other fly families also tunnel in relatively fresh wood [e.g., *Temnostoma* syrphids (Fig. 5.2h, i)], but rotting logs generally support a greater variety of species from families including Bibionidae, Canthyloscelidae, Cecidomyiidae, Ditomyiidae, Pachyneuridae, Psychodidae, Scatopsidae, and Syrphidae (Krivosheina 2006). Some species have very specific substrate requirements with respect to moisture levels. For example, axymyiids tunnel into logs partially submerged in streams and only use wet portions of the log exposed to the air (Wihlm and Courtney 2011). Wood with a high moisture content is generally preferred by saproxylic flies, and many taxa are more abundant in downed than in standing trees, as Dennis et al. (2017) recently reported from Canada. Some species are known to occur in snags, however. For example, Krivosheina (2006) reported that *Pachyneura oculata* Kriv. et Mam. (Pachyneuridae) can be found within the relatively dry wood of standing dead trees in Russia.

Although flies associated with dying and dead wood in tropical forests have been less studied than those in temperate regions, they include some of the most

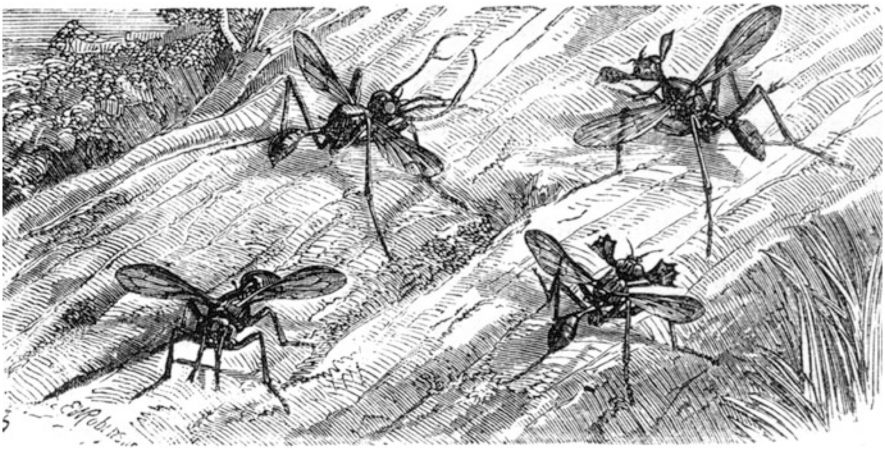

Fig. 5.4 An illustration of four "horned fly" species (Tephritidae: Phytalmiinae) from New Guinea observed by Alfred Russel Wallace in the mid-1800s. Wallace (1869) was the first naturalist to report on their association with dead wood (Glaubrecht and Kotrba 2004). Species shown include *Phytalmia cervicornis* Gerstaecker (top left), *P. alcicornis* (Saunders) (top right), and. *P. megalotis* Gerstaecker (lower right) (Gary Dodson, personal communication)

remarkable fly species in the world. Among these are 6 genera and 15 species of Phytalmiinae tephritids that breed in rotting logs in New Guinea, Northern Australia, Borneo, and Sulawesi (Dodson 2000). The males of these taxa have dramatic forward-curving cheek projections that are, depending on the species, often paddle-shaped, sometimes resembling the antlers of a moose, or thin and branch-like (Fig. 5.4). The males use these structures to signal body size and, if necessary, to fight over breeding sites and females (Wilkinson and Dodson 1997). Similar examples of sexual dimorphism are seen in other saproxylic fly species associated with rotting logs. The males of many clusiid species, for example, have broadened heads, cheek projections (e.g., certain *Hendelia* and *Procerosoma*), or elongated antennae (e.g., *Hendelia* from Australia) used to defend mating territories from rivals (Marshall 2012). These examples are reminiscent of the exaggerated mandibles of lucanids and the horns of dynastine scarabs, certain ciids, tenebrionids, and other saproxylic beetle taxa, underscoring the frequency of resource-defense mating systems and associated sexually dimorphic structures among saproxylic insects (Hamilton 1978).

Fungivorous flies, especially those belonging to the families Mycetophilidae, Sciaridae, and Cecidomyiidae, are among the most abundant and diverse fly taxa associated with rotting wood (Derksen 1941; Hövemeyer and Schauermann 2003; Krivosheina 2006) where they are thought to primarily feed on mycelia (see Sect. 5.2.5 on associates of fungal fruiting bodies). These flies remain mostly undescribed throughout much of the world (Amorim 2009), and the habits of most described species remain unknown. Stokland et al. (2012) suggest that saproxylic flies may prove to be more diverse than saproxylic beetles in Scandinavia once the habits of these fungus gnats are more fully known. Given the same uncertainties, it should not be assumed that all fungus gnats and other fly taxa that emerge from rotting wood are saproxylic as many taxa may also breed in other decomposing plant material. A study of Collembola in North America, for example, found that species occurring in rotting stumps represented just a subset of the soil-dwelling fauna (Setälä and Marshall 1994). However, this does not appear to be the case for fungus gnats based on a comparison of flies associated with rotting wood and leaf litter. In Germany, Irmler et al. (1996) found that 46% and 32% of mycetophilid species were found only in association with wood and leaf litter, respectively, with the remainder occurring in both substrate types. The respective figures for sciarids in that study were 30% and 45%. These findings indicate that many but not all of the fly species associated with dead wood are in fact saproxylic and underscore the need for more life history information.

In addition to the many saprophagous fly species found in dead wood, a wide variety of predatory taxa are present as well. Some predatory taxa have a wide host range. The North American tachinid, *Zelia vertebrata* (Say) (Fig. 5.2g), for instance, is known to parasitize a wide range of wood-boring beetle taxa including passalids, tenebrionids lucanids, etc.

5.2.4 Tree Holes

Tree holes are highly variable habitats depending on their age, position relative to the ground, opening size, water content, and insect community composition. All of these factors have been shown to influence saproxylic fly assemblages (Sánchez-Galván et al. 2014). Water content is a particularly important determinant, ranging from hollows that are usually or seasonally water-filled to those that are always dry. Flies typically dominate insect assemblages in the wettest tree holes, as Yanoviak (2001) observed in Panama, Majumder et al. (2011) reported from India, and Blakely et al. (2012) reported from New Zealand. Although some of these species are opportunists that utilize a wide range of water bodies, many of them are restricted to these structures (Blakely et al. 2012). Of the 25 species of Syrphidae collected by Ricarte et al. (2009) in Spain, 23 were collected from trunk cavities or tree holes and 12 of these were found nowhere else. Fly species dependent on water-filled tree cavities are perhaps best exemplified by Culicidae. In North America alone, for example, there are 21 species of mosquitoes from four genera (*Aedes*, *Anopheles*, *Orthopodomyia*, and *Toxorhynchites*) that are found only in these habitats and are thus saproxylic (Teskey 1976). Other fly taxa found only in or at the edge of water in wet tree holes include ceratopogonids (e.g., *Dasyhelea*, *Culicoides*, and *Atrichopogon*), syrphids (e.g., *Callicera*, *Mallota*, and *Myathropa*), chironomids (e.g., *Metriocnemus*), and dolichopodids (e.g., *Systenus*, a predator of ceratopogonids), whereas other fly genera (e.g., *Brachyopa*, *Fannia, Forcipomyia*, and *Phaonia*) are found in drier parts of the hole away from the water surface (Teskey 1976; Speight 1989). Syrphids exhibit a wide range of variation with respect to their affinity to water in tree hollows, with some species requiring it and others being restricted to drier substrates (Sánchez-Galván et al. 2014). Moreover, Rotheray (2013) showed that four species of syrphids that coexist within pine stump rot holes in Scotland inhabit distinct depths, as permitted by differences in behaviors and lengths of their respiratory tubes. In addition to water content, Sánchez-Galván et al. (2014) showed cavity height, size, and orientation to also be important determinants of hollow-dwelling syrphid assemblages in Spain. The most important predictor in that study was cetoniine beetle activity, however, and the frass from these beetles was shown to enhance the larval growth rate and adult wing length of *Myathropa florea* (L.). In addition, scolytine galleries were particularly important for one species, *Criorhina pachymera* Egger. While these findings suggest interspecific interactions may strongly influence the occurrence and abundance of hollow-dwelling insect assemblages, not all studies have shown this to be the case (Schmidl et al. 2008). Fly taxa dependent on tree hollows are probably among the most vulnerable of all saproxylic fly species due to the rarity of hollow-bearing old trees and the length of time required for these structures to form. Although similar estimates for flies are lacking, Floren and Schmidl (2008) estimated that 86% of beetle species dependent on rot holes in Germany are threatened.

5.2.5 Fungal Fruiting Bodies

Elton (1966b) distinguished between the fruiting bodies of non-saproxylic and saproxylic fungi and noted that, whereas flies dominate the insect fauna associated with the former, beetles more commonly dominate the fruiting bodies of saproxylic fungi. A survey of insects utilizing *Fomes fomentarius* (L. ex Fr.) in Canada largely supports this conclusion, at least for this species of hard sporocarp. Matthewman and Pielou (1971) reported Diptera from only 4.7% of the sporocarps inspected in that study, and they accounted for just 18% and 14% of the total numbers of species and individuals collected, respectively (Fig. 5.5). Beetles, by contrast, were found in 34% of all sporocarps and made up about 33% and 37% of all species and individuals collected. Although flies make up a smaller proportion of the fauna in fungal fruiting bodies than in some other saproxylic habitats, they are nevertheless represented by a wide variety of taxa and are generally thought to be more numerous in fruiting bodies that are softer and that decompose more rapidly [i.e., annual vs. perennial species; see Komonen et al. (2001)]. In a survey of Diptera associated with fungi (including saproxylic fungi) in the Czech and Slovak Republics, Mycetophilidae was the most diverse family, accounting for 41% of species, followed by Phoridae (9%), Cecidomyiidae (8%), Drosophilidae (6%), Bolitophilidae (4%), Platypezidae (4%), and Muscidae (4%) (Ševčík 2010).

Once established, all wood-rotting basidiomycetes produce fruiting bodies. In some cases these are short-lived and soft, whereas in perennial species harder fruiting bodies continue to grow for several years before dying and slowly decomposing (Gilbertson 1984). Elton (1966b) recognized that fungal fruiting

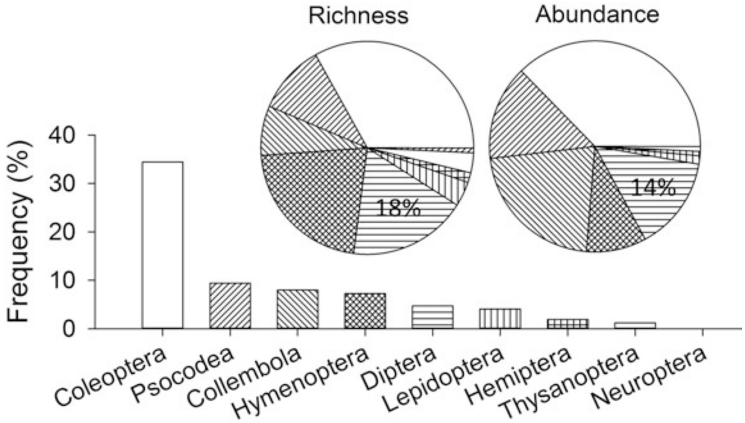

Fig. 5.5 Relative richness, abundance, and occupancy rates of Diptera and other insect orders reported by Matthewman and Pielou (1971, see Table 3) from sporocarps of *Fomes fomentarius* in Canada

bodies provide insects with four main resources: (1) spores, (2) living fungal tissue, and (3–4) aging or dead fungal tissue which, depending on the species, can be hard and long-lasting or soft and ephemeral. There are saproxylic flies specific to all four of these categories. An example of a spore-feeding species is the threatened European keroplatid, *Keroplatus tipuloides* Bosc, which feeds on the spores of *Fomes fomentarius* (L. ex Fr.) within mucilaginous webs they construct beneath the sporocarps (Speight 1989). A variety of fly species feed on living fungal tissue (e.g., Cecidomyiidae, Platypezidae, Mycetophilidae, Sciaridae, etc.), and these taxa tend to be more host specific, but fewer in number, than those feeding on decomposing fungi (Matthewman and Pielou 1971; Marshall 2012; Jonsell et al. 2001). Most sporocarp-inhabiting fly species are found in dead rather than living fruiting bodies. Those associated with dead soft fungi (Fig. 5.1c, d) are generally less host specific than those utilizing hard perennial sporocarps. Graves (1960) distinguished between dying or recently dead sporocarps and those that are dead and decomposing and suggested the former support the greatest diversity of insects. A variety of intrinsic and extrinsic factors are important in influencing the occurrence of saproxylic flies in fungal fruiting bodies. In a comparison of insect assemblages associated with *Fomitopsis pinicola* and *Fomes fomentarius*, for example, Jonsell et al. (2001) showed that most common fly taxa correlated positively with sporocarp size. Height above the ground was also important for some species (e.g., mycetophilids) as was tree diameter and sun exposure.

Predatory flies can often be found inhabiting fungal fruiting bodies. Jonsell et al. (2001) reported two species of Tachinidae (*Elodia* and *Phytomyptera*), both parasitoids, from sporocarps in Sweden, for example. Similarly, Komonen et al. (2001) found another tachinid, *Elfia cingulata* (Robineau-Desvoidy), parasitizing a tineid moth in fungal fruiting bodies in Finland. Keroplatids are often associated with spores from polypore fungi, but will also feed on small invertebrates trapped in their webs, sometimes very efficiently (Mansbridge and Buston 1933) (Fig. 5.1b).

5.2.6 *Insect Galleries*

Many fly taxa are predators within the tunnels of wood-boring beetles and other insects. Pachygasterine stratiomyids can be found wherever their hosts occur, including their tunnels. Laphriinae asilids are active predators within the tunnels of xylophagous beetles and are morphologically adapted for this habitat (Krivosheina 2006). Dolichopodids of the genus *Medetera* are also confined to the galleries of various bark beetle species (Fig. 5.1e). Clusiids and odiniids are also among the predators found within the tunnels of wood-boring insects. Not all fly species found in beetle tunnels are predators, however. For instance, species of Ulidiidae associated with dead wood are also thought to feed on frass and other particulate matter in beetle galleries (Marshall 2012).

5.2.7 *Social Insect Nests*

A number of flies exist as inquilines within the nests of social saproxylic insects. The family Braulidae consists of two genera and eight species that are wingless, mite-like inquilines of honey bees. The larvae live in honeycombs where they feed on pollen, and the adults can be found clinging to the hairs of their hosts (Marshall 2012). Species from at least six fly families (Calliphoridae, Cecidomyiidae, Phoridae, Sarcophagidae, Scenopinidae, and Tephritidae) are known to be associated with termite nests. Within the family Phoridae alone, there are 190 species known to associate with termites (Dupont and Pape 2009), including parasitoids, opportunistic scavengers, and inquilines. The inquilines are often highly specialized, either protected by armor or by a physical or chemical similarity to their termite hosts (e.g., see Fig. 1 in Dupont and Pape 2009).

5.3 Substrate Requirements

5.3.1 *Successional Patterns*

As with beetles and other insects, there is a succession of flies as decomposition proceeds, with many species exhibiting distinct preferences for fresh or highly decomposed wood. An excellent demonstration of this was provided by Hövemeyer and Schauermann (2003) who studied the emergence of flies from decomposing beech wood over a 10-year period in Germany. Consistent with other studies (Derksen 1941; Irmler et al. 1996; Kleinevoss et al. 1996; Selby 2005), they showed that fly abundance and richness generally increased as the logs decomposed. While many fly taxa were more abundant later in the decomposition process (e.g., species of *Tipula*, *Caenosciara*, *Euthyneura*, *Cordyla*, and *Neolimonia*), some were restricted to medium-aged logs (*Symmerus*), and others were more strongly associated with younger logs including predatory taxa such as *Medetera* and *Xylophagus*. In Canada, Vanderwel et al. (2006) also found predatory flies (Dolichopodidae and Lonchaeidae but not Empididae, which showed the opposite pattern) to be more abundant in younger decay classes, whereas saprophagous and fungivorous taxa were generally more abundant in later stages of decomposition. The higher abundance of predatory flies in younger decay classes probably reflects the higher abundance of phloem- and wood-feeding beetle prey in young logs as was shown in the same study. The pattern of greater saprophage and fungivore abundance in highly decomposed wood is complicated by the migration of leaf litter fauna into the wood as decomposition proceeds, as found by Irmler et al. (1996) in Germany. Clearly, more detailed information on habitat associations will be needed to better understand the successional patterns of saproxylic Diptera.

Some saproxylic fly taxa are restricted to ephemeral resources or microhabitats present only at the beginning of the decomposition process. Fermenting sap under bark, for example, is a breeding substrate for many fly taxa but dries out and disappears quickly (Rotheray et al. 2009). The subcortical space itself is an important microhabitat for many species but lasts only as long as the bark remains in place. Among the North American taxa of *Forcipomyia* (Ceratopogonidae), for example, some species are restricted to wood prior to bark loss, whereas others occur only in highly decomposed wood (Teskey 1976).

Living sporocarps support a different fly fauna than dead sporocarps, and the hard sporocarps produced by perennial fungal species decompose slowly and host a succession of fly species. As summarized by Elton (1966a), mycetophilids associated with the living sporocarps of *Piptoporus betulinus* (Bull.) P. Karst. in England were replaced, soon after the death of the fungus, by the larvae of cecidomyiids and other taxa. Jonsell et al. (2001) reported a similar pattern for flies associated with *Fomitopsis pinicola* in Sweden. Økland and Hågvar (1994) showed that living *F. pinicola* sporocarps support few species before, compared to after, the development of hymenium and that dead sporocarps support the most species. Graves (1960) suggested that dying or recently dead sporocarps support more insects than those at latter stages of decomposition. Those associated with decomposing fungi (Fig. 5.1c, d) are generally believed to exhibit less host specificity. In Canada, Matthewman and Pielou (1971) found a species of *Gaurax* (Chloropidae) to be found only in dead sporocarps of *Fomes fomentarius*.

5.3.2 Diameter Preferences

Wood diameter probably matters for saproxylic fly communities just as it does for other insect taxa, but few studies have tested this. In Switzerland, Schiegg (2001) collected a significantly greater number of species from beech limbs than from beech trunks, with only a 55.3% similarity between the two diameter classes compared to 82.6% for beetles. Halme et al. (2013) found nematoceran fly communities emerging from the bases and tops of aspen trunks to be highly variable in Finland and attributed compositional differences between these locations to random assembly rather than to diameter preferences. They suggested that the difference in diameters compared in that study was not large enough to detect strong differences.

5.3.3 Host Specificity

Host tree specificity is common among saproxylic insects, and many saproxylic fly taxa are largely or entirely restricted to a single genus of trees. Among the species of *Phytalmia* (Tephritidae) associated with the wood of decaying rainforest trees, for example, two are restricted to a single tree species (Dodson 2000). Irmler et al. (1996) reported a fairly high degree of host specificity among fungus gnats (mycetophilids and sciarids) in a comparison of three wood genera in Germany. About 71% and 30% of mycetophilid and sciarid taxa, respectively, were collected from beech wood but not from the *Alnus* or *Picea* wood included in that study. By contrast, Rotheray et al. (2001) found fly diversity to vary widely among tree species in Scotland, but relatively few species were restricted to a single genus or species. Taken together, these findings indicate that the degree of host specificity exhibited by saproxylic flies varies widely among species but that some species depend on the presence of particular host tree taxa.

Although some tree species are more likely to form hollows than others, Kitching (2000) suggested that tree species has little influence on the composition of the insect fauna occupying a hollow. This appears to be true for many hollow-dwelling fly species (Ricarte et al. 2009), but some species are known to be strongly associated with particular tree taxa. The European syrphid species *Blera fallax* (L.), for example, is found in water pockets or rot holes of *Pinus sylvestris* L. stumps (Rotheray et al. 2016). Another threatened syrphid, *Callicera rufa* Schummel, also appears to be restricted to tree holes in conifers (Rotheray and MacGowan 2000).

Saproxylic flies associated with fungal fruiting bodies, especially with living sporocarps, often exhibit a high degree of host specificity. According to Jonsell et al. (2001), living fungal species that produce soft ephemeral sporocarps tend to support a less distinct fauna than those producing perennial sporocarps. Perennial sporocarps are thought to contain more secondary compounds used in defense, and this likely gives rise to specialization among fungivorous insects. In a comparison of insects associated with six species of sporocarps in Norway, Økland (1995b) found some cecidomyiid species to be restricted to particular genera or species. In Finland, Komonen et al. (2001) found that species of annual and perennial fungal fruiting bodies (*Amylocystis lapponica* (Romell) and *Fomitopsis rosea* (Alb. et Schw.: Fr.) Karst., respectively) supported distinct communities of flies and other insects.

5.3.4 *Effects of Sun Exposure*

Saproxylic flies prefer wetter substrates than many other saproxylic insect taxa, and many are adapted to aquatic or semiaquatic microhabitats. Rotheray et al. (2001) conducted perhaps the single greatest effort to describe the microhabitat associations of saproxylic Diptera. Over a 10-year period in Scotland, they collected 32 families and 258 species from sap runs, tree holes, loose bark, and dead wood from a variety of tree species. They found that some tree genera supported more species than others and that the occurrence of key microhabitats varied among tree taxa. Saproxylic fly larvae were almost always collected from damp or wet conditions in that study, with most coming from decaying sap under bark and decaying sapwood on the ground. In a study of saproxylic fly succession in Germany, Hövemeyer and Schauermann (2003) found that flies were most numerous the year following very moist summers and suggested that log conditions, particularly moisture content, may be more important than log age in determining substrate suitability. Indeed, of the six saproxylic fly species abundant enough to analyze individually in that study, the abundances of all but one were positively and significantly correlated with wood water content.

Such findings suggest that saproxylic flies may be sensitive to sun exposure. In a study of insects associated with fungal fruiting bodies in Sweden, Jonsell et al. (2001) found *Medetera* to be significantly less frequent under open conditions, whereas the frequency of Cecidomyiidae and Mycetophilidae did not differ among exposure categories. Some saproxylic fly taxa are considered thermophilic, however, such as the European syrphid *Mallota dusmeti* Andréu (Quinto et al. 2014). Moreover, open conditions may provide important resources for the adult stage of many saproxylic fly species, such as those that visit flowers.

5.4 Status and Conservation

The literature is full of examples of saproxylic fly species known or suspected to be in decline if not already extirpated across much of their historic range. Stubbs (1972) highlighted seven such species from Britain in his early report on the conservation value of dead wood. Threatened flies also featured prominently in Speight's later assessment of the status of saproxylic insects in Europe (Speight 1989). Jonsell et al. (1998) reported 46 species of saproxylic flies red-listed in Sweden (making up nearly half of all red-listed Diptera for the country), but noted that this probably underestimates the number of threatened species due to limited knowledge. Some saproxylic fly species have the potential to serve as indicators of habitat quality. Many of the largest and most charismatic tipulid species are saproxylic, for example, and these are sensitive to the amount and continuity of dead wood (Oosterbroek et al. 2006). In some cases, flies are suspected of being saproxylic and limited to old-growth forests even though their biology remains incompletely known. In northeastern North

America, for example, the rare sphaerocerid *Volumosina voluminosa* (Marshall) has been collected only from old-growth forests and almost exclusively from large woody debris (Roháček and Marshall 2017).

The question of how much dead wood is needed to sustain diverse saproxylic insect assemblages remains an active area of study. This question has received less attention for flies than for beetles, however. Vanderwel et al. (2006) showed that the abundance of fungivorous flies (Cecidomyiidae, Mycetophilidae, and Tipulidae, which were also combined with the beetle family Melandryidae for the analysis) emerging from decomposing logs was positively correlated with the volume of dead wood present within both the surrounding 20 ha and the surrounding 79 ha. It was not possible to determine which spatial scale was more relevant in that study, however. As discussed in that paper, these patterns may be due to fungal richness correlating with coarse woody debris abundance and influencing the richness of fungivorous insects as has been shown in previous studies (Vanderwel et al. 2006 and references therein). Similarly, Schiegg (2000) found a positive correlation between the richness of flies emerging from dead wood and the average volume of subplots within a 150 m radius in Switzerland. In Norway, Økland (1994) found mycetophilid diversity to be much higher in seminatural forests when compared to managed forests (clear-cut 70–120 years previously) or recent clear-cuts (2–3 years previously), suggesting this family may be especially sensitive to the temporal continuity of forests. Økland (1996) also found a positive correlation between mycetophilid species richness and the amount of old-growth forests in the surrounding 100 km^2 in Norway. It was suggested in the same article that because mycetophilids must wait until late summer or early autumn for sporocarps suitable for oviposition to become available, they generally conserve energy by waiting in humid microhabitats such as under logs rather than wasting energy on dispersal. Later work by the same author found mycetophilids to be largely unaffected by harvests that removed, on average, 26% of the basal area (Økland et al. 2008). Taken together, these findings indicate that mycetophilids may be less impacted by partial harvests than clear-cuts.

Although rarely studied, the dispersal abilities of saproxylic flies probably vary widely among taxa as have been shown for beetles and other groups. Species that utilize ephemeral and infrequent resources are generally expected to be capable of travelling long distances. Support for this was provided by a mark-recapture study by Rotheray et al. (2014) which showed that the syrphid *Hammerschmidtia ferruginea* can disperse at least 5 km in Scotland. More limited dispersal abilities have been reported for other species, however. Jonsell et al. (1999) studied the ability of insects to colonize fungal fruiting bodies placed at various distances from source populations in Sweden and found two fly taxa, *Leucophenga* and *Medetera* (Drosophilidae and Dolichopodidae, respectively) to be more affected by distance than beetles in that study. Jonsell and Nordlander (2002) also found *Medetera* to be generally more common in forests with a long history of dead wood continuity compared to forests with a shorter history, although there were too few records for statistical analysis. In Finland, Komonen et al. (2000) found *Elfia cingulata*, a tachinid that parasitizes larval tineids in fungal fruiting bodies, to be completely absent from forest fragments that had been isolated for the longest period of time.

In the Netherlands, Reemer (2005) found that 59% of saproxylic syrphid species have increased in recent years, whereas 26% have decreased. The increases are thought to be due to an increase in forest cover since the 1950s, the presence of more large diameter trees, and efforts to protect dying trees and dead wood. These numbers suggest that efforts to protect old trees and dead wood in forests can be expected to benefit saproxylic flies, although the specific requirements of declining species need to be taken into account. The protection of old trees is likely to be particularly beneficial to flies dependent on tree hollows (Blakely et al. 2012; Ricarte et al. 2009). Because these structures take such a long time to develop naturally (Micó 2018), management interventions that promote their formation are of great interest. Traditional pruning practices such as pollarding and coppicing have been shown to do so in Europe where orchards, parks, old forest pastures, and similar habitats provide some of the most important habitats for hollow-dependent insects (Sebek et al. 2013). Indeed, Quinto et al. (2014) suggest that pollarding may benefit vulnerable hollow-dependent syrphids such as *Mallota dusmeti* in Spain. Suitable breeding sites for some species (e.g., *Callicera rufa* in Europe) can be created more directly and immediately by simply cutting holes into trees or stumps (Rotheray and MacGowan 2000). Active recovery efforts for *Blera fallax*, a syrphid species on the edge of extinction in Scotland, involve captive rearing of the fly and reintroducing it into areas where pine stump rot holes have been artificially created (Rotheray et al. 2012).

Efforts to conserve saproxylic Diptera should recognize that these insects typically exhibit a stronger affinity for moist or wet habitats than most beetles or other saproxylic groups. Quinto et al. (2014) found syrphid abundance to be positively correlated with the amount of water in tree cavities, for example, whereas the opposite was the case for beetles. Rotheray et al. (2001) showed that even small young trees can provide breeding habitat for many flies, including red-listed species, provided that the necessary wet microhabitats are provided. Whereas the results from beetle studies often suggest that more open forests and sunnier conditions will promote the conservation of saproxylic insects, this may not be true for other groups, including flies. In Scotland, the endangered syrphid *Hammerschmidtia ferruginea* is known to breed in the wet fermenting sap beneath bark as well as in sap runs. The former resource is more productive but is also more ephemeral. The speed at which fermenting sap beneath bark dries out is thought to be one of the major challenges facing efforts to conserve this species (Rotheray et al. 2009), suggesting such taxa may be sensitive to efforts aimed at creating more open conditions.

Finally, aquatic flies dependent on submerged wood are thought to be sensitive to forest clearance. In Brazil, for instance, Valente-Neto et al. (2015) showed that deforestation decreased the abundance and richness of saproxylic flies (chironomids) in wood submerged in streams. The researchers attributed these effects to increased sedimentation caused by the harvesting operations.

5.5 Conclusions

Flies are extremely diverse members of saproxylic insect assemblages and commonly exceed even beetles in abundance and richness. This is especially true in the wettest microhabitats including sap runs, wet tree holes, and submerged wood. Although the diversity, ecology, and conservation status of these insects have received little attention, it is clear that many species are declining or have experienced significant range contractions. Because saproxylic Diptera exhibit a strong affinity for wet or even saturated substrates, they deserve special consideration when developing conservation strategies for saproxylic insects. Studies addressing their sensitivity to forest management interventions are urgently needed.

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Chapter 6
Ecology, Diversity and Conservation of Saproxylic Hymenopteran Parasitoids

Jacek Hilszczański

Abstract The ecological adaptations of parasitoids associated with bark- and wood-boring insects, i.e. saproxylic insects, are presented principally from examples of Ichneumonoidea but also other families of saproxylic parasitoids typically associated with insects inhabiting dead wood. Morphological adaptations to hosts living in wood, behaviours related to parasitism of the host and life strategies of saproxylic idiobionts and koinobionts are characterised. From the example of *Doryctes leucogaster* (Nees) (Doryctinae, Braconidae), details of searching behaviour and the oviposition process are described. Brief summaries of the main "saproxylic" subfamilies of Ichneumonidae and Braconidae followed by Stephanidae, Aulacidae, Ibaliidae and Orussidae are included. Habitat requirements of saproxylic ichneumonoid parasitoids in boreal and temperate forests are presented in relation to forest successional stage and the type and position of woody substrates. The potential role of saproxylic parasitoids as indicators of saproxylic habitat quality is discussed, and the lack of ecological knowledge for most saproxylic parasitoid taxa, especially from tropical zones, is indicated.

6.1 Introduction

Parasitoids comprise one of the most numerous groups of insects (Gaston 1991) and are distinguished from parasites in that they are parasitic only as larvae and eventually kill their hosts. Moreover, unlike many solitary wasps, female parasitoids do not attempt to move a host after parasitising it (Godfray 1994). Although many insect orders include saproxylic parasitoid taxa [e.g. Diptera (Tachinidae), Coleoptera (Bothrideridae) and Lepidoptera (Sesiidae)] (Hellrigl 1984; Hilszczański, pers. obs.), Hymenoptera contains the highest number of species. This chapter is limited to hymenopteran parasitoids that are saproxylic (hereafter referred to as parasitoids

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for brevity), i.e. meaning they specifically target hosts that depend directly or indirectly on dead wood (Speight 1989).

Saproxylic insects pose unique challenges to parasitoids as hosts hidden beneath bark or within wood are inherently harder to locate and parasitise than are exposed hosts (Gross 1991). Although many parasitoid species target insects feeding within the phloem layer beneath the bark (e.g. Cerambycidae, Buprestidae, Curculionidae, etc.), bark thickness and ovipositor length limit host availability for some species (Abell et al. 2012). How far insects bore into wood can be expected to similarly influence the susceptibility of a species to parasitism. Indeed, saproxylic insects with the most cryptic habits experience the lowest rates of parasitism. Wood-dwelling termites, for example, and especially those that nest below ground, are parasitised by few species and more often by Diptera (e.g. Phoridae) than Hymenoptera (e.g. Bethylidae attacking drywood termites) (Culliney and Grace 2000). In this chapter, I first provide a brief overview of the ecology of saproxylic parasitoids before summarising the global diversity of these insects and groups of particular importance in European forests (e.g. Braconidae, Ichneumonidae and various other families such as Aulacidae, Stephanidae, Orussidae and Ibaliidae) which are exclusively or almost exclusively associated with hosts of typical saproxylic families such as wood-boring beetles (Cerambycidae, Buprestidae, Ipinae, Anobiidae) and wood wasps (Siricidae, Xiphydriidae). The chapter ends with a discussion of parasitoid habitat requirements and conservation considerations.

6.2 Ecological Importance

A key ecosystem service provided by saproxylic hymenopteran parasitoids is reducing host populations which can, in turn, result in measurable benefits to forest health. This is especially relevant with respect to reducing populations of bark beetles and various wood-boring insect species, including those that pose a threat to healthy trees during outbreaks (Kenis and Hilszczanski 2004). Moreover, in the case of invasive insect species, parasitoids and other biocontrol agents, including both native species and those intentionally introduced from the pest's native range, sometimes represent one of the best available options for reducing mortality in native host trees (Van Driesche and Reardon 2014; Duan et al. 2016). Although relatively few studies have attempted to quantify the ecosystem services provided by saproxylic hymenopteran parasitoids, those that have been conducted support the idea that these insects have a significant top-down effect on host populations. The most detailed assessments have involved bark beetles such as *Dendroctonus frontalis* Zimmermann in North America and *Ips typographus* (L.) in Europe, and the parasitoid communities associated with these species are thought to play an important role in reducing population growth and perhaps also outbreak severity (Wermelinger 2004; Berisford 2011). Particularly strong experimental evidence that hymenopteran parasitoids have significant negative impacts on their host populations was recently provided by Duan et al. (2015) who found that both native and introduced (i.e. classical biocontrol agents) hymenopteran parasitoids significantly reduce population growth rates of the invasive emerald ash borer in North America.

6.3 Parasitoid Natural History

Parasitoids can be variously categorised on the basis of host stage specificity (e.g. eggs, larvae, pupae or adults), whether they are solitary or gregarious (i.e. one or multiple eggs laid per host), whether eggs are laid internally or externally and whether the host is killed at the time of oviposition or continues to grow after eggs are laid. Although a detailed review of these differences is beyond the scope of this article, and can be found elsewhere (e.g. Godfray 1994), it is worth briefly discussing differences between koinobionts and idiobionts.

6.3.1 Koinobionts vs. Idiobionts

As in most ecological groups of parasitoids, saproxylic species can be divided into koinobionts and idiobionts according to the classification proposed by Haeselbarth (1979) and further developed by Askew and Shaw (1986). The main feature of that classification is whether or not the host insect continues its development after it has been paralysed.

Koinobionts do not paralyse or immediately kill their hosts, allowing them to instead continue feeding and growing. Some koinobionts are known to manipulate the growth physiology of their hosts, sometimes causing them to delay maturation and suppress pupation (Godfray 1994). Most koinobionts are associated with exposed hosts; however, there are species which parasitise concealed hosts including saproxylic ones. Saproxylic koinobionts attack larvae and very often early instars, sometimes even eggs, of insects living in wood. Examples include several braconid genera such as *Eubazus* (Helconinae) (Kenis and Mills 1998) and certain eulophids (e.g. *Tetrastichus*) that attack beetles and species of Aulacidae and Ibaliidae that attack wood wasps. Hosts parasitised by koinobionts often reach a late larval or pupal stage before getting entirely consumed and killed. Saproxylic koinobionts are necessarily endoparasitoids as it would be impossible to live externally attached to a host larva which is moving inside narrow galleries. Because the larvae of koinobionts live inside the bodies of active hosts, their physiology is adapted to that way of life, which implies adaptations to overcome the immunological system of the host. This specific adaptation makes koinobionts rather host-specific although it is known that species are sometimes related to a specific niche rather than strictly to a host species and are sometimes able to parasitise several host species which are characterised by similar biology. Although most saproxylic koinobionts are known from single host species, there are quite a few exceptions, though often based on unreliable data (Shaw 2017). For example, the koinobiotic braconid *Helcon tardator*

Nees (Helconinae) is recorded from at least 14 cerambycid hosts associated with coniferous and deciduous trees. Koinobionts are rather pro-ovigenic which means that emerged females have a full set of developed small eggs. Data on longevity of parasitoid adults, especially in the field, are very scarce, but typically koinobionts are shorter-lived than idiobionts. Unlike the adults, larvae of koinobionts tend to live longer than idiobionts and do not have “to be in hurry” inside their developing host.

Saproxylic idiobionts paralyse or kill their hosts permanently, and because of that they have to look for bigger larvae, rarely pupae, of wood-inhabiting insects to fully support the development of their larvae. Idiobionts have developed the ability to determine the sex of the egg to match the host’s size, which has not been observed in koinobionts. Idiobionts are ectoparasitoids with few exceptions, and their larvae are not in danger from the immovable larva of the host (Quicke 2015). Idiobionts have not evolved sophisticated physiological adaptations to their host; however they do possess abilities to make their lives easier. To protect their paralysed or killed host from rotting away, some species produce antifungal or antibacterial secretions which is probably the case in the braconid *Histeromerus mystacinus* Wesmael (Rhyssalinae) whereby larva of the lepturine host (Cerambycidae) was found to be fresh during the whole lifetime of the parasitoid larvae (Shaw 1995). Saproxylic idiobionts tend to be generalists, and most of them are known from numerous hosts. One of the most common Palaearctic xoridines, *Xorides praecatorius* (F.) (Ichneumonidae), for example, has been reared from galleries of at least 30 species of mostly cerambycids and buprestids and from both dead and living coniferous and deciduous trees and shrubs (Hilszczański 2002). Idiobionts are synovigenic which means that they produce relatively big eggs successively during their adult life. This requires supplementary feeding on flowers, honeydew or hosts (host feeding), although the latter has not been actually observed in saproxylic idiobionts. Adults drink water, and the presence of water, for example, dew, is probably a limiting factor for these insects (Vanlaerhoven et al. 2005). Idiobionts are generally longer-lived than koinobionts, which is explained mainly by their successive development of large well-yolked eggs, which is an ongoing process, and the consequent limits to the frequency of ovipositions that can be achieved.

6.4 Behavioural and Morphological Adaptations of Saproxylic Parasitoids

Compared to parasitoids of exposed hosts (e.g. such as those attacking caterpillars that feed externally on leaves), saproxylic parasitoids face a number of unique challenges arising from their specificity for hosts concealed under bark or within dying or dead wood. Host location is the first challenge, followed by ovipositing through hard layers of bark or wood and finally emerging as new adults from deep within the galleries of host insects. As discussed below, these insects have developed a wide variety of behavioural and morphological adaptations to cope with these challenges.

6.4.1 Host Location

Successful parasitism involves a sequence of steps including host habitat location, host location, host acceptance and host suitability (Godfray 1994). To find a host concealed in wood, parasitoids use a combination of chemical and physical cues. Vibrations made by the host are often a very good indication of host presence [see example of *Doryctes leucogaster* (Nees) below]. However some parasitoids use a form of echolocation, i.e. vibrational sounding, whereby vibrations are made by the parasitoid female with the use of special antennal hammers (Fig. 6.2c, f) (Vilhelmsen et al. 2001). The response of the substrate is then detected in subgenual organs located in the swollen fore tibia (Fig. 6.2d) (Broad and Quicke 2000).

6.4.2 Oviposition

A long ovipositor is the most obvious feature which is very often connected with morphological adaptations of parasitoids to lay eggs on hosts concealed in wood. Indeed a long ovipositor is one of the main tools, but the ovipositor itself has many other adaptations which enable parasitoid females to assure reproductive success (Quicke 2015).

Typically the ovipositor of ichneumonoids consists of a single upper and a pair of lower valves, which are protected by sheaths when not in use. In the case of saproxylic species, the ovipositor is used to penetrate the substrate, and because of that it is constructed to be able to get through sometimes hard wood. The most commonly seen ovipositors in saproxylic parasitoids are equipped with a sharp strong tip, sometimes pre-apical protuberances (nodus) on the upper valve, and distinct lower valve serrations (Fig. 6.2a). Variations in those features are sometimes used as important morphological features used in species identification (Zwakhals 2010). The ovipositor works similarly to a ratchet drill; finding the right place for the tip of ovipositor to start the whole process is of paramount importance (see below for the example of *Doryctes leucogaster*). “Drilling” or cutting through a hard substrate requires a strong cuticle on the ovipositor teeth. The apex of the ovipositor was found in some species to largely consist of a zinc- or manganese-protein complex (Quicke et al. 1998). Some species of parasitoids use oviposition holes made by females of the host species, and such females have a much more “delicate” ovipositor which is thinner than the host one and does not possess strong serrations. For example, *Aulacus striatus* Jurine (Aulacidae) lays its eggs using the hole made by wood wasps (*Xiphydria* sp.), while in a similar fashion, the ichneumonid kleptoparasitoid *Pseudorhyssa* (Poemeniinae) uses the boring made by the female of the primary ichneumonid rhyssine parasitoids *Rhyssa* sp. or *Rhysella* sp. to steal the host of these primary parasitoids. Despite its narrower ovipositor, *Pseudorhyssa* lays much bigger eggs than the primary parasitoids, and its first instar larva has a great advantage over them in having far more powerful mandibles, through which it is able to kill their egg or win contests with the primary parasitoid larva. In the case of saproxylic species which are able to reach their host in other ways than by drilling through substrate, the ovipositor can be small and with reduced serrations as in the case of *Histeromerus* sp. (Braconidae, Histeromerinae) (Shaw 1995).

An important thing for species having a long ovipositor, which might be five to ten times longer than the body, is to stabilise it and prevent it from buckling. To penetrate a woody substrate, the ovipositor has to be pushed with force. A thin and long ovipositor is prone to buckle, so many species have special adaptations to reduce the effective (force-bearing) length of the ovipositor by clamping it using grooves located on the hind coxae (*Pristaulacus* sp., Aulacidae (Fig. 6.1f); Cenocoelinae, Braconidae) or special guides with hooks on the metasomal sternites

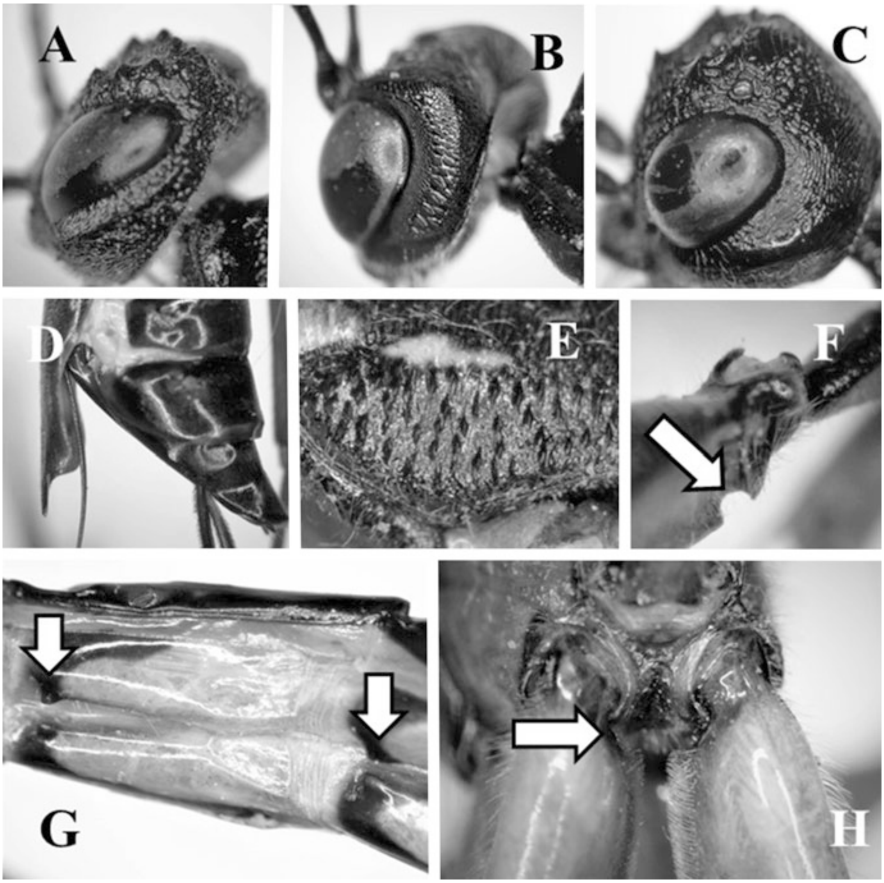

Fig. 6.1 Morphological features of saproxylic parasitoids. (**a**) *Orussus abietinus* (Scopoli) spines on the head; (**b**) *Neoxorides* sp. scalelike ridges on the head; (**c**) *Stephanus serrator* (F.) spines on the head; (**d**) *Coleocentrus croceicornis* (Gravenhorst) enlarged hypopygium; (**e**) *Megarhyssa* ridges on mesosoma; (**f**) *Pristaulacus* sp. groove on hind coxa; (**g**) *Megarhyssa* sp. groove with hooks; (**h**) *Megarhyssa* sp. groove on the base of hind coxa (Photos by Jacek Hilszczański)

in some Rhyssinae (*Megarhyssa* sp.) (Fig. 6.1g). In some *Megarhyssa*, the ovipositor can be looped in an internal membranous sac between tergites 6 and 7 of the metasoma, which facilitates the use of a much longer ovipositor. To use long ovipositors, many parasitoids also have thin and long legs, which enable them to position the ovipositor perpendicularly to the wood when starting the process of penetration (Fig. 6.4b, g).

Megarhyssa and other Rhyssinae and some Ephialtini (*Dolichomitus*) stabilise the ovipositor by positioning it in a special groove at the base of the hind coxae (Figs. 6.1h and 6.4e, g). In the case of Acaenitinae, a stabilisation role is played by the enlarged hypopygium (Fig. 6.1d), which reduces the effective length of the ovipositor by a factor of about two. Species with shorter ovipositors, or those associated with a host occupying a softer substrate such as bracket fungi, manage without additional stabilisation (Fig. 6.4d).

Although it is not well studied in saproxylic parasitoids, it is known that some species are able to steer the distal part of the ovipositor through fissures as an adaptation to reach their host in its galleries. The mechanism for this is similar to a bimetallic strip, i.e. the shortening of one side causing bending of the ovipositor to the shorter side. The effect is achieved with the help of various modifications of the valves such as swollen parts, scarped butts and notches which work as the valves are moving.

Another function of the ovipositor that is provided by sense organs on the tip is to locate the host in the substrate and assess whether it is acceptable for ovipositing.

The next task for the ovipositor is to temporarily paralyse or kill the host by injecting venom. Most probably the saproxylic host larva is not indifferent to what is going on and is able to escape or defend itself by trying to bite the emerging ovipositor tip, as has been observed in the case of *Diprion* sp. sawfly larvae attacked by the cryptine *Agrothereutes adustus* (Gravenhorst) (Hilszczański, pers. obs.).

The last thing is to lay an egg. Saproxylic parasitoids typically have long highly elastic eggs which are able to pass along the thin egg canal of the ovipositor. The inner walls of the ovipositor are equipped with ctenidia-like microsculpture to drag the chorion of the egg down it.

6.4.3 Emergence from Dead Wood

Newly hatched saproxylic parasitoid adults have to egress from the substrate, which usually involves passing a certain distance through wood or bark. They have to chew their way out, which is made easier by having the chisel-like mandibles found in several groups (Fig. 6.2e). Mandibular teeth are hardened by zinc- or manganese-protein complex (Quicke et al. 1998). While chewing their way out, it is important to get sufficient purchase, and many saproxylic parasitoids have evolved a variety of spines and ridges on the head and mesosoma (Fig. 6.1a, b, c, e) and pegs or spines on legs. The characteristic set of spines located on the head of stephanids and orussids is called the ocellar corona (Fig. 6.1a, c) (Vilhelmsen 2011).

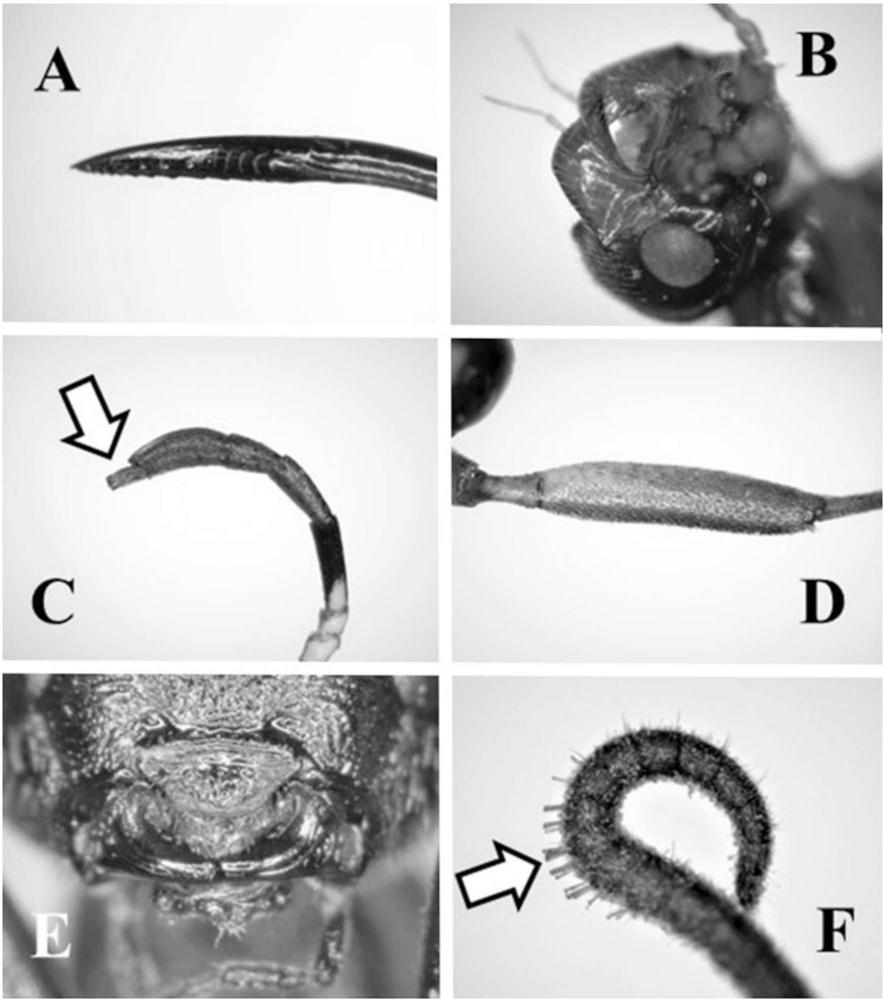

Fig. 6.2 Morphological features of saproxylic parasitoids. (**a**) *Dolichomitus* sp. tip of the ovipositor; (**b**) *Cosmophorus regius* Niezabitowski strong mandibles for keeping adult host; (**c**) *Orussus abietinus* (Scopoli) antennal hammer; (**d**) *Xorides irrigator* (F.) swollen front tibia; (**e**) *X. irrigator* chisel-like mandibles; (**f**) *X. propinquus* (Tschek) antennal hammers (peglike setae) (Photos by Jacek Hilszczański)

Some species have a strongly dorsoventrally depressed body, such as *Aplomerus* sp., *Xorides gracilicornis* (Gravenhorst), *X. depressus* (Holmgren) (Xoridinae) and *Chartobracon* (Braconinae) (Fig. 6.5f). This is most probably an adaptation to move in host galleries or under the loose bark of infested trees.

An exceptional group of saproxylic parasitoids are species attacking adult beetles living under bark. Those species have special adaptations to handle the host, for example, strong mandibles with which they can grasp the host while ovipositing, as in the case of *Cosmophorus regius* Niezabitowski (Euphorinae) (Fig. 6.2b).

6.5 Saproxylic Parasitoids Have to Be Patient and Precise: The Case of *Doryctes leucogaster* (Nees) (Doryctinae, Braconidae)

Doryctes leucogaster is a common idiobiont, ectoparasitoid of larvae of wood-boring beetles. It is recorded to parasitise numerous species of families Cerambycidae, Buprestidae and Anobiidae in both coniferous and deciduous woody species. Records of the species from lepidopterans or phytophagous beetles are most probably mistakes (Yu et al. 2012). The larva of House borer *Hylotrupes bajulus* (L.) (Cerambycidae) is a typical host of the parasitoid. During summer 1995, I made careful observations of the behaviour of several female *D. leucogaster* individuals staying on common fir beams heavily infested by house borer larvae on the roof construction of a barn.

The first specimens of *D. leucogaster* on roof beams were observed on the 25th of June, but I was able to make observation of searching and ovipositing behaviour only between the 5th and 11th of August of the same year. Individuals of the parasitoid were concentrated on a single beam about 2 m in length and about 18 cm in diameter. There were permanently 3–8 specimens (max. 5♀♀ and 3♂♂) of *D. leucogaster* around the beam. During that time no courtship or any signs of feeding was observed. Adults are very slow and especially females stay motionless sometimes for many hours. Searching for host larvae takes the female a very long time, and they move slowly for 2–3 cm and then stand still. They could move from time to time practically 24 hours a day but the highest activity takes place in the evening (17:00–19:00). There is no doubt that the females are able to feel vibrations made by house borer larvae during feeding. The sound made by these larvae is very well audible even for humans. Those vibrations most probably provide great information for the parasitoid female on the size of the host, its location and its viability (Quicke 2015). Females move with widely splayed antennae and hind legs, which takes them sometimes hours. In this species no vibrational sounding (drumming by antennae) was observed. After finding the appropriate place, the female starts to turn in a circle. It looks as though the female searches for the best place (coordinates) indicated by vibrational information and received by the tips of antennae and hind legs. Dry beams have plenty of pores, so there is no problem for the female to position her ovipositor in an appropriate place and launch the process of "drilling". While drilling, female moves her abdomen on her sides which makes the stabilised ovipositor by enlarged hypopygium turn. At the same time the female moves her ovipositor upwards and downwards. The whole process of drilling takes the female from 1 to 2.5 h, probably depending on the depth at which the host larva is located (usually 0.5–1.0 cm). After finishing drilling, but with the ovipositor still in the wood, the female stands still and looks as though it is waiting for something. Most probably the host larva defends itself by assaulting the emerging ovipositor. This kind of behaviour was observed in the case of *Diprion* larva attacked by parasitoid *A. adustus* (see section on oviposition). A host larva could also escape along the galleries, so the female parasitoid has to wait patiently for the right moment to sting and paralyse the passing larva. Indeed after some time, the female executes a fast movement with her abdomen (stinging) and after a while start to "pump" with her abdomen (egg laying). It takes 7 min from stinging to extraction of the ovipositor. Extraction of the ovipositor lasts just a few seconds. Not all attacks are successful: after opening a gallery in the place of oviposition in three cases, I did not find any larvae. Only once was I able to find a motionless paralysed larva. Females oviposit more or less in the same place several times, which means that the same female, or perhaps another one, tries to parasitise the same unparasitised host larva a few times. The first naturally dying female was observed on the 11th of August. On the barn beam *D. leucogaster* had competition from other species of parasitoids such as *Rhoptrocentrus piceus* Marshall, *Spathius curvicaudus* Ratz., *S. rubidus* (Rossi) and *Helcon redactor* Thunberg (Braconidae), but those species were much more actively moving and flying around and were difficult to observe for a long period.

6.6 Diversity of Saproxylic Parasitoids, with a Brief Overview of Major Families

Although many hymenopteran families are likely to include saproxylic members, the ecology of this fauna remains poorly characterised outside Europe and other well-studied temperate zones. In the following sections, I review families known to contain saproxylic species in Holarctic forests. These taxa were targeted specifically because of their known importance as parasitoids of typically wood-living insects including certain forest pests such as woodborers. Although not specifically addressed below, it should be noted that many other families of hymenoptera include saproxylic members in forests throughout the world, including the extremely diverse superfamily Chalcidoidea.

6.6.1 Ichneumonidae

6.6.1.1 Acaenitinae

Members of this subfamily are typically large koinobiont endoparasitoids, often rare in collections. Their biology is poorly known except for the Palaearctic non-saproxylic *Acaenitus dubitator* (Panzer) (Shaw and Wahl 1989) and *Coleocentrus excitator* (Poda) which was investigated by Kinelski (1964). *C. excitator* is an endoparasitoid of cerambycid larvae, mainly *Corymbia rubra* L., living in the dead wood of pine and very often in pine stumps infested by the cerambycid where Kinelski found many of them parasitised by *C. excitator*. Most acaenitines have a long ovipositor which they stabilise during oviposition using the enlarged hypopygium (Fig. 6.1d).

6.6.1.2 Xoridinae

This is a subfamily of idiobiont ectoparasitoids of larvae and pupae of wood-boring beetles (Fig. 6.3f). Species of *Xorides* (Fig. 6.4a, c), *Odontocolon* (Fig. 6.4f), *Ischnoceros* and *Aplomerus* are recorded in woody substrates infested by cerambycids, buprestids or anobiids (Hilszczański 2002). It is often possible to recognise these species by the shape and colour of their characteristic cocoons (Fig. 6.3a–e). Most species are usually solitary, but *Ischnoceros rusticus* (Geoffroy) have been found to be normally gregarious (Fig. 6.3b). Records of xoridines from wood wasps are doubtful and require confirmation. Xoridines use vibrational sounding when searching for host larvae. Females possess peg-like setae on subterminal segments of the antenna (Fig. 6.2f) which are cuticular structures used to transmit vibrations to the substrate (Quicke 2015). The swollen front tibia (Fig. 6.2d) of females contains a vibration-detecting subgenual organ. Egression out of the wood is made easier by having chisel-like mandibles (Fig. 6.2e).

6.6.1.3 Rhyssinae

This is one of the best known groups of parasitoids, represented by large (often reaching 5 cm in length with ovipositors up to 10 cm) easily noticeable species with striking coloration as in *Rhyssa* and *Megarhyssa*. Rhyssines are idiobiont ectoparasitoids of wood wasps (Siricidae and Xiphydriidae). They are able to detect the presence of infested trees through volatiles from the fungal symbiont of the host larvae (Madden 1968). Rhyssines are used as control agents of invasive siricids in coniferous plantations in Australia and New Zealand (Heatwole et al. 1962). On the same host siricid, *Tremex columba* (L.), three species of rhyssines exhibit niche partitioning driven by ovipositor length (Gibbons 1979). Males of rhyssines often aggregate in the place where a female is about to emerge. In *Megarhyssa*, males have long, slender abdomens which enable them to reach the female and copulate prior to her complete emergence. Rhyssines have developed various adaptations for ovipositing in and emerging from woody substrates, such as ridges on the mesosoma and grooves for stabilising the ovipositor on sternites and hind coxae (Fig. 6.1e, g, h).

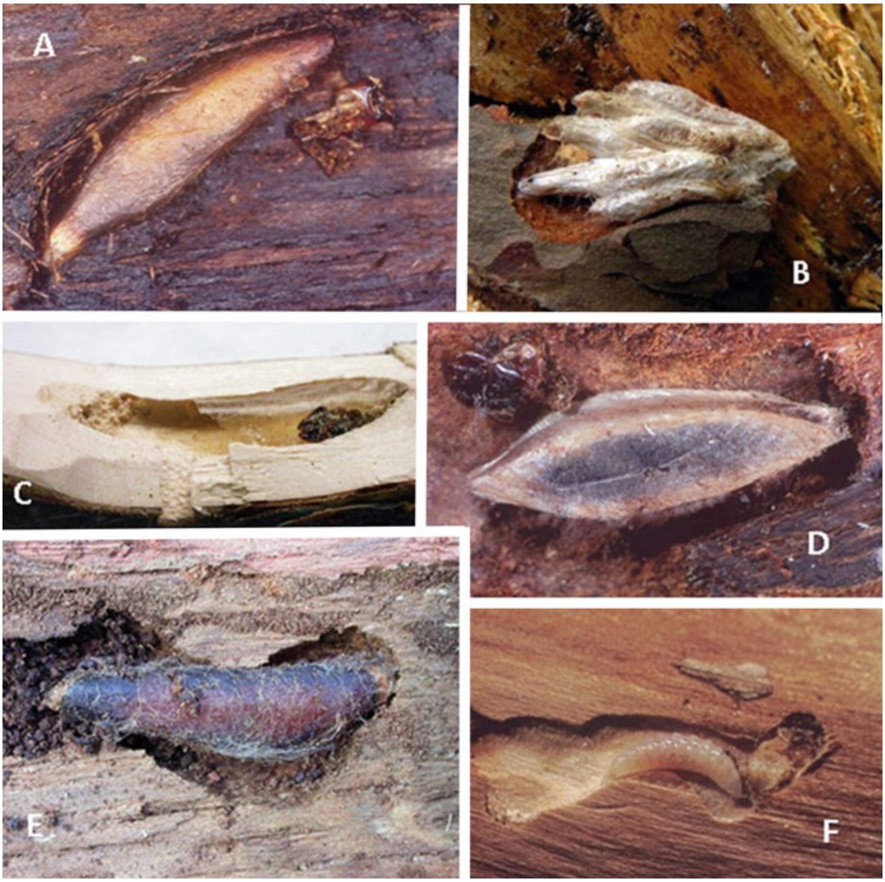

Fig. 6.3 Various cocoons of Xoridinae (Ichneumonidae). (**a**) *Xorides indicatorius* (Latreille); (**b**) *Ischnoceros rusticus* (Geoffroy); (**c**) *X. fuligator* (F.); (**d**) *I. caligatus* (Gravenhorst); (**e**) *X. filiformis* (Gravenhorst); (**f**) *X. praecatorius* (F.) larvae near host remains before spinning up cocoon (Photos by Jacek Hilszczański)

6.6.1.4 Labeninae

This is a small subfamily comprising parasitoids of wood-boring Coleoptera and siricid wood wasps. Similarly to rhyssines some species of labenines, such as *Apechoneura* sp., have adaptations for parasitising hosts concealed in the wood, such as ridges on the mesosoma and grooves on the hind coxae for stabilising the ovipositor (Gauld and Wahl 2000).

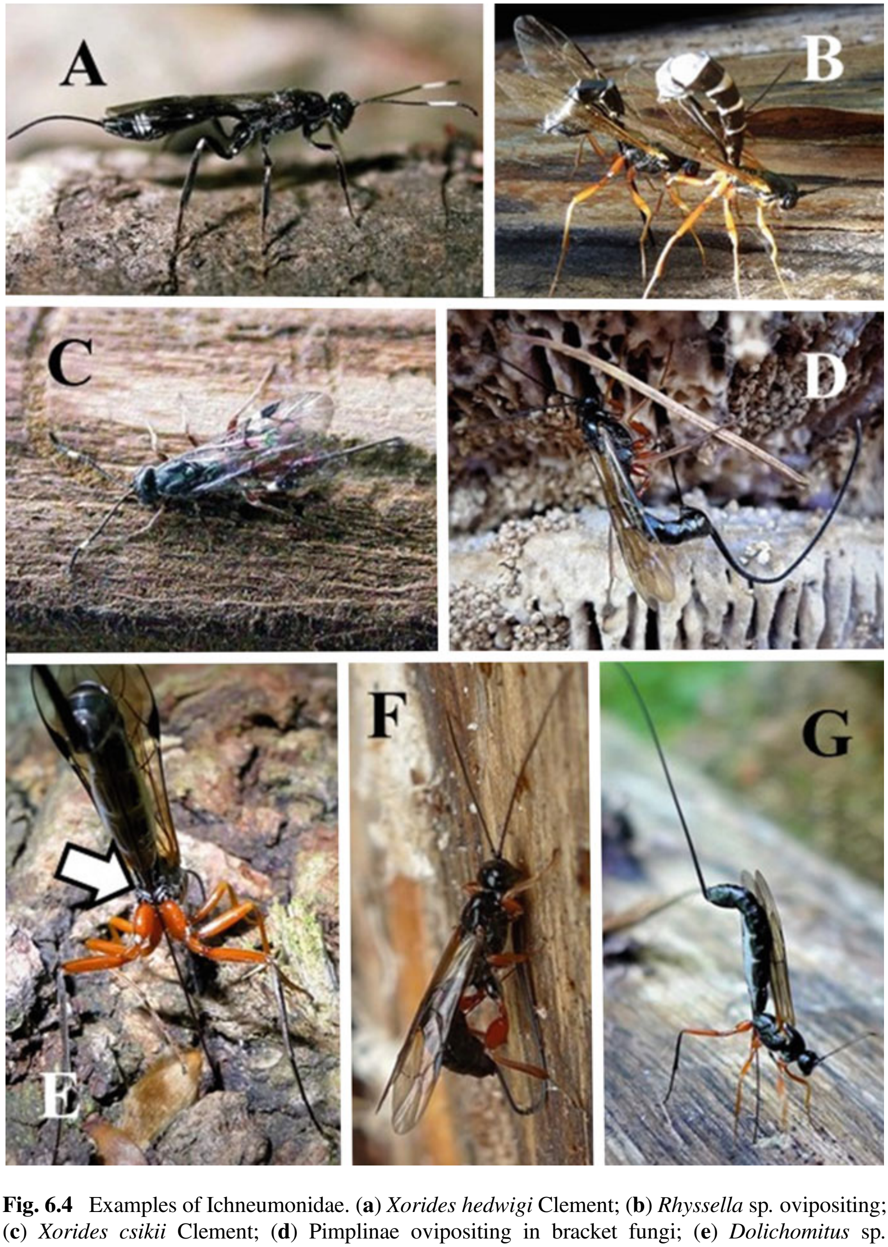

Fig. 6.4 Examples of Ichneumonidae. (**a**) *Xorides hedwigi* Clement; (**b**) *Rhyssella* sp. ovipositing; (**c**) *Xorides csikii* Clement; (**d**) Pimplinae ovipositing in bracket fungi; (**e**) *Dolichomitus* sp. ovipositing keeping and stabilising ovipositor with the help of grooves on the base of hind coxae; (**f**) *Odontocolon dentipes* (Gmelin) ovipositing; (**g**) *Dolichomitus* sp. ovipositing (Photos by Jacek Hilszczański)

6.6.1.5 Poemeniinae

These are idiobiont ectoparasitoids of insects living in concealed places, such as beetle larvae (*Deuteroxorides*, *Neoxorides*, *Cnastis*, *Podoschistus*) or solitary wasps (*Poemenia*). Some species have evolved adaptations for emerging from the substrate, such as ridges on the head (Fig. 6.1b). The sister group for other poemeniines, *Pseudorhyssa* spp., are kleptoparasitoids of *Rhyssa* and *Rhyssella* (Rhyssinae) (Fig. 6.4b).

6.6.1.6 Pimplinae

Some genera of this large subfamily, such as *Dolichomitus* and *Ephialtes*, utilise saproxylic hosts (Fitton et al. 1988). All species are idiobiont ectoparasitoids of larvae and sometimes pupae of insects living in wood, mainly beetles but sometimes also wasps nesting in wood, as in the case of *Ephialtes* sp., or in bracket fungi (Fig. 6.4d). These species typically have very long ovipositors reaching sometimes six to eight times the length of the body as in the case of the Holarctic *Dolichomitus cephalotes* (Holmgren) or Peruvian *D. hypermeces* Townes. Some of these parasitoids are able to stabilise the ovipositor by locating it in the base of hind coxae (Fig. 6.4e, g).

6.6.1.7 Cryptinae

This is a large subfamily of mostly idiobiont ectoparasitoids. Some species, such as *Echthrus* sp., *Helcostizu*s or *Stenarella*, are related to hosts living in wood. *Cryptus genalis* Tschek is known to parasitise pupal chambers of cetonid beetles living in tree cavities (Schwarz et al. 2013).

6.6.1.8 Campopleginae

This large subfamily is related mostly to lepidopterans and sawflies; however, species of *Pyracmon* and especially *Rhimphoctona* are important parasitoids of wood-boring beetle larvae (Luo and Sheng 2010). Campoplegines are koinobiont endoparasitoids.

6.6.2 Braconidae

6.6.2.1 Braconinae

This is one of the biggest subfamilies of braconids. All the saproxylic braconine species are idiobiont ectoparasitoids. Many species are effective enemies of economically important pests, such as *Coeloides* sp. (Fig. 6.5a), *Atanycolus* sp. and some *Bracon* sp. (Fig. 6.5e) parasitoids of bark beetles and other phloem feeders. Some species are very flat and produce flat cocoons as adaptations to the restricted space under loose bark (Fig. 6.5d, f).

6.6.2.2 Doryctinae

This is a very large cosmopolitan subfamily with many genera and species that utilise saproxylic hosts. Doryctines are idiobiont ectoparasitoids that are usually solitary but sometimes gregarious [e.g. *Doryctes*, *Spathius*, *Heterospilus*, *Jarra* and *Gildoria* (Fig. 6.5b)] (Shaw and Huddleston 1991). Some target important pests such as *Spathius agrili* Yang, a parasitoid of emerald ash borer (*Agrilus planipennis* Fairmaire); *Ontsira mellipes* (Ashmead), a parasitoid of the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) (Golec et al. 2017); or *Syngaster lepidus* Brullé and *Jarra* sp., parasitoids of eucalypt borers *Phoracantha* sp. The last two species partition the larval resource based, in part, on bark thickness and size of the host; solitary *Syngaster* prefers smaller larvae located deeper in the substrate, whereas gregarious *Jarra* targets bigger larvae closer to the surface (Paine et al. 2000). The gregarious *S. agrili* have been found to rely on host vibration during host location, and immobile hosts, including already parasitised ones, are not attacked. Females of this species lay about 23 eggs, and there are 5 larval instars (Wang et al. 2010). Males of some species, such as *Dendrosoter* sp., aggregate in places where they are able to locate a female before she emerges from the substrate (Fig. 6.5c).

6.6.2.3 Rhyssalinae

The biology and host associations of this subfamily remain poorly known. *Histeromerus mystacinus* Wesmael is an interesting gregarious ectoparasitoid (up to 47 larvae on 1 host larva) which parasitises larvae, pupae or prepupae of wood-boring beetles (mainly cerambycids and burpestids). Females reach the host by digging through the substrate with the help of strong mandibles and spinose front tibiae. After paralysing the host, the female exhibits a form of parental care, remaining close to its developing brood (Shaw 1995). Species of *Dolopsidea* are also associated with dead trees although the hosts targeted by this genus remain unclear (Shaw 1993).

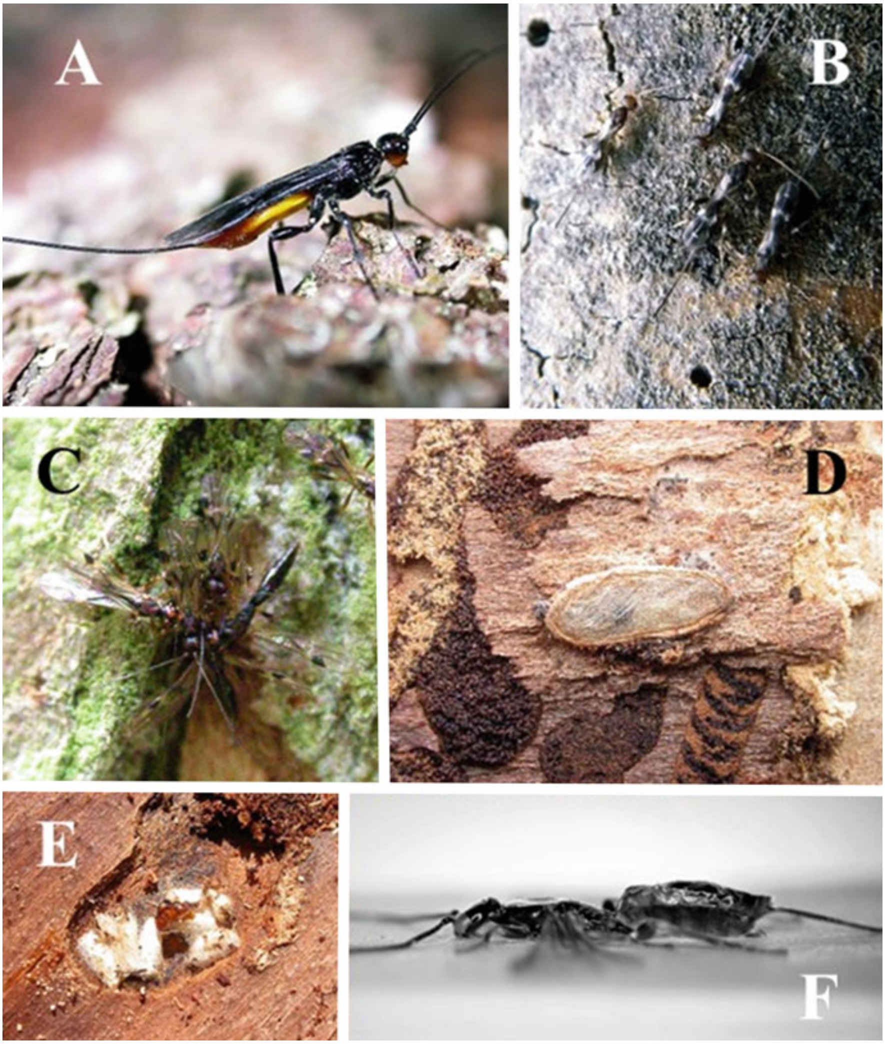

Fig. 6.5 Examples of Braconidae. (**a**) *Coeloides* sp.; (**b**) *Gildoria* sp. females gathering in a good place for ovipositing; (**c**) *Dendrosoter* sp. aggregation of males where a female is about to emerge; (**d**) *Coeloides* sp. flat cocoon under the bark; (**e**) *Bracon* sp. gregarious brood with remains of the host; (**f**) *Chartobracon huggerti* van Achterberg strongly depressed body (Photos by Jacek Hilszczański)

6.6.2.4 Helconinae

Koinobiont endoparasitoids comprising relatively big parasitoids of larvae of woodboring beetles (Cerambycidae, Buprestidae). Some species are important enemies of common woodborers such as *Helconidea dentator*, a parasitoid of larvae of *Tetropium* sp. (Kenis and Hilszczanski 2004).

6.6.2.5 Cenocoeliinae

This is a small mainly tropical subfamily of koinobiont endoparasitoids. Cenocoeliines parasitise larvae of wood-boring beetles living usually in thin twigs, and probably because of that these parasitoids have the metasoma inserted high on the propodeum as in *Lestricus secalis* (L.) common parasitoid of *Pogonocherus* sp. (Cerambycidae) larvae in Central European pine forests (Hilszczański 1998). The species very often exhibit a special groove for stabilising the ovipositor on the inner side of the hind coxae, similar to aulacids.

6.6.2.6 Euphorinae

This subfamily of parasitoids develops as koinobiont endoparasitoids of adult insects, in the case of saproxylic ones (*Cosmophorus*, *Cryptoxilos*, *Ropalophorus*), mainly on adults of bark beetles. *Cosmophorus* females grasp the host beetle with their enlarged mandibles (Fig. 6.2b) while temporarily paralysing it and ovipositing. Some species of the genus *Meteorus* are recorded from larvae of saproxylic beetles belonging to the families Melandryidae, Erotylidae, Biphyllidae, Cerambycidae, Ciidae and Scolytinae (Huddleston 1980; Tobias 1986). *Meteorus corax* Marshall has been often collected in traps mounted on dead spruce trees (Hilszczański, pers. obs.) and recorded presumably as parasitoid of cerambycids larvae or more probably of *Pytho depressus* L. (Coleoptera: Pythidae) (Martikainen and Koponen 2001).

6.6.3 Aulacidae

Found worldwide, this small family of koinobiont endoparasitoids mostly parasitises the larvae of wood-boring Coleoptera. A single species of *Aulacus* is known to parasitise wood wasp larvae of the family Xiphydriidae. Two worldwide genera are known: *Aulacus* and *Pristaulacus* (Fig. 6.6f). Females are able to lay eggs in hard wood using their long ovipositor which is stabilised by locating it in special grooves on the hind coxae (Fig. 6.1f). In the case of *Aulacus* parasitising Xiphydria, the female threads her ovipositor down the drill shaft made by the female *Xiphydria* and oviposits into the group of host eggs.

6.6.4 Ibaliidae

This small family of koinobiont endoparasitoids represents an exceptional group within Cynipoidea parasitising larvae of siricids in coniferous and deciduous trees. *Ibalia* (Fig. 6.6e) has been introduced to South America, Australia and New Zealand

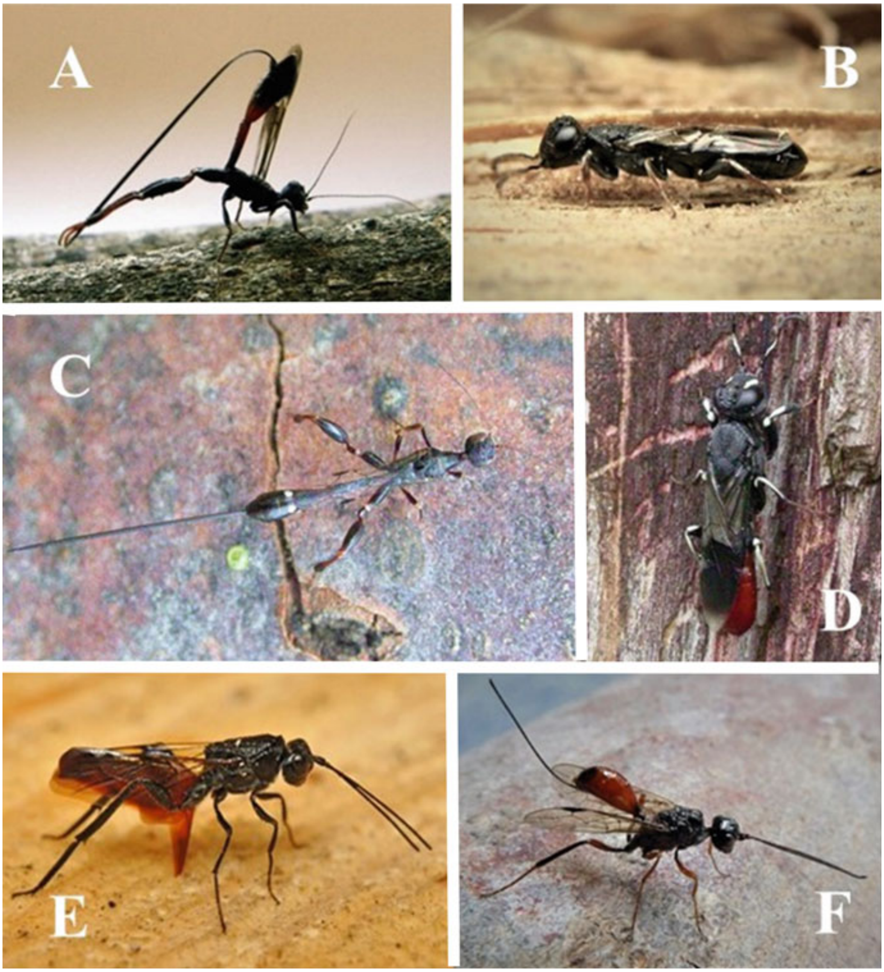

Fig. 6.6 Examples of various families. (**a**) *Stephanus serrator* (F.) (Stephanidae) cleaning ovipositor; (**b**) *Orussus moroi* Guiglia (Orussidae); (**c**) *Foenatopus turcomanorum* (Semenov) (Stephanidae); (**d**) *Orussus abietinus* (Scopoli) (Orussidae); (**e**) *Ibalia* sp. (Ibaliidae) ovipositing; (**f**) *Aulacus striatus* Jurine (Aulacidae) (Photos **a**–**d**, **f** by Jacek Hilszczański, **e** by Jacek Nowak)

to control introduced Siricidae infesting pine wood (Cameron 2011). The most distinct features of ibaliids are their strongly laterally compressed gaster and a series of transverse ridges on the mesosoma. Females possess a hypopygium used to stabilise the ovipositor during wood penetration (Fig. 6.6e).

6.6.5 Stephanidae

Stephanids (Fig. 6.6a, c) comprise a small cosmopolitan family occurring mostly in tropical and subtropical forest ecosystems where these idiobiont parasitoids are associated with wood-boring beetles. *Schlettererius cinctipes* (Cresson) is known to parasitise *Sirex noctilio* F. (Siricidae) and was introduced as a control agent to Australia and Tasmania (Hong et al. 2011; Collett and Elms 2009). Stephanids have characteristic ocellar coronae which helps them to emerge from wood (Fig. 6.1c). They also bear modified hind legs with subgenual organs which in some species play an important role in host vibration detection (Vilhelmsen et al. 2008). Hind legs have a swollen femur that has large teeth on the underside. The role of the teeth is unknown although it could also be related to emergence from the wood.

6.6.6 Orussidae

This is a basal group of saproxylic parasitoids, the sister group of Apocrita, (Vilhelmsen 1997, 2003) (Fig. 6.6b, d). Utilising hosts living deep in wood, e.g. buprestid larvae, orussids possess ovipositors that are several times the length of the body. The ovipositors extend all the way into the prothorax, where they are coiled before extending posteriorly to lie between the third valvulae distally. The ovipositors lie in a membranous sac attached posteriorly to the proximal parts of the ovipositor apparatus and the posterior margin of sternum 7 (Vilhelmsen et al. 2001). Orussids search for host larvae by using vibrational sounding. To make vibrations they use special antennal hammers (Fig. 6.2c). Emergence from wood is facilitated by special spines located around the ocelli on the head, called the ocellar corona (Fig. 6.1a). Adult orussids are able to jump, which is probably an effective method to escape from predators.

6.7 Habitat Requirements

Habitat requirements of saproxylic parasitoids have been investigated only sporadically, except for some particular species which are considered to be important enemies of saproxylic pests, especially bark beetles (Kruger and Mills 1990). Recently some research has been done on that issue, especially in the boreal forests of the Northern Hemisphere (Gibb et al. 2008; Hilszczański et al. 2005; Jonsell et al. 1999; Komonen et al. 2000; Stenbacka et al. 2010) and temperate forests of North America (Ulyshen et al. 2011). Most saproxylic parasitoids are completely unknown concerning their host associations, which is especially typical for tropical species. Even for well-studied Holarctic species, host records are often of unknown reliability or based on mass rearing efforts that provide no insight into habitat associations (Kenis and Hilszczanski 2004).

Being at a high trophic level, parasitoids often depend on unreliable resources. Many species of saproxylic parasitoids are specialised, which is especially the case in koinobiotic endoparasitoids (see koinobionts vs. idiobionts), and in general more specialised species are more sensitive to changes in the trophic level on which they depend (Shaw and Hochberg 2001). Parasitoids appear to be more affected by landscape structure than their hosts, probably because of poor dispersal capacity (Weslien and Schroeder 1999; Jonsell et al. 1999). This diverse group of highly specialised insects may act as much better indicators of quality and continuity of woody resources than their hosts. Despite their potential to inform conservation efforts, parasitoids have been mostly neglected due to their largely unknown ecology (Shaw and Hochberg 2001).

Studies in boreal forests (Hilszczański et al. 2005; Hedgren 2007; Gibb et al. 2008; Stenbacka et al. 2010) clearly showed that forest management history (managed vs. reserve) and substrate posture have a distinct impact on the species assemblage of saproxylic parasitoids. Snags or standing dead trees host a distinctive assemblage of parasitoids and usually support higher numbers than prostrate logs (Ulyshen et al. 2011). Snags are preferred and exclusively inhabited by many species associated with common cerambycids and other wood borers. Also communities associated with the upper parts of standing trees and crowns of snags are different in this respect from those in lower parts of snags (Ulyshen et al. 2011). These results indicate the importance of creating a diversity of potential dead wood habitats in managed forests, including retaining entire snags during harvest operations. It is known that the location of the appropriate habitat usually occurs first in the sequence of host searching behaviour in parasitoids (Quicke 1997) which implies that the type of substrate (standing vs. on the ground) may be especially important for highly selective species.

Saproxylic parasitoids clearly differ in their ability to utilise particular wood substrates as determined by the presence and accessibility of suitable hosts. For example, cenocoelines such as *Cenocoelius analis* (Nees) or *Lestricus secalis* (L.) are exclusively associated with specific cerambycid hosts within the thin twigs of coniferous and deciduous trees, respectively. On the other hand, parasitoids such as *Ischnoceros caligatus* (Gravenhorst) (Xoridinae) attack many species of cerambycid larvae, regardless of the size and kind of host tree (Hilszczański, pers. obs., 1998; Yu et al. 2012). *Histeromerus mystacinus* Wesmael is adapted to search for cerambycid larvae digging through their galleries and has been known to attack several species, mostly larvae of big lepturines like *Leptura scutellata* F., *L. aurulenta* F. and *L. thoracica* Creutzer (Shaw 1995; Yu et al. 2012; Hilszczański, pers. obs.). Because of this, *H. mystacinus* is looking for big woody substrates preferred by its hosts. Many parasitoids are restricted by the length of the ovipositors, being unable to reach larvae deep within wood or beneath thick bark. Mancini et al. (2003), for example, found *Caenopachys hartigii* (Ratzeburg) (Braconidae, Doryctinae) to be restricted to twigs less than 7 cm in diameter as bark was otherwise too thick for the wasps to reach the bark beetle larvae concealed underneath.

Some parasitoids are also well adapted to clear-cuts, while others are associated only with older successional stages of forest. Koinobionts appear to be generally more abundant in forests than on clear-cuts, while the opposite pattern was found for idiobionts (Hilszczański et al. 2005). Idiobionts are not so closely restricted to particular hosts and thus usually have more potential hosts and at the same time tend to be less restricted in habitat selection. Saproxylic koinobionts, being endoparasitoids, are usually more specialised than idiobionts and are adapted to stable habitats where the hosts are not as affected by disturbances of the kind often seen in late succession habitats. In some forest habitats such as tree plantations, where hosts are especially abundant, koinobionts can become more common (e.g. *Ibalia* in Australian pine plantations, Carnegie et al. 2005).

Some parasitoids might be more substrate-specific than their hosts, as has been shown for some species in boreal forests. For example, *Helcon dentator* F. (Braconidae, Helconinae), a parasitoid of *Tetropium* sp. (Cerambycidae), was absent at experimental sites lacking snags, even though its host was present in other substrate types (Hilszczański et al. 2005). Saproxylic parasitoids may act as important early indicators of changes in woody resource availability, which could affect saproxylic biodiversity. One can conclude that the different tree species, stand types and types of dead wood are complementary in the composition of saproxylic parasitoid assemblages but that none hold a complete diversity of them. Thus, the full range of successional stages has to be retained to help conserve the entire saproxylic parasitoid community.

6.8 Conclusions

Saproxylic parasitoids are well recognised taxonomically, especially in temperate and boreal zones. Also the host associations of many species are known, even though a considerable part of that is still based on mass rearings and incorrect conclusions as to the correct host identity are quite common. There is still a big need to improve our knowledge on the habitat requirements of many saproxylic parasitoids. The tropical fauna in this respect is almost completely unknown. At the same time, many behavioural adaptations, and the role of physiological and morphological features of saproxylic parasitoids, remain unstudied.

There is no doubt that if we know so little about host relationships and habitat requirements of most of the saproxylic parasitoid fauna, it is impossible to anticipate what effects the loss of habitats would bring, especially in tropical forests for certain groups or species of parasitoids. It follows that, until much more knowledge is obtained, it is very difficult to imagine any system of nature protection which would take the requirements of these remarkable insects properly into consideration.

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Chapter 7
Saproxylic Bees and Wasps

Petr Bogusch and Jakub Horák

Abstract Bees and wasps are usually known to occur in open habitats, with most species recorded from sand, loess, and open rock biotopes. Although most species nest underground (45% of the fauna of the Czech Republic), followed by parasitic species (31%), many species from various groups use dead wood for nesting. Of the group of species nesting in various cavities (21% of all species), one quarter is represented by species highly preferring cavities in dead wood. These species, especially of the families Crabronidae, Vespidae, and Megachilidae, are real saproxyles, as are also many members of the families Chrysididae, Sapygidae, Tiphiidae, and Scoliidae. The European honeybee is also saproxylic, with its preference for cavities in tree trunks for nesting, as well as several species of bumblebees. Dead wood is the most important building material used by many wasps and paper wasps for making nests. Saproxylic bees and wasps are endangered due to the loss of old trees, as well as due to the removal of dead wood. We can support saproxylic hymenopterans in forests by retaining standing dead trees and other forms of sun-exposed dead wood. In urban or residential environments, populations of these insects can be supported using insect hotels and other types of artificial nests.

7.1 Introduction

Aculeate hymenopterans (Hymenoptera: Aculeata), and, namely, bees and wasps, are quite numerous members of saproxylic insect communities that inhabit a range of dead wood habitats. The number of studies on saproxylic bees and wasps remains rather low despite the diversity and ecological importance of these insects. Studies

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on bees are largely focused on their importance as pollinators (e.g., Klatt et al. 2014), and wasps are mainly studied as important predatory taxa (e.g., Schenk and Bacher 2002). Currently, there is particular interest in better understanding the habitat requirements of bees given global declines in pollinator communities (Potts et al. 2010; Burkle et al. 2013). Because many bees move readily between different habitats, the conservation of bees in forests can be expected to benefit agricultural production (Taki et al. 2011; Blitzer et al. 2012; Monasterolo et al. 2015). Despite growing recognition that forests provide important habitats for bees and wasps and that these insects are sensitive to management decisions (Hanula et al. 2016), few specific guidelines have been developed for the saproxylic members of these groups. In this chapter we provide an overview of saproxylic Aculeata. Focusing on the well-known fauna of the Czech Republic, we discuss the biology and habitat associations of these insects and end by briefly discussing implications for conservation.

As recently reviewed by Russo (2016), another globally relevant issue concerning saproxylic bees and wasps involves their intentional or unintentional (~73% of non-native species) movement through international trade and travel. Overall, 69% of non-native species, including 77% of those introduced unintentionally, nest in wood or other cavities. Once introduced into a new area, these insects can have major impacts on ecosystems. Negative impacts can include competition with native bee species for floral or nesting resources, introduction of diseases, pollination of invasive plants, and changing the structure of pollination networks (Russo 2016). On the other hand, positive impacts of non-native bees can include improved pollination of agricultural crops and increased resilience of ecosystems impacted by human activities or climate change (Russo 2016). In many cases, introduced bees can have both positive and negative effects. Honeybees (*Apis* spp.) are not native to North America, for example, but are now considered to be incredibly important to agricultural production. At the same time, however, there is some concern that the large honeybee colonies can result in large reductions in local floral resource availability, thus negatively impacting native bee populations (Cane and Tepedino 2016).

7.2 Knowledge About Saproxylic Bees and Wasps

Although saproxylic bees and wasps were not much studied as a community in the past, insights can be gained from published life history information on individual species that have some relationship to dead wood. An example is the review of contemporary knowledge of carpenter bees (genus *Xylocopa* Latreille, 1802) in North America. Ackerman (1916) cited that the eastern carpenter bee, *Xylocopa virginica* (Linnaeus, 1771), was frequently found nesting in the railings of porches, in posts, rafters, doors, palings of fences, door frames, or window sills, which classifies this species among the saproxylics in the current classification. However, this information is outdated, and if we would like to know more about the relationship of saproxylic bees and wasps to the environment, the studies have to be designed regarding this aim. Malyshev (1935) and Krombein (1967) have published the most comprehensive studies on bees and wasps nesting in cavities. Both of these studies are very useful, but much more work is needed to fully understand the habitat requirements of these species.

The number of studies on saproxylic bees and wasps appears to be slowly increasing over time, both in Europe and in other parts of the world. In Europe, the development of the European Red List of Bees (Nieto et al. 2014), which will probably be followed by the red list of other aculeate hymenopterans in the near future, will greatly advance efforts to conserve this fauna. Presently, it is known that one of the important factors for the survival of saproxylic bees in forests and similar habitats is the retention of standing dead wood (Westerfelt et al. 2015), which is corroborated by findings from other regions including the tropics (Thiele 2005). On the other hand, most studies dealing with bees and wasps include them as a part of multi-taxa investigations. Furthermore, these insects are sometimes predicted to be saproxylic based on passive trapping (e.g., flight intercept traps) in forests (Sebek et al. 2016) or from the emergence of individuals from wood (Horák et al. 2014).

On the one hand, it is understandable that bees and wasps have not been the main focus of many studies on saproxylic insects as their foraging strategies are very complex and difficult to catch and their identification is often difficult. On the other hand, it is quite surprising this fauna has received so little attention, particularly given the immense importance of pollinators, including the European honeybee, which is itself saproxylic. Indeed, the specific tradition of beekeeping in artificial tree cavities underscores the importance of dead wood habitats to honeybees and to pollination more broadly (e.g., Horák et al. 2012; Oleksa et al. 2013; Tofilski and Oleksa 2013). Moreover, beetles are the most studied saproxylic insects; thus, from this point of view, it is also important that the interaction between saproxylic bees and beetles might be found in the nature. Many cavity-nesting bees and wasps in forests utilize the galleries created by wood-boring beetles, for example (Westerfelt et al. 2015). Other examples include parasitism by species like the skin beetle, *Megatoma undata* (Linnaeus, 1758), in the nests of solitary bees (Steffan-Dewenter and Schiele 2008) or the rove beetle, *Velleius dilatatus* (Fabricius, 1787), which lives only in the nests of the European hornet (*Vespa crabro* Linnaeus, 1758) (Herman 2001).

From this perspective, it can be concluded that the knowledge about saproxylic bees and wasps is still quite limited, but there are many possible approaches for studying them—and some of them appear to belong to the most important research issues (like natural honeybee nesting demands). Because a global review of this topic is beyond the scope of this chapter, we limit our discussion here largely to the situation in the Czech Republic which probably provides an accurate representation of the demands of saproxylic bees and wasps in many temperate landscapes.

7.3 Systematics of Aculeate Bees and Wasps

Bees and wasps, as reviewed in this chapter, are a diverse group of hymenopteran insects, belonging to a monophyletic group, Aculeata, which contains the superfamilies Chrysidoidea, Vespoidea, and Apoidea.

Members of Chrysidoidea are globally classified into seven families and are all parasitic while larvae of most of them live as parasitoids of other insects, usually other bees and wasps. Chrysididae is a particularly important family of parasitoids commonly associated with the nests of saproxylic bees and wasps. Also several species of Bethylidae attack the larvae of saproxylic beetles (Goulet and Huber 1993; Macek et al. 2010; Wiśniowski 2014).

Species of the superfamily Vespoidea are divided into 9–13 families (this group is highly diversified, and the phylogeny is still unclear). While several families are parasitic (Tiphiidae, Mutillidae, Sapygidae, Scoliidae), others include species that provide their nests with paralyzed specimens of invertebrates (Goulet and Huber 1993; Wiśniowski 2009; Macek et al. 2010). Moreover, a variety of nest parasites are known within these (e.g., species belonging to the pompilid genera *Evagetes* Lepeletier, 1845, and *Ceropales* Latreille, 1796, and the vespid genera *Polistes* Latreille, 1802; *Vespula* Thomson, 1869; and *Dolichovespula* Rohwer, 1916 (O'Neill 2001; Macek et al. 2010)). Most species of the subfamilies Polistinae and Vespinae are eusocial (West-Eberhard 1969; Ross and Matthews 1991). Note that ants (Formicidae) are also members of the superfamily Vespoidea, but they are typically studied separately and are not discussed further here (see Hölldobler and Wilson 1994).

The last and most species-rich superfamily, Apoidea, contains many families and is usually divided into two big groups—the Spheciformes (digger wasps) and the Apiformes (true bees). Spheciformes is a paraphyletic group containing four families: Ampulicidae, Heterogynaidae, Sphecidae, and Crabronidae (Blösch 2000; Macek et al. 2010). Ampulicids are ectoparasitoids of cockroaches, while the other three families are usually nest predators of various insects and invertebrates. Several genera contain nest cleptoparasites including, in Europe, *Nysson* Latreille, 1796; *Brachystegus* A. Costa, 1859; and *Stizoides* Guerin-Meneville, 1844 (Blösch 2000; O'Neill 2001; Macek et al. 2010). Apiformes, a monophyletic group (Roig-Alsina and Michener 1993; Hedtke et al. 2013), contains seven bee families: Melittidae, Megachilidae, Apidae, Andrenidae, Colletidae, Stenotritidae, and Halictidae. Bees make nests and feed their larvae with pollen, nectar, and floral oils. Around 20% of bee species worldwide are nest cleptoparasites, and several groups of Apidae and Halictidae are eusocial (Michener 2007).

7.4 Situation in the Czech Republic as an Example

Here we summarize the saproxylic habits of Aculeata known from the Czech Republic. Because this fauna was studied intensively in the 1930s–1950s (Baťa et al. 1938; Zavadil et al. 1937; Kocourek 1966; Wolf 1971) and more recently beginning 1995 (Bogusch et al. 2007; Macek et al. 2010), information on the ecology of nearly all species has been gathered. The diversity of species and their nesting strategies are very high, including many saproxylic taxa (see Bogusch and Straka 2011). Altogether 1305 species are known in the country (more accurately, 1410 species of the Aculeata minus 105 species of Formicidae) according to the newest comprehensive publication—the new Czech Red List (Bogusch and Straka 2017a, b; Straka and Bogusch 2017a, b). In addition to Macek et al. (2010), which provides information on the ecology of many species, we also consulted Wiśniowski (2014) for the ecology of Chrysididae, Wolf (1971) and Wiśniowski (2009) for the ecology of Pompilidae, Blösch (2000, 2012) for the ecology of digger wasps, and Westrich (1989), Amiet and Krebs (2012), and Scheuchl (2016) for the ecology of the bees. Data from several other studies were also used, and they are cited in the appropriate parts of this chapter. In addition, knowledge gained after nearly 20 years of study by the first author was very useful in providing information on saproxylic Aculeata summarized below.

7.5 Nesting Behavior

Many species of the Aculeata do not make nests. Most of them are parasitic—usually parasitoids of other insects (superfamily Chrysidoidea; families Tiphiidae, Mutillidae, Sapygidae, and Scoliidae of the superfamily Vespoidea; and family Ampulicidae of the superfamily Apoidea). Nest cleptoparasites are quite numerous—they form number of species within the bee families Apidae, Megachilidae, and Halictidae; several species are known also within the digger wasp family Crabronidae and spider wasps, Pompilidae. Social parasites are well distributed in the bee family Apidae and the family Vespidae. The overall number of parasitic aculeate hymenopterans is 408 and comprises 31% of all species. Several species of Pompilidae do not build nests but use spider prey's burrows (e.g., *Aporus pollux* (Kohl, 1888); *Aporus unicolor* Spinola, 1808; *Eoferreola manticata* (Pallas, 1771); *Eoferreola rhombica* (Christ, 1791); *Ferreola diffinis* (Lepeletier, 1845); and *Homonotus sanguinolentus* (Fabricius, 1793); Wiśniowski 2009; Macek et al. 2010). Unfortunately, we still do not know the nesting biology of seven rare species. For the main nesting strategies in the Czech Republic, see Fig. 7.1.

Nesting species of bees and wasps make their nests usually as burrows or tracks in many kinds of materials, including dead wood. Most of the species make their nests only in the ground. Ground nesting is typical for some families of bees—Melittidae, Andrenidae, and Halictidae (Westrich 1989; Celary 2005; Scheuchl 2016). In other

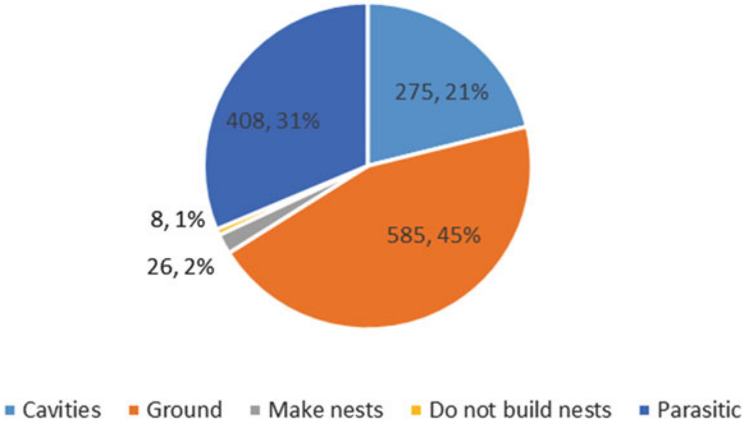

Fig. 7.1 Proportions of life strategies and nesting types among aculeate Hymenoptera in the Czech Republic

families of bees, this type of nesting is also widespread, and in several cases, it is used by majority of the species (Pompilidae, Sphecidae, and Apidae). Thus, nearly half of all aculeate species are ground-nesters (551 species; 45%). A small group of 26 species usually build mud nests on various surfaces. These species often have very predictable habits, e.g., digger wasps of the genus *Sceliphron* make nests of mud on rocks and on and inside the buildings. This behavior facilitated the movement of *S. curvatum* (Smith, 1870) on aircraft from Asia and *S. caementarium* (Drury, 1773) on ships from the USA (Bogusch et al. 2005; Lukáš et al. 2006; Mader 2013).

Altogether 275 species (around 21%) of all Czech Aculeata use various types of cavities for their nesting (Fig. 7.2). Many of these species are facultative saproxylics, making their nests in a wide variety of cavities including those found in dead wood (140 species; 51% of all cavity nesters). The second most numerous group is the group of the main interest of this book—obligate saproxylics, i.e., species that predominantly or only nest in dead wood (82 species; 30%). Only several species are specialized for nesting in various types of galls, usually those of cynipids (e.g., *Pemphredon austriaca* (Kohl, 1888) in galls of *Andricus kollari* (Hartig, 1843) (Blommers 2008)) or frit flies (e.g., *Pemphredon fabricii* (Müller, 1911); *Hylaeus pectoralis* Förster, 1871; and *Stenodynerus clypeopictus* (Kostylev 1940) using galls of *Lipara lucens* Meigen, 1830, and *L. pulitarsis* Doskočil and Chvála, 1971) which was recently described and reviewed by Astapenková et al. (2017). Many species (38.14%) are specialized for nesting in stems and stalks, most of which are specialists of genera known to nest in various cavities including those in dead wood (e.g., *Passaloecus clypealis* Faester, 1947; *Trypoxylon deceptorium* Antropov, 1991; *Crossocerus cetratus* (Shuckard, 1837); *Ectemnius confinis* (Walker, 1871); *Hylaeus moricei* (Friese, 1898); *H. pfankuchi* (Alfken, 1919); *H. rinki* (Gorski, 1852); and others). In addition to dead wood, several species also sometimes use rocks and

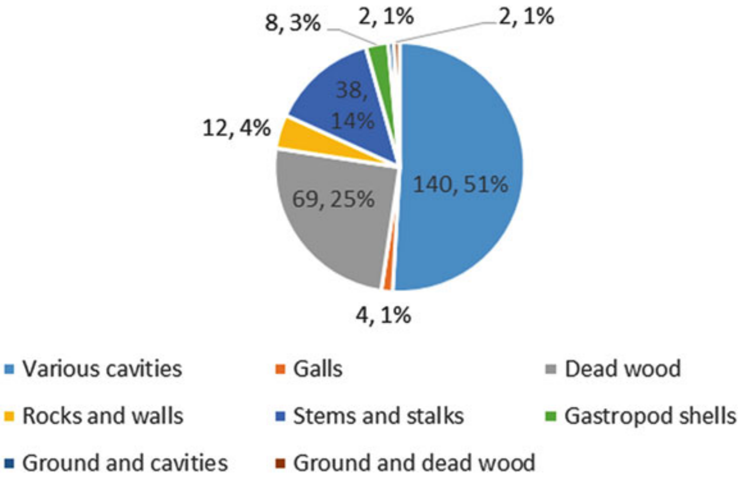

Fig. 7.2 Proportions of cavity-nesting types among aculeate Hymenoptera in the Czech Republic

walls for their nesting (12.4%). This group primarily consists of species from ground-nesting genera, but several other species have also adopted these habits, including several species of the bee genus *Osmia* and spider wasps of the genus *Agenioideus* Ashmead, 1902 (Macek et al. 2010). A small group of eight species (3%), consisting of bees of the family Megachilidae (*Osmia andrenoides* Spinola, 1808, *Osmia aurulenta* (Panzer, 1799), *Osmia bicolor* (Schrank, 1781), *Osmia rufohirta* (Latreille, 1811), *Hoplosmia spinulosa* (Kirby, 1802), *Rhodanthidium septemdentatum* (Latreille, 1809)) and two small solitary wasps (*Leptochilus alpestris* (Saussure, 1855) and *Leptochilus regulus* (Saussure, 1855)) are interesting in that they nest only in empty gastropod shells (Müller 1994; Zurbuchen and Müller 2012). Two species are known to nest in various cavities and in the ground (spider wasps *Anoplius alpinobalticus* Wolf, 1965, and *Anoplius nigerrimus* (Scopoli, 1763)), and two others use dead wood for their nesting, but they also could nest in the ground (digger wasps *Crossocerus distinguendus* (Morawitz, 1866) and *Crossocerus elongatulus* (Van der Linden, 1829); Macek et al. 2010). This is an interesting fact regarding the known specialization of most species belonging to this group.

7.6 Relationship with Dead Wood

Dead wood is a very important nesting habitat for aculeate Hymenoptera. The group of species using dead wood for their development includes 82 species, which represents 30% of cavity nesters and 5.3% of all known species. Additional 129 species are wood nesters.

Most species use dead wood as a substrate for their nesting, with the majority of them creating nests in the abandoned galleries of saproxylic beetles, sawflies, clearwing moths, or other insects (Blösch 2000; Macek et al. 2010). Many species, especially those belonging to the family Crabronidae, do not nest directly in tree trunks or thick parts of wood but prefer to nest in smaller, thinner branches (e.g., many species of the genera *Crossocerus* Lepeletier and Brullé, 1834; *Nitela* Latreille, 1809; *Trypoxylon* Latreille, 1796; and other Crabronidae). Several species prefer to nest in dead wood at later stages of decomposition. Several apid species, for example, including *A. furcata* and three species of *Xylocopa*, exhibit a strong preference of more decomposed wood. Only a few species can excavate their own cavities in wood, including *Xylocopa* bees; two species of the genus *Lithurgus* Latreille, 1825 (Megachilidae); and also several species of the family Crabronidae (usually genera *Crossocerus* and *Trypoxylon*; Malyshev 1930; Blösch 2000; Macek et al. 2010). Interestingly, most wood-nesters do not use wood to build septa or plugs in their nests, instead using plant leaves, resin, or mud (see Grandi 1961; Janvier 1961a, b, 1962, 2012; Banaszak and Romasenko 1998).

Other bee and wasp species use dead wood as a construction material for building their nests, as it is typical for all three *Vespula* species and four species of *Dolichovespula* and all five species of *Polistes*. All these taxa mix chewed dead wood with their saliva to build paperlike nest material. The difference between the nests of Polistinae and Vespinae is apparent at first sight, because the second group makes the cover for their brood cells (Ross and Matthews 1991). Related wasp species of the genus *Discoelius* Latreille, 1809 (two species) use dead wood to make special paperlike septa and closing plugs in their wood-cavity nests (Macek et al. 2010). In contrast, other species build nests on stones or mud surfaces including the mason bee, *Anthidiellum strigatum* (Panzer, 1805), which builds its nest with resin and little stones.

Saproxylic species occur in 7 of the 19 aculeate families known from the Czech Republic (see Table 7.1). Crabronidae is the most diverse, with 91 species (34.5%) being strictly or facultatively saproxylic, and more than half of them (52 species) nest only in dead wood (Table 7.2). Nesting in dead wood is widespread within this family, with examples from 14 genera.

The second most species-rich family of wood-nesting Aculeata is Megachilidae, which includes 56 species (52.3%) using dead wood, and 15 of these nest only in dead wood. Most of the other facultative saproxylic species are non-specific nesters using many types of cavities for their nesting (like *Hoplitis leucomelana* (Kirby, 1802) nesting also in stems, stalks, and galls; Astapenková et al. 2017).

Species of the family Vespidae frequently use dead wood for their nesting (33 species, 40.7%), but only three of them (*Discoelius dufourii* Lepeletier, 1841, *Discoelius zonalis* (Panzer, 1801), and *Symmorphus murarius* (Linnaeus, 1758)) are dead wood specialists. The other 30 species usually nest in various types of cavities.

Facultative saproxylic species are known in the families Colletidae (14 species of the genus *Hylaeus*, 30.4%) and Pompilidae (11 species of the genera *Auplopus* Spinola, 1841, and *Dipogon* Fox, 1897, 10.3%). Only several species (e.g., *Hylaeus punctulatissimus* Smith, 1842; *Dipogon austriacus* Wolf, 1964; *D. subintermedius*

Table 7.1 Proportions of saproxylic species within the families of aculeate Hymenoptera in the Czech Republic

Superfamily/family	Total species	Saproxylic	%	Fac. saproxylic	%
Chrysidoidea					
Bethylidae	41	0	0	0	0
Chrysididae	107	0	0	0	0
Dryinidae	41	0	0	0	0
Embolemidae	1	0	0	0	0
Vespoidea (wasps)					
Tiphiidae	8	0	0	0	0
Mutillidae	16	0	0	0	0
Sapygidae	4	0	0	0	0
Pompilidae	107	0	0	11	10.28
Scoliidae	4	0	0	0	0
Vespidae	80	3	3.75	30	37.50
Apoidea (bees s. l.) Spheciformes					
Ampulicidae	2	1	50	0	0
Sphecidae	16	0	0	0	0
Crabronidae	264	52	19.70	39	14.77
Apiformes (bees s. s.)					
Melittidae	10	0	0	0	0
Megachilidae	107	22	20.56	34	31.78
Apidae	171	4	2.34	1	0.58
Andrenidae	145	0	0	0	0
Colletidae	46	0	0	14	30.43
Halictidae	134	0	0	0	0

(Magretti, 1866); and *D. vechti* Day, 1979) prefer nesting in dead wood. One of the two Czech species of the family Ampulicidae—*Ampulex fasciata* Jurine, 1807—uses wood cavities for nesting. This species does not build nests but puts paralyzed cockroaches into wood cavities and lays eggs on them (Blösch 2000).

7.7 Well-Known, but Not Due to Dead Wood Preference

The European honeybee and some species of bumblebees can be also classified as saproxylic. Before domestication, the European honeybee, *Apis mellifera* Linnaeus, 1758, was saproxylic, nesting almost exclusively in tree cavities (Michener 2007; Nieto et al. 2014). Although some subspecies in warmer regions are also known to nest in tree cavities, related species such as *Apis cerana* Fabricius, 1793; *Apis dorsata* Fabricius, 1793; and *A. florea* Fabricius, 1787, frequently nest freely on trees and shrubs (Oleksa et al. 2013; Tofilski and Oleksa 2013). Presently, no populations of native *Apis mellifera mellifera* Linnaeus, 1758, are known to occur

Table 7.2 List of strictly saproxylic species of the Aculeata in the Czech Republic

Family/species
Vespidae
Discoelius dufourii (Panzer, 1801)
Discoelius zonalis (DuBuysson, 1905)
Symmorphus murarius (Linnaeus, 1758)
Ampulicidae
Ampulex fasciata Jurine, 1807
Crabronidae
Crossocerus acanthophorus Kohl, 1892
Crossocerus annulipes Lepeletier et Brullé, 1834
Crossocerus barbipes (Dahlbom, 1845)
Crossocerus binotatus Lepeletier et Brullé, 1834
Crossocerus congener (Dahlbom, 1845)
Crossocerus dimidiatus (Fabricius, 1781)
Crossocerus leucostoma (Linnaeus, 1758)
Crossocerus megacephalus (Rossi, 1790)
Crossocerus nigritus (Lepeletier & Brullé, 1835)
Crossocerus podagricus (Vander Linden, 1829)
Crossocerus styrius (Kohl, 1892)
Crossocerus vagabundus (Panzer, 1798)
Crossocerus walkeri (Shuckard, 1837)
Ectemnius cavifrons (Thomson, 1870)
Ectemnius cephalotes (Olivier, 1811)
Ectemnius continuus (Fabricius, 1804)
Ectemnius dives (Lepeletier et Brullé, 1834)
Ectemnius fossorius (Linnaeus, 1758)
Ectemnius guttatus (Vander Linden, 1829)
Ectemnius lapidarius (Panzer, 1804)
Ectemnius lituratus (Panzer, 1805)
Ectemnius meridionalis (A. Costa, 1871)
Ectemnius nigritarsus (Herrich-Schaeffer, 1841)
Ectemnius ruficornis (Zetterstedt, 1838)
Ectemnius schlettereri Kohl, 1888
Ectemnius sexcinctus (Fabricius, 1775)
Ectemnius spinipes (A. Morawitz, 1866)
Lestica clypeata (Schreber, 1759)
Mimumesa dahlbomi (Wesmael, 1852)
Nitela fallax Kohl, 1883
Passaloecus borealis Dahlbom, 1845
Passaloecus eremita Kohl, 1893
Passaloecus vandeli Ribaut, 1952
Pemphredon clypealis Thomson, 1970
Pemphredon lugens Dahlbom, 1842

(continued)

Table 7.2 (continued)

Family/species
Pemphredon lugubris (Fabricius, 1793)
Pemphredon montana Dahlbom, 1845
Pemphredon morio Vander Linden, 1829
Pemphredon mortifer Valkeila, 1972
Pemphredon podagrica Chevrier, 1870
Pemphredon rugifer Dahlbom, 1843
Polemistus abnormis (Kohl, 1888)
Psenulus fuscipennis (Dahlbom, 1843)
Rhopalum austriacum Kohl, 1899
Solierella compedita (Piccioli, 1869)
Spilomena beata Blüthgen, 1953
Spilomena curruca (Dahlbom, 1843)
Spilomena differens Blüthgen, 1953
Stigmus pendulus Panzer, 1805
Stigmus solskyi A. Morawitz, 1864
Tracheliodes curvitarsis (Herrich-Schäffer, 1841)
Tracheliodes varus (Panzer, 1799)
Megachilidae
Chelostoma campanularum Stoeckhert, 1929
Chelostoma distinctum (Nylander, 1856)
Chelostoma emarginatum (Linnaeus, 1758)
Chelostoma florisomne (Lepeletier, 1841)
Chelostoma rapunculi Schletterer, 1889
Chelostoma ventrale (Fabricius, 1787)
Heriades crenulatus Pérez, 1890
Heriades truncorum (Dufour et Perris, 1840)
Hoplitis adunca (Schenck, 1853)
Hoplosmia bidentata (Kirby, 1802)
Lithurgus cornutus Fonscolombe, 1834
Lithurgus chrysurus Alfken, 1924
Megachile analis Spinola, 1808
Megachile ligniseca (Kirby, 1802)
Megachile nigriventris Nylander, 1852
Megachile pyrenaea Smith, 1844
Osmia inermis (Kirby, 1802)
Osmia leaiana Spinola, 1808
Osmia nigriventris (Fabricius, 1804)
Osmia niveata Curtis, 1828
Osmia parietina Smith, 1846
Osmia uncinata (Kirby, 1802)
Apidae
Clisodon furcatus (Panzer, 1798)

(continued)

Table 7.2 (continued)

Family/species
Xylocopa iris (Christ, 1791)
Xylocopa valga Gerstaecker, 1872
Xylocopa violacea (Linnaeus, 1758)

in Central Europe, and all honeybees there are hybridized with other subspecies (especially *Apis mellifera carnica* Pollman, 1879). Thus, we cannot study the nesting preferences of the central European honeybee (although the most domesticated subspecies from Slovenia has probably very similar nesting biology).

Bumblebees usually nest under the ground but will sometimes nest in cavity-like spaces aboveground as well. It is not common but sometimes bumblebee colonies are reported from tree cavities (Goulson 2003), for example. Many species of bumblebees can be kept in small hives simulating tree cavities, but usually these are placed only several centimeters above the ground. Of European species, *Bombus hypnorum* (Linnaeus, 1758) is known to frequently nest in bird houses and tree cavities more than 1 meter above the ground (Rasmont et al. 2014). That species is parasitized by another *Bombus* species, *B. norwegicus* (Sparre-Schneider, 1919), which is, thus, also saproxylic.

The nests of wood-nesting species usually differ from those in the soil. They typically involve a single main chamber containing a row of brood cells separated by thin septa (for comparison see Fig. 7.3a, b). Nest structure can vary within individual species (see Batra 1984; Westrich 1989; Cane et al. 2007; Michener 2007), but most of them (except for those capable of excavation, e.g., *Lithurgus*, *Xylocopa*, etc.) are dependent on the structures of the existing cavities in dead wood. It is not uncommon for more than one species to utilize the same cavity. This was described for species nesting in reed galls, for example, where a nest occupying only part of the gall from one species leaves space for other species to nest nearby (Bogusch et al. 2015; Astapenková et al. 2017). Parasitoids and nest cleptoparasites usually use a similar strategy—often waiting near the nest entrance for females of their host species to prepare the brood cell and lay an egg. When the brood cell is nearly finished, containing the food and egg, and the cell is almost sealed, the parasitic female lays her egg (Michener 2007). For this reason, females of saproxylic cuckoo bees of the genera *Coelioxys* Latreille, 1809, and *Dioxys* Lepeletier and Serville, 1825, have conical abdomens (Westrich 1989; Michener 2007).

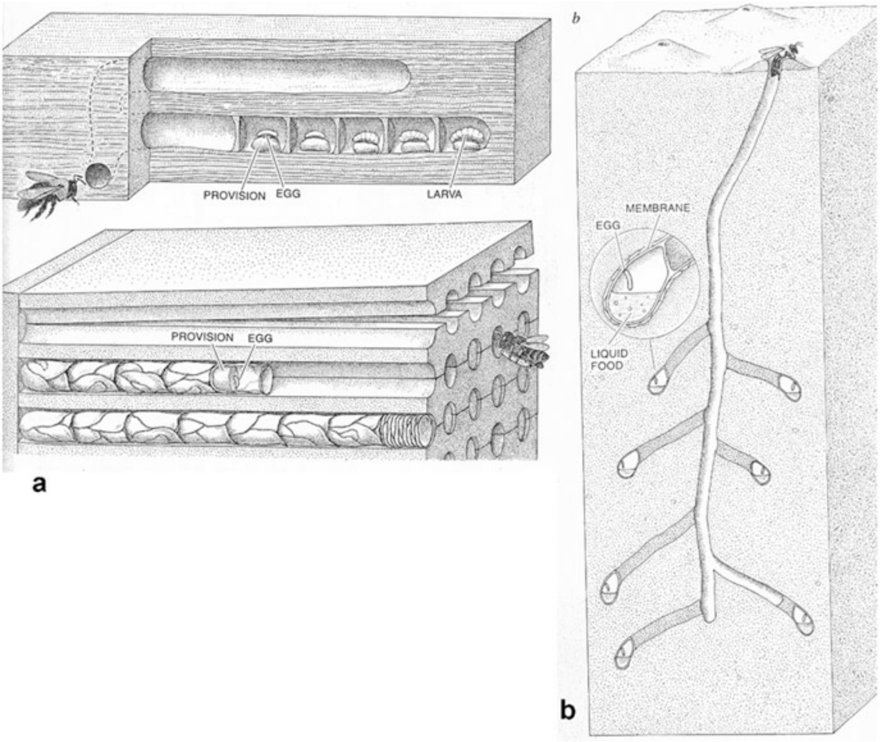

Fig. 7.3 Types of nests of Hymenoptera: Aculeata. (**a**) Nest in soil with one main way and more chambers, (**b**) nest in wood with only one cavity and brood cells one by one. From Batra (1984)

7.8 Opportunities for Research on Saproxylic Bees and Wasps

Wood-nesting bees and wasps offer a number of interesting research opportunities. Trap-nests can be used for their study, which is a big advantage in comparison with studies of bees and wasps nesting in the ground (see Malyshev 1935; Krombein 1967; Bogusch 2008). There are plenty of types of trap-nests, both commercial and for hobbyists. Recently, so-called insect hotels have become very common in Europe, being available in special shops or built at home (Fig. 7.4). These blocks of trap-nests use various types of cavities—reed stalks, plant stems with hollows and with parenchyma, tree branches, blocks of wood with holes, bricks and roof tiles, as well as boxes with clay and many others (see, e.g., manuals in the recent literature—Günzel 2007; Von Orlow 2011, 2013; Büsche 2016). For a long time, simple blocks of wood have been used to provide nesting resources for the Alfalfa leafcutter bee (*Megachile pacifica* Panzer, 1798) and some other related species in the USA (Klostermeyer and Gerber 1969; Richards 1984; Cane 2006). These blocks are commercially produced and very often used for maintenance of this species. In

Fig. 7.4 Nesting house (insect hotel) for solitary bees and wasps in garden of first author. Photo: Petr Bogusch

addition to providing important habitats for cavity-nesting bees, nest blocks also provide a useful tool for researchers. There is very limited information about the nesting biology of many species including their substrate preferences and natural enemies. Observing such species in trap-nests can thus shed light on their ecology, larval morphology, and development. Artificial nests consisting of transparent tubes can be very effective in this regard (Jung 1996), allowing the developing brood to be easily viewed without disturbance (Bogusch 2008).

Species of the families Tiphiidae and Scoliidae are parasitoids of scarabaeid beetle larvae (O'Neill 2001; Macek et al. 2010). Although most of the species prefer the larvae of beetles feeding in sandy soil, several of them parasitize larvae feeding on decaying wood. *Megascolia maculata* (Drury, 1773), the Europe's largest aculeate, is a good example, because it parasitizes the larvae of the European rhinoceros beetle, *Oryctes nasicornis* Linnaeus, 1758, and the stag beetle, *Lucanus cervus* Linnaeus, 1758 (Zavadil et al. 1937). In addition, the common scoliid *Scolia hirta* (Schrank, 1781) lays its eggs on larvae of the common rose chafer beetle (Cetoniidae) within decaying wood. Because the larvae of these scoliids develop on saproxylic hosts, they also classify as saproxylic.

7.9 Conservation of Saproxylic Bees and Wasps

As reviewed above, a substantial fraction of bee and wasp diversity is saproxylic, and thus it is necessary to help these species in recent and future landscape. Because there are differences among the species in the character of wood they use for their nesting, protecting a wide variety of dead woody habitats is key to conserving these species. When dead wood is cut and removed from a site, the number of cavities available to saproxylic bees and wasps is drastically reduced. Saproxylic bees and wasps utilize cavities in wood ranging widely in diameters and stages of decomposition. They also utilize standing solitary trees as well as trees in groups or forests. It is especially important to preserve remnants of old trees because they host an exceptional diversity of saproxylic insects including many bees, wasps, and their parasites. Although fallen trees can also be colonized by many species of this group, many studies have shown that standing and sun-exposed dead trees provide preferred habitats for many species (Thiele 2005; Sobek et al. 2009; Westerfelt et al. 2015). The protection of snags in managed forests is thus likely to promote the conservation of saproxylic bees and wasps. If a locality does not contain dead wood, such as in many urban or residential areas, we can help bees and wasps by providing suitable resources at the site, including the creation of insect hotels. It is important to place these pieces of wood in both sunny and shady environments due to preferences among the different species.

Saproxylic bees and wasps will readily nest in a variety of wooden structures. Observations made in Kleneč, Czech Republic, provide a good example of this. Although no dead wood and only young trees were present at this location, 14 species of bees and wasps made their nests in the wooden frame of a sign describing the protected site. The following year, dead wood was transferred to the site and they were quickly used for nesting by many species of bees and wasps (P. Bogusch, personal observations). Even remnants of burned trees were utilized by many saproxylic species, including several of high conservation interest (Bogusch et al. 2015).

7.10 Conclusions

Although bees and wasps are usually known as species occurring in open habitats and most of them make their nests under the ground, there is also a high proportion of species nesting in various cavities. Many of these species nest primarily or only within dead wood and are thus inherently sensitive to losses of dead wood. Among the other cavity nesters, many species use dead wood as one type of a cavity suitable for their nesting. Comprehensive studies of bees and wasps show that saproxylic species form an interesting guild within this group and they are distributed both in warm alluvial forests and cool beech or spruce forests in the mountains. Many species have also adapted to anthropogenic forests or other sites with trees (e.g., orchards, gardens, or parks) and use various types of wood for their nesting. Conservation of saproxylic bees and wasps and the study of their biology are thus very important. Though this ecological group is much better suited for studies using artificial nests, studies addressing their habitat associations in forests would be of particular value to land managers. Cavity-nesting bees and wasps are also readily moved through the international trade of goods. Steps to prevent the unintentional introduction of these insects into new regions will help promote the conservation of native species.

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Chapter 8
Ants: Ecology and Impacts in Dead Wood

**Joshua R. King, Robert J. Warren II, Daniel S. Maynard,
and Mark A. Bradford**

Abstract Although rarely considered as a saproxylic insect group, ants are an important, highly abundant insect taxon in dead wood environments worldwide. Ants directly impact the dead wood environment primarily through nesting in standing dead trees, logs, stumps, and coarse and fine woody materials, contributing to the physical breakdown of woody materials. Ants indirectly impact the dead wood environment through predation of a wide variety of arthropods, particularly termites, and by serving as a food source for other animals, particularly birds (woodpeckers) and bears that physically break down dead wood to prey upon ant colonies. The known impacts of ant nesting and predation in dead wood are reviewed with a case study that provides new information on the role of abiotic factors affecting nesting site location in dead wood in the eastern temperate US forests. Results showed horizontal and vertical nest stratification of ant nests that shifted with spatial scale. At broad scales, climate determines disparate ranges among species across a latitudinal gradient. At the scale of a forest floor, however, microsite temperature, moisture, and biotic interactions affect nesting locations in downed logs. Future research aimed at better understanding the interactions between ants and other organisms in dead wood environments is necessary to improve our understanding of the importance of ants in shaping dead wood communities and ecosystem processes like decomposition.

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Foraging and nesting by ants belowground in soils and in live tree canopies has been thoroughly documented, and these are often considered primary domains of ants (Hölldobler and Wilson 1990). However, ants commonly nest and forage within downed and standing dead wood and have been shown to be the most, or among the most, abundant animal taxa in those environments (Wilson 1959; Lindgren and MacIsaac 2002; King et al. 2013). The term "saproxylic" refers to any species that depends either directly or indirectly on dying or dead wood, and thus this chapter is focused primarily upon ant activities in dead wood. Ant activity in live trees and shrubs (including myrmecophytic trees) and in ecosystems largely devoid of dead wood (e.g., some grasslands, deserts) is not considered.

Globally, forests sequester ~50% of the world's terrestrial carbon (Mahli 2002), with dead wood constituting 10–20% of this C (Weedon et al. 2009). In certain regions, dead wood can account for 20–30% of the forest C stock and as much as 40% of forest respiration (Pan et al. 2011). Controls on the decay rate and partitioning of this dead wood pool are affected by organismal interactions in the dead wood environment, and understanding these interactions refines both regional and global C budgets (Boddy et al. 2008; Cornwell et al. 2009; Crowther et al. 2012; Warren and Bradford 2012; Bradford et al. 2014; Maynard et al. 2017). Ant activities in dead wood are important controls in forest ecosystems at all latitudes where standing and downed dead wood is abundant (Warren and Bradford 2012; Bradford et al. 2014; Parr et al. 2016).

Recent work has shown that wood-rot fungi and termites are key interacting players in determining the rate of wood decomposition at local scales in many forest ecosystems and that ants interact with both fungi and termites—and a multitude of other organisms– in dead wood environments (Abe et al. 2000; Warren and Bradford 2012; Bradford et al. 2014; Maynard et al. 2015; Neupane et al. 2015; Parr et al. 2016). Little is known, however, about the activity of ants in dead wood —which presents a major gap in our understanding of the natural history and ecology of this key group of organisms and their effects on a central, global ecosystem function: decomposition of dead wood. Here we review existing knowledge of the activities and impacts of ants in dead wood, present evidence of factors affecting the movement of and location of ant colonies in dead wood in eastern US temperate forests, and suggest key research needs to improve our understanding of the role of ants in shaping conditions and communities in dead wood environments.

8.1 Impacts of Ants in Dead Wood

8.1.1 Nesting Ecology

Ant nests take a number of forms, ranging from arboreal nests in preformed cavities in living trees, carton nests formed from processed (e.g., chewed and mixed with saliva or bound with silk) vegetative material, nests in soil or rock cavities, and nests in dead woody material of all sizes. Ant nests are a key component of their eusocial life history; a nest is the extended phenotype of eusociality, used as a tool for organizing the colony social structure, including division of labor and protection of the colony members especially reproductive castes and young, and the nest acts as a thermoregulatory device that buffers temperature and moisture extremes (Tschinkel 2006, 2015). Accessible dead wood with cavities of dimensions appropriate for entrance or defense (Powell 2009) makes an ideal nesting substrate. Ants do not consume dead wood, and most ant species—with the exception of carpenter ants in the genus *Camponotus*—lack the ability to excavate sound wood. More commonly, ants occupy preformed cavities excavated, for example, by wood-boring beetles or termites. The creation of channels and occupancy and possible expansion of existing channels by ants may be an important component of the channelization and successional processes of the decomposition of wood (Ulyshen 2016). Channelization typically occurs after trees are mechanically damaged during mortality events (e.g., treefall due to wind, mechanical damage during harvest events by humans, fire scarring) which is followed by the initial stages of wood decay when fungi attack the pith, bark, and wood surface (Ausmus 1977). A large number of ant species frequently nest in wood, but the majority of species found in wood may also nest in soil in temperate and tropical forest ecosystems (Hashimoto et al. 2006; King et al. 2013). Standing trees, stumps, coarse woody material (CWM), and fine woody material (FWM, including stems, seedpods, acorns, etc.) with preformed cavities are all subject to colonization for nesting by ants (Herbers 1989; Hansen and Klotz 2005; de Souza et al. 2012).

Among the most conspicuous dead wood-nesting genera are carpenter ants in the genus *Camponotus*. This genus contains species that excavate cavities in heartwood of live trees and in dead wood (Hansen and Akre 1990; Hansen and Klotz 2005). This genus was recently revised and the subgenera *Colobopsis* and *Dinomyrmex* were elevated to genera (Ward et al. 2016) removing these largely arboreal genera from inclusion in the genus *Camponotus*. Currently, the genus *Camponotus* is estimated to contain over 1000 species worldwide. Many of the species in the genus nest in live trees; however, the remaining species nest in dead wood or soil and can be found in temperate, subtropical, and tropical forests across the globe (Hansen and Akre 1990; Wilson 2003). Many species of *Camponotus* are large-bodied, have large colony sizes (many hundreds to thousands of workers), and are predominately crepuscular or nocturnally active (Hansen and Klotz 2005).

Mature *Camponotus* colonies or founding queens enter dead wood that has become softened due to fungal decay or enter using holes and channels previously created by larger wood-boring beetle larvae such as Cerambycids or Buprestidae (Hansen and Klotz 2005). Once the wood is occupied, the workers channelize opportunistically through the softer parts of stumps, standing dead trees, and CWM (Akre and Hansen 1990; Hansen and Akre 1990). In human-built structures, damage by carpenter ants may also occur in rotting wood, sound softwood materials, or even in other soft building materials such as drywall (Akre and Hansen 1990). Among temperate species there is evidence of specialization among dead wood habitats. For example, some species prefer large logs or standing dead trees in the earliest stages of decomposition (Torgersen and Bull 1995), whereas others nest in later-stage stumps and logs (Klotz et al. 1998) or small logs and CWM (Chen et al. 2002).

In north temperate, subboreal ecosystems where termites may be rare or absent, carpenter ants are often some of the first arthropods that channelize decaying wood (Hansen and Akre 1990; Hansen and Klotz 2005). In many north temperate ecosystems, *Camponotus* species are also among the most abundant ants in dead wood of all stages of decomposition, although a number of species in the genera *Formica*, *Myrmica*, *Temnothorax*, and *Lasius* are also common, often collectively comprising upward of 100% of species present in dead wood (Franch and Espadaler 1988; Torgersen and Bull 1995; Francoeur 1997; Swenson et al. 1999; Lindgren and MacIsaac 2002; Raley and Aubry 2006). Species in these genera have variable mature colony sizes, ranging from hundreds to tens of thousands of workers (Hölldobler and Wilson 1990; Hansen and Klotz 2005; King 2010; King et al. 2013). In open areas along forest edges or areas cleared by human activities, *Formica* species may become increasingly abundant as *Camponotus* species become less common and as wood becomes increasingly decayed and soft (Lindgren and MacIsaac 2002). As wood becomes more decayed and soft, species other than *Camponotus* may then be able to excavate wood to create nests, suggesting that decay stage of wood may be an important variable regulating ant distributions by governing nest-site availability. In regions outside the cool temperate zones, *Camponotus* remains a conspicuous member of the dead wood-nesting ant fauna although in the tropics they are only one of many genera that occupy dead wood environments (Wilson 1959; Hashimoto et al. 2006; De la Mora and Philpott 2010).

In warm temperate, subtropical, and tropical forests, the diversity of ant species increases and the predominant genera inhabiting dead wood environments shift away from *Camponotus*, *Formica*, and *Lasius*, which typically dominate dead wood nesting in cool temperate and boreal forests. In warm temperate zones, species in the genera *Aphaenogaster*, *Pheidole*, *Rhytidoponera*, *Solenopsis*, and *Temnothorax* become predominant genera in dead wood (Andersen 1986; Herbers 1989; King et al. 2013). Species in these genera also vary considerably in mature colony sizes, ranging from hundreds to tens of thousands of workers (Baroni-Urbani and Pisarski 1978; Hölldobler and Wilson 1990; Hansen and Klotz 2005; King 2010; King et al. 2013). In many tropical forests, the number of ant species found in dead wood is high, comprising up to ~20% of total ant diversity (including arboreal species) and ~50% of ground-dwelling species diversity (Hashimoto et al. 2006; Sagata et al. 2010). The genus *Pheidole* becomes especially common and abundant in dead wood of various sizes and decomposition stages in the subtropics and tropics (Wilson 2003, 1959; Levings and Franks 1982; Eguchi 2001; Watt et al. 2002; Eguchi and Yamane 2003; Hashimoto et al. 2006; De la Mora and Philpott 2010; Sagata et al. 2010; de Souza et al. 2012; Fernandes et al. 2012). A variety of specialist predators also become common nesters in dead wood environments. Species from the genera *Strumigenys*, *Gnamptogenys*, and *Cerapachys* are common, and mature colony sizes of many of these species tend to range from several tens to several hundreds of workers (Baroni-Urbani and Pisarski 1978; Hölldobler and Wilson 1990; King 2010).

In subboreal and cool temperate forests, a majority of species (≥70%) use logs, stumps, and CWM (≥10 cm diameter) for nesting (Franch and Espadaler 1988; Higgins and Lindgren 2006, 2015; Higgins et al. 2017). These larger pieces of wood provide a substrate that warms rapidly when exposed to sunlight and retains heat after sunset, making these nesting locations favorable relative to soil for thermoregulation by colonies in cooler climates (Higgins and Lindgren 2006, 2012). Standing dead trees, logs, stumps, and CWM are nesting sites for many species in warmer climates as well, although the diversity of species in leaf litter, soil, and in live trees surpasses the diversity of ants nesting in larger pieces of dead wood (Wilson 1959; Levings and Franks 1982; Watt et al. 2002; Hashimoto et al. 2006; De la Mora and Philpott 2010; Sagata et al. 2010). Fine woody material (≤10 cm diameter) including small twigs and even seed pods and nuts are used by ants in the temperate (Booher et al. 2017) and especially tropical zones (De la Mora and Philpott 2010; de Souza et al. 2012; Nakano et al. 2012). These substrates are an important nesting site for a large diversity of species and may be occupied at various stages of decomposition (De la Mora and Philpott 2010; Booher et al. 2017). It is likely that these dead wood substrates are favored by many small-bodied ant species because they represent a contained, defensible location for an entire small colony that provides consistent humidity and temperature conditions relative to other nesting sites, such as soil (Wilson 1959; Booher et al. 2017).

Suitable nesting sites in dead wood may be limiting at local scales due to the inability of many species to excavate sound wood or to limited availability of preformed cavities of appropriate size (Herbers 1986; Powell 2009; Sagata et al. 2010; Booher et al. 2017). For example, when FWM nesting sites are experimentally increased in forest plots, nest site occupancy typically increases up to ~20% whether in tropical or temperate forest (Kaspari 1996; Foitzik et al. 2004; Sagata et al. 2010). The most likely competitors for nesting sites for ants in dead wood are other ants (Hölldobler and Wilson 1990; Sagata et al. 2010). However, multiple species may often occupy the same wood piece, and many dead wood pieces (large or small) are often unoccupied, suggesting that factors other than competition may be driving dead wood occupancy rates (Franch and Espadaler 1988; Sagata et al. 2010; Higgins and Lindgren 2012). Termites may also compete with ants for dead wood space but also appear to inadvertently provide nesting sites in dead wood for ants, especially in the tropics (Wilson 1971; Hölldobler and Wilson 1990; Dejean et al. 1997; Mertl et al. 2012; Warren and Bradford 2012; Warren et al. 2012). Co-nesting of termites and ants in single dead wood pieces has been observed in temperate and tropical forests (Buczkowski and Bennett 2008; Mertl et al. 2012). In temperate forests, much of the co-nesting is likely occurring between multiple piece nesting termites (the "lower" termites) that feed upon and nest within dead wood and a variety of ant genera with similar nesting requirements (Buczkowski and Bennett 2008; Lubertazzi 2012; Maynard et al. 2015). In tropical forests, termite communities are much more diverse, and thus a much broader diversity of ants and termites are likely to co-nest in dead wood pieces (Mertl et al. 2012). The creation of physical barriers by termites and specialized antipredatory strategies against ant predators likely make co-nesting possible (Jaffe et al. 1995; Buczkowski and Bennett 2008; Oberst et al. 2017).

8.1.2 Ants as Predators and Prey

The majority of ants are broadly omnivorous and highly opportunistic in their diet, taking prey or plant-derived food resources according to colony needs (e.g., high demand for protein during reproductive phases) or simply because of availability (Stradling 1978; Hölldobler and Wilson 1990; Tschinkel 2006). It is likely that the interactions between ants and termites impact the decomposition process, potentially affecting nutrient cycling rates and even the pathways by which C and nitrogen enter the soil (Warren and Bradford 2012; Bradford et al. 2014). Ants, as a group, long have been recognized as the most important termite predators wherever termites occur (Wood and Sands 1978; Deligne et al. 1981; Hölldobler and Wilson 1990). Species from almost every ant subfamily prey upon termites, whether opportunistically or as specialized predators (Wood and Sands 1978; Deligne et al. 1981; Hölldobler and Wilson 1990).

Ants may be an especially important limiting factor for termite populations as they are a specific predator on termite kings and queens in dead wood, preying upon alates (winged reproductives) during mating flights and during the founding stage when termite colonies are especially vulnerable, due to small colony size (Blake 1941; Basalingappa 1970). Some of the most common ants in dead wood are substantial termite predators. For example, species from the genus *Aphaenogaster* often are among the most common dead wood nesting species in eastern US forests, and termites from the genus *Reticulitermes* are an important part of their diet (Buczkowski and Bennett 2007; King et al. 2013). The genus *Pheidole* often is the most abundant group of ants in dead wood in the warm temperate through tropical zones, and the genus contains a number of species that prey on termites (Sheppe 1970; Deligne et al. 1981; Hölldobler and Wilson 1990). Although many of these ant genera are generalist predators in dead wood and likely opportunistically preying upon adult worker termites, or even whole colonies, their high abundance and common occurrence in dead wood in forests worldwide likely limits termite activity (Wood and Sands 1978; Deligne et al. 1981; Wilson and Brown 1984; Wilson and Holldobler 1986; Hölldobler and Wilson 1990; Raimundo et al. 2009).

Other ant species are specialized predators of termites with morphological, physiological, and behavioral adaptations that suggest that termites are their primary prey item (Deligne et al. 1981; Traniello 1981; Hölldobler and Wilson 1990; Lemaire et al. 1990). The entire Ponerinae genus *Centromyrmex* (15 species) is termitophagous and has morphological adaptations, including short, stout legs apparently adapted to moving through narrow, tubular termite galleries, making this a conspicuous, if not especially common, group of termite predators from the New and Old World tropics (Weber 1949; Kempf 1966; Bolton and Fisher 2008). Other termitophagous ant species (several genera) form hunting parties that specialize upon raiding termite nests (and, in some cases, other ant nests) in which they attack and eat termite colony members (Wheeler 1936; Levieux 1966; Longhurst et al. 1978, 1979; Leal and Oliveira 1995; Yusuf et al. 2014; Lampasona 2015). Termitolestic species, in the genus *Solenopsis* and *Carebara*, are very small ant species that specialize in stealing the eggs and young nymphs of termite colonies (Wheeler 1936; Deligne et al. 1981). These highly specialized termite predators are widespread throughout the subtropical and tropical regions of the New and Old World regions.

Ants likely also are the most important predators of other arthropods in dead wood due to their abundance and their foraging activities in most terrestrial environments (Petal 1978; Hölldobler and Wilson 1990; King et al. 2013; King 2016). For example, ant species prey upon oribatid mites, isopods, millipedes, and wide variety of larvae, such as fly larvae commonly found in dead wood environments (Wilson and Brown 1984; Masuko 1994; Dejean and Evraerts 1997; Ito 1998; Wilson 2005). Moreover, ants surpass other predatory macroinvertebrate groups, such as spiders and predatory beetles, both in total abundance and impact on arthropod prey populations (Kajak et al. 1972; Petal 1978). Ant predation may eliminate as much as ~50% of the individuals produced per unit area per year for some groups of arthropods, such as flies and bugs, (Kajak et al. 1972; Petal 1978). Spiders and other predators, such as beetles, also are common ant prey items, and thus ant predation likely has cascading impacts throughout dead wood communities, although these impacts may be localized nearest colony activity (Petal 1978).

Ants, due to their enormous abundance in dead wood in forests, are important sources of food for other animals, including vertebrates. Ants comprise a major component of the diet of a variety of birds, especially woodpeckers that forage in dead wood. More than 50% of their diet may be composed of ants foraged from dead wood (Levieux 1972; Torgersen and Bull 1995; Raley and Aubry 2006; Horn and Hanula 2008). A variety of reptiles, frogs, and especially dead-wood-dwelling salamanders depend upon ants as a major component of their diet (Hamilton 1932; Anderson and Mathis 1999; Caldwell and Vitt 1999; Hirai and Matsui 2000; Moseley et al. 2005). Specialist ant- and termite-eating mammals (monotremes, marsupials, and eutherians) that occur in forests and woodlands primarily consume ants and termites in dead wood, and these insects typically comprise greater than 90% of their diet (Calaby 1960; Redford 1987). Bears, including black, brown, sun, and sloth bears, are another group of mammals that depend upon ants in dead wood as a key component of their diet (Swenson et al. 1999; Mattson 2001; Große et al. 2003; Bargali et al. 2004; Steinmetz et al. 2011). Among other taxa, ants in dead wood are food for a wide variety arthropods, invertebrates, and even fungi (Petal 1978; Roberts and Humber 1981; Hölldobler and Wilson 1990).

8.2 Colony Movement in Dead Wood

Ant colonies move, and, in some cases, species may be highly transient to the point that entire colonies change location on a regular basis (Smallwood 1982a; Miyata et al. 2003; McGlynn et al. 2004; Moyano and Feener 2014). The regular movement of colonies, at the population scale, represents an important ecological phenomenon affecting the spatial distribution of colony impacts, including predation, channelization, availability as a prey item, and, ultimately, the rate of ecosystem processes such as dead wood decomposition (Kaspari et al. 2011; Bradford et al. 2014).

Frequent colony relocation may be prompted by a number of factors including thermoregulation, competition, predator avoidance, and resource acquisition (McGlynn et al. 2004; Jones and Oldroyd 2006; Tschinkel 2014). Colony relocation among microhabitats (e.g., soil, decomposing wood, under rocks, leaf litter) might be considered “horizontal” movement, but it often corresponds with “vertical” positioning along a continuum from the soil column to the upper reaches of fallen logs or even into trees (Ofer 1970; Miyata et al. 2003; Hashimoto et al. 2006; Lubertazzi 2012; Moyano and Feener 2014). In tropical, subtropical, and temperate forests, temperature and moisture levels are heterogeneous both across the forest floor and, vertically, from soil to leaf litter, to tree trunks, and to canopy (Christy 1952; Warren 2010; Warren and Bradford 2011). Microhabitat conditions also change with season, as do colony requirements (e.g., many subtropical and temperate species need warmer temperatures for brood development), prompting nest relocation for optimal temperature and moisture regulation (Carlson and Gentry 1973; Smallwood and Culver 1979; Smallwood 1982b; Miller 1994; Kuriachan and Vinson 2000; Chen et al. 2002; McGlynn et al. 2010; Warren et al. 2010, 2012). Many eusocial colonies also move vertically on a seasonal basis as they shift from winter hibernacula to summer nests (Talbot 1951; Ofer 1970; Snyder and Herbers 1991; Miller 1994; Banschbach et al. 1997; Laskis and Tschinkel 2009) or daily to maximize optimal temperature and moisture for colony health and brood development (Headley 1949; Roces and Nunez 1989; Cabrera and Kamble 2001; Houseman et al. 2001; Pranschke and Hooper-Bùi 2003; Higgins and Lindgren 2006, 2012; Jones and Oldroyd 2006; Penick and Tschinkel 2008; Moyano and Feener 2014).

8.2.1 A Case Study of Ant and Termite Colony Movement in Eastern US Forests

Despite our understanding of segregation of nesting locations at local scales, we still have relatively little understanding of fine-scale vertical and horizontal nesting choices and how those choices may change under different climatic conditions. Whereas horizontal segregation (Levings and Traniello 1981; Ryti and Case 1992; Brown 1999) or vertical segregation at a coarse scale such as litter versus arboreal strata (Lynch 1981; Longino and Nadkarni 1990; Zelikova et al. 2008) has been examined, vertical colony placement across the scale of soil to downed dead wood (~1 m) among co-occurring, interacting ground-dwelling social insects (ants and termites) rarely has been examined. We examined horizontal (presence/absence, abundance) and vertical (soil up to downed dead wood) nest placement, across a regional climate gradient in eastern US temperate forest, for the three dominant social insects inhabiting soil and CWM: the woodland ant species *Aphaenogaster rudis* and *Pheidole dentata* and the temperate forest termite *Reticulitermes flavipes.* We examined the relative contribution of abiotic (temperature, moisture, CWM class) versus biotic (interspecific interactions between *R. flavipes*, *A. rudis*, *P. dentata*, and other ants) variables in predicting horizontal and vertical nest placement at both broad and fine spatial scales.

8.2.2 Methods

8.2.2.1 Study Sites

King et al. (2013) conducted a forest arthropod survey from Connecticut to Florida (in eastern US temperate mixed forests) and found that macroinvertebrate abundance and biomass in dead wood was dominated by ants and termites. Species of the *Aphaenogaster fulva-rudis-texana* species complex (Umphrey 1996) include *A. picea* Wheeler and *A. rudis* Enzmann (hereafter "*A. rudis*"). These species dominated dead wood ant communities in the northern portion of the latitudinal gradient and then gave way to *Pheidole dentata* Mayr as the dominant ant in the southern reach of eastern US forest—coinciding with a marked increase in *Reticulitermes flavipes* Kollar termite colonies from north to south (King et al. 2013; Maynard et al. 2015). Working in the same study sites and sampling plots as King et al. (2013), ant and termite colonies were sampled in August to September 2011. The four study locations spanned ~12° latitude (approximately 1600 km): Yale-Myers Forest (Connecticut, 41°57′N 72°07′W), Coweeta Hydrologic Laboratory (North Carolina, 35°03′N 83°25′W), Whitehall Forest (Georgia, 33°53′N 83°21′W), and San Felasco State Park (Florida, 29°43′N 82°26W).

8.2.2.2 Study Species

Aphaenogaster rudis is a widespread and abundant species complex that ranges from southern Canada to Georgia and west to the Mississippi River (Lubertazzi 2012; King et al. 2013) in the eastern United States. *Aphaenogaster rudis* are dietary generalists acting as scavengers, predators, and keystone woodland seed dispersers (Ness et al. 2009). Colonies are typically monogyne (single queen) with fewer than 500 workers. Nests are constructed in a variety of substrates but most commonly in rotten wood extending into the soil (personal observations, King et al. 2013). *Pheidole dentata* is an abundant, widespread ant species mainly located in forests in the southeastern United States but reaching as far northward as Maryland and westward to Texas (Wilson 2003). *Pheidole dentata* have two physical worker castes, soldiers as well as workers, and may have multiple queens (polygyne), although they are typically monogyne. Colonies are >ca. 600 workers. Nests are constructed in a variety of substrates, especially rotten wood, and extend into the soil. *Pheidole dentata* workers are scavengers and generalist predators.

Reticulitermes flavipes, the eastern subterranean termite, occurs throughout the eastern United States, but its density increases greatly moving southward (Emerson 1936; Maynard et al. 2015). *Reticulitermes flavipes* feed on dead wood, but, unlike the ant species, reproductive members of the colony often remain belowground (Thorne et al. 1999). However, the vast majority of the colony and the standing biomass of *Reticulitermes* colonies—when temperatures are warm enough to facilitate feeding (i.e., ~>10 °C)—are found in aboveground dead wood connected by subterranean tunnels (Abe 1990; Korb 2007; King et al. 2013).

8.2.2.3 Sampling

Two 10 × 10 m plots were established on two north- and two south-facing slopes (except at YMF, where slopes face east-west) at each of the four study sites ($n = 8$ plots per study site and 32,100 m^2 plots across all four locations). Study ants and termites were sampled in all CWM (dead wood >10 cm dia.) within each plot, with an emphasis on collecting whole colonies (ants) or feeding groups (subterranean termites) of social insects. Although termite foraging congregations may or may not be true "nests," they were measureable units typically representing the majority biomass of the colony (Deheer and Vargo 2004; Vargo and Husseneder 2009; King et al. 2013). All CWM was measured along the center axis for length, and at either end for diameter. We categorized the state of decay in each individual CWM using the "class" index developed by Pyle and Brown (1998), where class I is sound wood and class V is heavily decayed to the point of almost becoming soil. See King et al. (2013) for more detailed methodology. The nest height of all colonies from the soil surface also was measured. Given that nest height is constrained by the diameter of available CWM, we also calculated relative nest height as the proportion of available diameter height used (i.e., nest height/CWM diameter). In each plot, soil temperature was measured at 5 cm depth and volumetric soil moisture (Campbell HydroSense™) to 12 cm depth across 10 distinct sub-locations.

8.2.2.4 Horizontal Nest Placement Analysis

We used analysis of covariance (ANCOVA) models in the R statistical program (Team 2014) to evaluate *R. flavipes*, *A. rudis*, and *P. dentata* abundance at the plot scale ($n = 32$). None of the ants we sampled occupied the same piece of CWM, so the abundance data were, in effect, analogous to presence/absence data. The biotic variables included in the model were *R. flavipes*, *A. rudis*, *P. dentata*, and other ant ("other," *Camponotus*, *Lasius*, *Nylanderia* spp.) abundance. Because ants eat termites, the ant species were included as predictors in the *R. flavipes* models, but *R. flavipes* was not included in ant statistical models because its presence should not deter ant colonization. Given that *A. rudis* and *P. dentata* ants never occurred in the same CWM, the influence of *P. dentata* presence on *A. rudis* plot-level abundance was evaluated, but the directional effect is unknown, making it redundant to include *A. rudis* as a predictor in *P. dentata* models. The abiotic variables were temperature, moisture and CWM class. We also used ANCOVA models to evaluate *R. flavipes*, *A. rudis*, and *P. dentata* abundance at the scale of individual CWM pieces ($n = 156$). Because the ant species never occurred in the same log, we used individual species presence and the same abiotic variables.

We included site ($n = 4$) as a factor in all ANCOVA models to capture unmeasured variance across sites as well as to evaluate contingent responses (interaction effects with site). We also evaluated second-order terms for the abiotic variables to examine intermediate responses. We used the "car" package (Fox and Weisberg 2011) in R to test for collinearity among fixed effects and found that soil moisture and temperature were collinear (variance inflation > 8), so they never were included in the same model. The inclusion or exclusion of variables was based on Akaike's Information Criterion (AIC) values (Akaike 1973), calculated using maximum likelihood with the best-fitting parameters (Δ 2AIC) retained. We then evaluated the slope value of retained fixed effects and considered coefficients with p-value ≤ 0.05 significant. We considered coefficients with p-value ≤ 0.10 to be "marginally significant" (Hurlbert and Lombardi 2009) and used this higher threshold given the noise in environmental data that decreases statistical power but, if randomly distributed, does not affect estimates of coefficient (or effect) size (Bradford et al. 2016).

8.2.2.5 Vertical Nest Placement Analysis

We used analysis of variance (ANOVA) models to evaluate differences among *R. flavipes*, *A. rudis*, and *P. dentata* nest height and relative nest height. We also used ANOVA to examine differences in CWM diameter by site. Post hoc tests for individual differences were done using Tukey's "Honest Significant Difference" tests. We evaluated *R. flavipes*, *A. rudis*, and *P. dentata* nest heights at the plot scales using ANCOVA models. We used an approach similar to that previously outlined for horizontal nest placement, except that interspecific ant influences on nest height could not be evaluated at the scale of individual CWM pieces because the ants did not co-occur in the same log.

8.2.3 Results

8.2.3.1 Study Species Occurrence

Whitehall Forest was the only location where we found all three study species (Table 8.1) in our plots. *Reticulitermes flavipes* was not found at Yale-Myers (Connecticut) but does occur in that region and at that site (pers. obs.); similarly

P. dentata was not found at Coweeta (North Carolina mountains) but also occurs in that region. The species distributions largely correspond with broad-scale climate drivers. Termite abundances correlated with increased temperature, increasing from the northernmost Yale-Myers site down to the southernmost San Felasco State Park site (Table 8.1). *Aphaenogaster* abundances directly correlated with precipitation and peaked at the Coweeta Hydrologic Lab; whereas *P. dentata* occurred most at the driest site, Whitehall Forest (Table 8.1).

8.2.3.2 Horizontal Nest Placement: Plot Scale

The best-fit model (ΔAIC < 2.0) predicting *R. flavipes* abundance at the plot scale retained temperature and site, but only the positive effect of temperature was significant (temperature, *df* = 1, *SS* = 1,525,934, *F-value* = 4.192, *p-value* = 0.050; site, *df* = 3, *SS* = 1,202,618, *F-value* = 1.101, *p-value* = 0.366). We only found termite colonies in plots with soil temperature >20 °C. The best-fit model for *A. rudis* abundance retained moisture and site, but only the positive effect of moisture was marginally significant (moisture, *df* = 1, *SS* = 1,082,269, *F-value* = 3.305, *p-value* = 0.080; site, *df* = 3, *SS* = 1,412,467, *F-value* = 1.438, *p-value* = 0.254). *Aphaenogaster* ants were most abundant where plots contained 5–20% soil moisture. The best-fit model for *P. dentata* abundance retained temperature and site, and the positive effect of temperature and site (given increased *P. dentata* abundance at Whitehall Forest and San Felasco) were significant (temperature, *df* = 1, *SS* = 637,037, *F-value* = 4.402, *p-value* = 0.045; site, *df* = 3, *SS* = 1,326,041, *F-value* = 3.054, *p-value* = 0.045). We only found *P. dentata* in plots with temperature >23 °C.

8.2.3.3 Horizontal Nest Placement: CWM Scale

The best-fit model (ΔAIC < 2.0) for *R. flavipes* abundance at the CWM scale contained *A. rudis* and *P. dentata* presence, temperature, temperature^2, CWM class and a *P. dentata* × site interaction term. The significant interaction term (*df* = 1, *SS* = 404,152, *F-value* = 11.267, *p-value* = 0.001) indicated that *R. flavipes* abundance was not impacted by *P. dentata* presence in CWM at San Felasco (mean ± SE, present = 544.71 ± 237 termites; absent 182.1 ± 83 termites), but decreased with *P. dentata* presence in CWM at Whitehall Forest (present = 6.8 ± 7 termites; absent 42.8 ± 18 termites). *R. flavipes* abundance decreased with *A. rudis* presence in all CWM (*df* = 1, *SS* = 154,849, *F-value* = 4.317, *p-value* = 0.040) (Fig. 8.1). We also found that *R. flavipes* abundance in CWM increased marginally significantly with temperature (*df* = 1, *SS* = 101,905, *F-value* = 2.841, *p-value* = 0.094), but CWM class and the temperature^2 terms were not significant.

The best-fit model (ΔAIC < 2.0) for *A. rudis* abundance retained *P. dentata*, other ants, soil moisture, CWM class, and site, but only the negative effect of *P. dentata* presence was marginally significant and the positive effect of soil

Table 8.1 Site conditions and social insects

	Climate[a]		*Reticulitermes* spp.		*Aphaenogaster* spp.		*Pheidole dentata*	
Site (latitude)	Temp (°C)	Prec (cm)	Colonies	Individuals	Colonies	Individuals	Colonies	Individuals
Yale-Myers Forest (41)	8.8	121.2	0	0	8	3865	0	0
Coweeta Hydrologic Lab (35)	12.5	183.0	12	1782	26	5720	0	0
Whitehall Forest (33)	16.6	119.5	13	2354	8	1617	6	4621
San Felasco State Park (29)	20.6	128.2	13	6262	0	0	7	2902

[a] Mean annual 1981–2000; PRISM Climate Data (http://www.prism.oregonstate.edu)

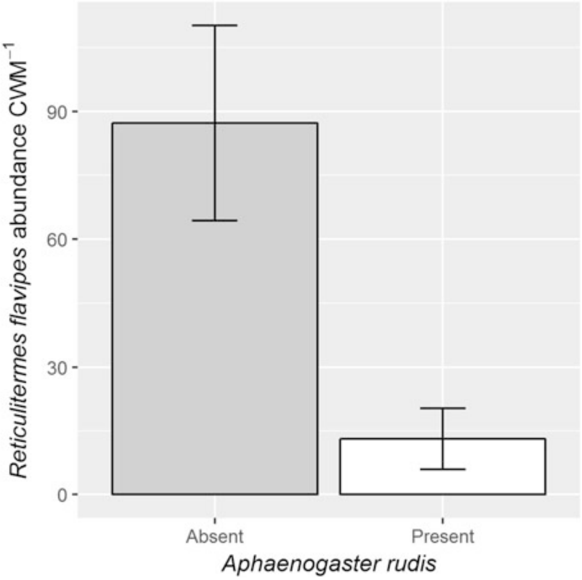

Fig. 8.1 *Reticulitermes flavipes* (subterranean termites) abundance in logs with the presence versus absence of *Aphaenogaster rudis* ants (values are means ± SE). The termite abundances are significantly lower in coarse woody material (CWM) containing the ants

moisture significant (*P. dentata*, *df* = 1, *SS* = 71,039, *F-value* = 3.160, *p-value* = 0.076; moisture, *df* = 1, *SS* = 527,843, *F-value* = 23.480, *p-value* < 0.001). *Aphaenogaster rudis* colonies contained (mean ± SE) 78.3 ± 14 individuals in CWM without *P. dentata* but never occurred in logs with *P. dentata* present (Fig. 8.2). The best-fit *P. dentata* model included CWM class and site, but only the site effect was significant (*df* = 3, *SS* = 132,566, *F-value* = 2.966, *p-value* = 0.034).

8.2.3.4 Vertical Nest Placement: Plot Scale

No significant differences occurred between species in nest height (*df* = 2, *SS* = 257, *F-value* = 1.585, *p-value* = 0.211) (Fig. 8.3a), but significant differences occurred in relative nest height (*df* = 2, *SS* = 0.880, *F-value* = 4.363, *p-value* = 0.016) (Fig. 8.3b). Tukey multiple comparison of means indicated *R. flavipes* relative nest height (0.54) was significantly greater (*adjusted p-value* = 0.011) than *A. rudis* relative nest height (0.31) (Fig. 8.3b). There was no difference in the diameter of the CWM colonized by the three species (*df* = 2, *SS* = 0.014, *F-value* = 0.015, *p-value* = 0.611).

The best-fit model (ΔAIC < 2.0) for *R. flavipes* nest height at the plot scale retained *A. rudis*, *P. dentata*, other ants, soil moisture, CWM class, and site, but none of the effects were significant. The best-fit model for *A. rudis* nest height retained *R. flavipes*, soil moisture, CWM class, and site, but only the positive effect of *R. flavipes* significantly correlated with *A. rudis* nest height (*df* = 1, *SS* = 3539,

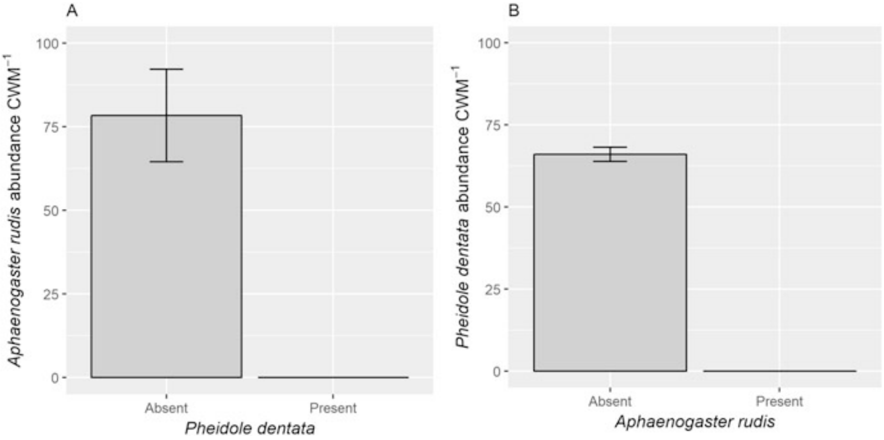

Fig. 8.2 *Aphaenogaster rudis* (**a**) and *Pheidole dentata* (**b**) ant abundance in logs in the absence versus presence of the other species. These two species did not coexist in the same piece of coarse woody material (CWM)

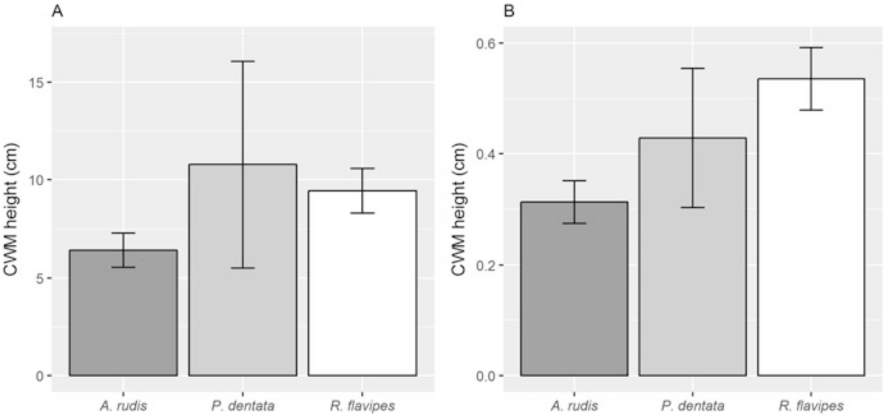

Fig. 8.3 Nest height (**a**) and nest height as a proportion of log diameter (**b**) for the dominant termites (*Reticulitermes flavipes*) and dominant ants (*Aphaenogaster rudis* and *Pheidole dentata*) [values are means ± SE] in eastern US temperate forest floors. None of the genera differed in absolute height of nests (**a**), but the *R. flavipes* colonies were significantly higher in larger logs than *A. rudis*—suggesting the termites used a greater proportion of available height than the ants

F-value = 29.233, *p-value* = 0.001) (Fig. 8.4). The best-fit model for *P. dentata* nest height retained soil temperature, temperature^2 and site, with only the temperature terms significant (temperature, *df* = 1, *SS* = 1814, *F-value* = 9.893, *p-value* = 0.014; temperature^2, *df* = 1, *SS* = 674, *F-value* = 3.675, *p-value* = 0.092; indicating a curvilinear response (Fig. 8.5)).

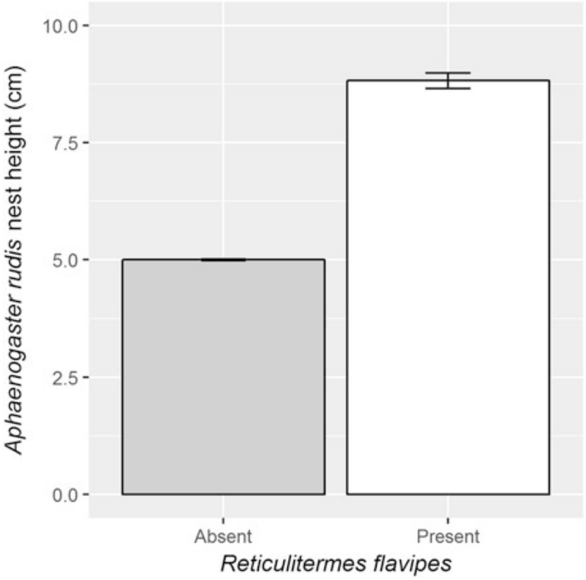

Fig. 8.4 Nest height of *Aphaenogaster rudis* ants where *Reticulitermes flavipes* termites were present and absent. The ants appeared to move their nests much higher in coarse woody material where termites also occurred

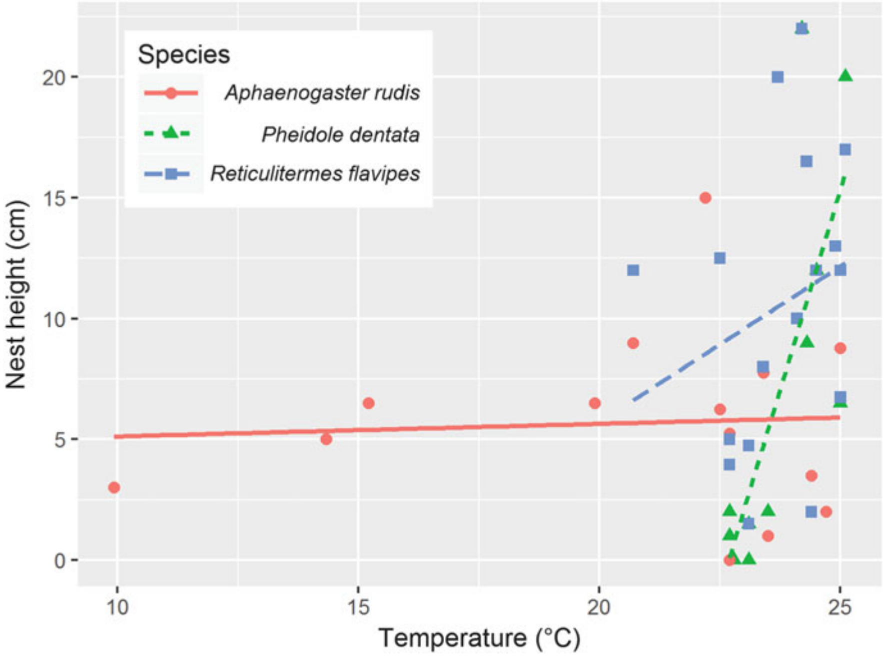

Fig. 8.5 Scatterplot showing *Aphaenogaster rudis*, *Pheidole dentata*, and *Reticulitermes flavipes* nest height increases with temperature. Whereas all species' nest height increased with temperature, only the slope value for *P. dentata* differed significantly from zero

8.2.4 Discussion

Our results suggest that the spatial scale of interest determines conclusions about the strength of biotic versus abiotic influences on eusocial insect nest placement. At broad scales (km), the distribution of *R. flavipes*, *A. rudis*, and *P. dentata* corresponded with climate. *R. flavipes* and *P. dentata* abundances increase with latitudinal increases in soil temperature, whereas *A. rudis* distributions peaked with high soil moisture. Similarly, at plot-level scales (*m*), temperature most influenced *R. flavipes* and *P. dentata* nest locations across the forest floor whereas moisture most influenced *A. rudis*. Temperature and moisture remained important at the scale of an individual log (cm), with interspecific interactions appearing to govern which species occupied the logs. None of the ant species, including additional ant species grouped together as "other ants," shared a log. *Reticulitermes flavipes* shared logs with *A. rudis* and *P. dentata* colonies but had significantly fewer termite workers present in the logs when they did. The consistency of the lack of co-occurring ants and reduced termite abundances in the presence of ants suggests that experiments are needed to verify underlying mechanisms for this relationship.

8.2.4.1 Horizontal Nest Placement

Aphaenogaster rudis appeared limited by moisture, preferring CWM in locations with moderately moist soils, whereas *R flavipes* and *P. dentata* only occurred in CWM in locations with the warmest soils. These interspecific microclimate requirements seem to map onto the broad-scale species distributions and the general natural history of this group of ants (Lubertazzi 2012).

Ant and termite species interact at very local scales (Hölldobler and Wilson 1990), and notably there was a conspicuous lack of shared logs between ant colonies, and a significant drop in *R. flavipes* abundance in logs shared with *A. rudis* (and site-specific effects in those shared with *P. dentata*). These findings suggest that local, negative biotic interactions influenced habitat selection for nests. Interestingly, at Whitehall Forest where *A. rudis* and *P. dentata* overlap, Giladi (2004) found that *P. dentata* dominated active floodplain habitat where *A. rudis* was absent, suggesting that negative interactions occur at scales greater than an individual log. In sum, these results suggest that manipulative field studies are required to definitively decouple biotic and abiotic drivers among these species.

We find dramatic declines in *R. flavipes* abundance in dead wood also colonized by *A. rudis*, whereas *P. dentata* appear to have contingent effects. Many ant species will prey upon termites (Feener 1988; Dejean and Feneron 1999; Bayliss and Fielding 2002; Buczkowski and Bennett 2007, 2008), and *R. flavipes* abundance decreases with *P. dentata* presence at Whitehall Forest. However, *R. flavipes* abundance is much greater at San Felasco, and it increases with *P. dentata* presence. In fact, because the density of termites is much greater in the southern range of *P. dentata*, any predatory impact may be relatively less, allowing greater microscale coexistence. Another possibility is that *P. dentata* outcompetes and excludes more effective termite predators, thereby alleviating an important top-down control on local termite abundances.

8.2.4.2 Vertical Nest Placement

Nest placement in logs helps regulate colony microclimate. Obvious vertical adjustments to microclimate are movements downward during winter to avoid freezing temperatures (Talbot 1951; Ofer 1970; Snyder and Herbers 1991; Miller 1994; Banschbach et al. 1997; Laskis and Tschinkel 2009) or during summer to avoid desiccation (Wilson 1971; Gordon et al. 2013). We only found one vertical microclimate response: *P. dentata* increased its nest height exponentially with temperature, likely maximizing optimal temperature conditions for colony functions such as brood development, queen egg laying, and even food storage (Tschinkel 2006; Gayahan and Tschinkel 2008).

All three species generally placed their nests at similar heights, but *A. rudis* used less available log diameter than *R. flavipes*. Given that ants use logs as housing for nests whereas *R. flavipes* also consumes dead wood as food, *R. flavipes* may occupy more log space to fully exploit consumable resources. *Aphaenogaster rudis* ants are also desiccation intolerant (Smallwood 1982b) and require highly mesic forest conditions for nesting (Warren et al. 2012). Given that dead wood dries from the top down, using the warmer, upper portions of the wood requires greater moisture to avoid desiccation, necessitating lower colony placement by *A. rudis* in drier locations. In addition, because *A. rudis* does not generally excavate wood itself, it is largely limited to those portions of the wood that have already been excavated by other soil animals. Interestingly, *A. rudis* locates colonies relatively higher in wood where termites are present, possibly a response to a food resource. Termites can fend off ants in dead wood colonies by filling in spaces and positioning soldiers at openings (Buczkowski and Bennett 2008), so an alternate possibility is that *A. rudis* nests higher to occupy abandoned tunnels in logs once occupied by termites.

8.3 Conclusions and Future Work

The drivers of horizontal and vertical colony locations in dead wood on a forest floor appear to change with scale for eusocial insects. At broad spatial scales, climate seems to shape disparate ranges among species across a latitudinal gradient, but we cannot rule out that a shift in interacting species (or some other unmeasured factor) also acts as an influence on range distributions. At the scale of a log, in contrast, biotic interactions appear to predominate, with species excluding one another, but not without some microclimate influences. Our results therefore highlight that the habitat distributions of dominant eusocial insects in eastern US temperate forest likely are structured by biotic and abiotic forces acting at different strengths depending on measurement scale. These results suggest that measures taken at a single spatial scale may misrepresent the strength of biotic or abiotic drivers and may lead to incorrect predictions about how eusocial insects will respond to climate change both within and among sites. This scale dependence of biotic vs. abiotic influence on eusocial insect distributions and abundance is likely also true for dead wood nesting ants in tropical forests (Kaspari 1996). Admittedly, our data are observational but suggest the need for experiments to tease apart and quantify biotic and abiotic influences on nest placement and how nest movements affect key ecosystem processes that are mediated by these species.

At the broadest scales, salvage logging, wildfire due to forest mismanagement, and land conversion present significant threats to dead wood environments and all of the species they support (Andrew et al. 2000; Watt et al. 2002; Majer et al. 2007; Ulyshen and Hanula 2009; Lemperiere and Marage 2010; Lindenmayer et al. 2012; Luke et al. 2014; Boucher et al. 2015). These threats lend urgency to improving understanding of the species and their interactions in dead wood. There are major gaps remaining, but a critical step in furthering our understanding of the role and importance of saproxylic insects is to better understand the most abundant taxa, like ants and termites, in dead wood, worldwide. We suggest three key areas of research for improving our understanding of the role of ants in dead wood environments. First, ants appear to act as top-down predators in dead wood, but their impact upon prey abundance and diversity in dead wood has only rarely been measured (Deligne et al. 1981). Quantifying their impacts as predators upon key groups, such as termites, in dead wood in relation to stage of decomposition should thus be a research priority. Second, because the impacts of ant nesting and other ant activities in dead wood are transitory, it is critical to understand the relationships between ant species and decay stage of dead wood. This is a necessary first step in understanding their impacts on the rate of decomposition, as the arrival and duration of ant impacts in decaying wood may create alternate pathways in carbon and nutrient cycling (e.g., redirecting termite- to fungal-mediated wood decomposition). This area of research is closely related to the third key area of research: the impact of ant nesting and activity upon microbial communities in dead wood. Ants may have important impacts upon microbial community assembly and succession in the dead wood environment because they produce a number of antimicrobial compounds that likely impact both fungal and bacterial communities, especially in the vicinity of their nests (Fernandez-Marin et al. 2006; LaRosa et al. 2012; Tranter et al. 2014). Thus, because of their high abundance in dead wood, through their interactions with other saproxylic insects like termites, and their potential impacts upon microbial communities, ants likely play a key role in the decomposition process of dead wood, worldwide. However, the magnitude and direction of these ant-mediated ecosystem effects are almost entirely unknown.

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Chapter 9
Diversity and Ecology of Saproxylic Hemiptera

Martin M. Gossner and Claas Damken

Abstract Saproxyly evolved several times independently within the insect order Hemiptera. Saproxylic Hemiptera are ancient groups of insects with approx. 5000 species described worldwide. They occur in all major zoogeographic regions but show the highest diversity in the tropics and subtropics. Species of this group are predominantly fungivores, sucking on fungal hyphae in deadwood, but also include a number of predators. They colonize a broad range of habitats, including deadwood structures of living trees as well as standing and downed logs of different diameters and decay stages. Also several pyrophilous species are known. Although most species have good dispersal capacities to find ephemeral deadwood structures, many species with reduced wings are known to occur in leaf litter, which provides a stable habitat, particularly in the tropics. Despite this numerical and ecological importance, our knowledge about the biology and ecology of these species is scarce. Most information is available from temperate and boreal forests, where many species are highly threatened due to intensive management and decreased fire frequency in fire-prone systems. It can be assumed that a high percentage of tropical species with their concealed lifestyle are still not discovered. More research on the ecology and habitat requirements of saproxylic Hemiptera is needed to protect this ancient and ecologically diverse group.

9.1 Introduction

Saproxylic behavior evolved several times independently within the Hemiptera (Fig. 9.1). We define saproxylic species as species that depend during some part of their life cycle, upon wounded or decaying woody material from living, weakened, or

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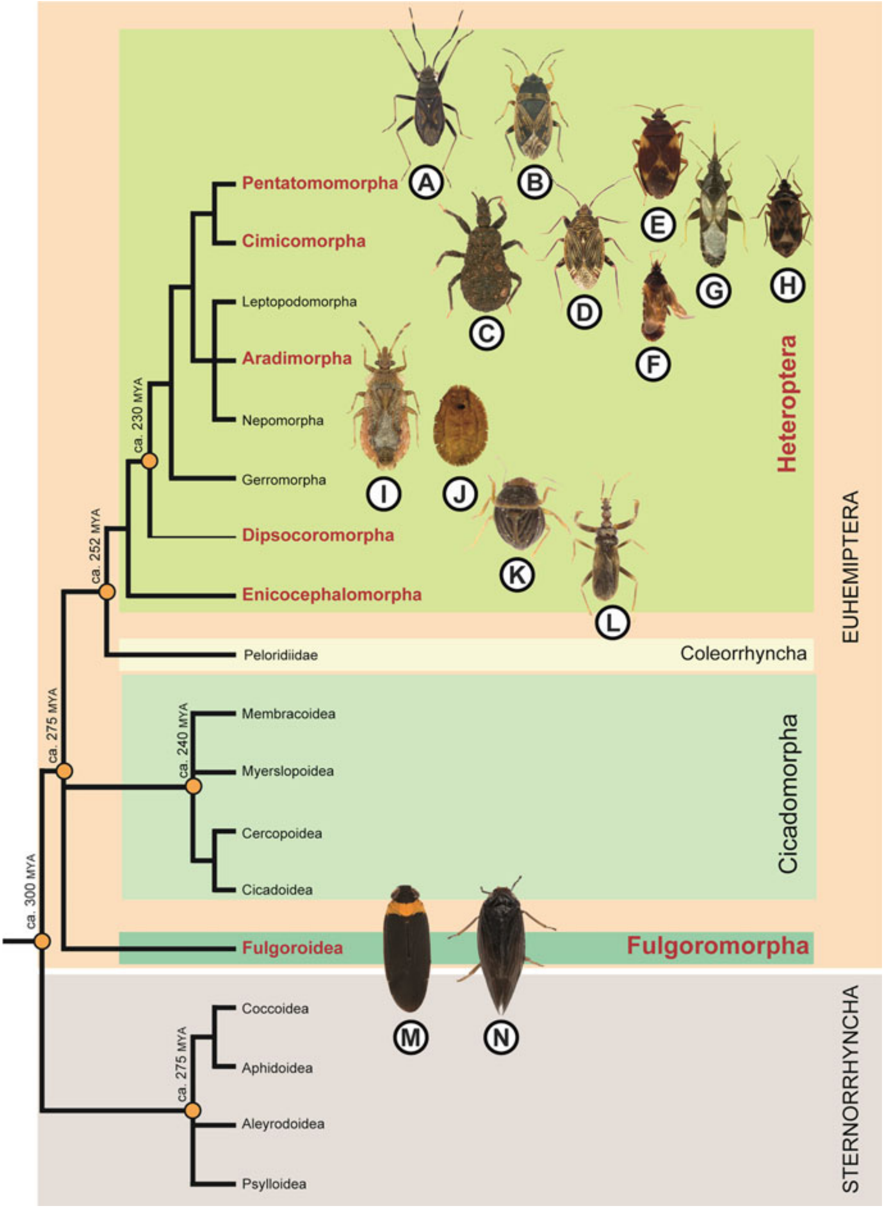

Fig. 9.1 Higher taxon phylogeny, showing the phylogenetic development of saproxylic species within the Hemiptera. Colored boxes indicate major groups (gray, red) and suborders (green colors) within the order Hemiptera. Groups in which saproxylic species evolved are marked in red. Each family is illustrated by a picture of one species (not scaled). Pentatomomorpha: (A) Pyrrhocoridae, *Ectatops* Amyot & Serville, 1843, sp. (Brunei), ♂ 9.2 mm; (B) Rhyparochromidae, *Trapezonotus dispar* Stål, 1872 (Germany), ♂ 4.9 mm. Cimicomorpha: (C) Reduviidae Physoderinae (Madagascar), juv. 5.5 mm; (D) Miridae Cylapinae *Peritropis javanica* Poppius 1909 (Brunei), ♀ 3.7 mm;

dead trees, following Stokland et al. (2012). The number of saproxylic species is not well documented, but there might be approx. 5000 species worldwide. Within the suborder Auchenorrhyncha, saproxylic species occur only in two families (Achilidae and Derbidae) of the superfamily Fulgoromorpha. Within the suborder Heteroptera, saproxylic species occur in 15 families of 5 superfamilies: Pentatomomorpha (Pyrrhocoridae and Rhyparochromidae), Cimicomorpha [following Schuh and Stys (1991)] (Reduviidae, Miridae, Medocostidae, Lasiochilidae, Lyctocoridae, and Anthocoridae), Aradimorpha (Aradidae and Termitaphididae), Dipsocoromorpha (Ceratocombidae, Hypsipterygidae, and Schizopteridae), and Enicocephalomorpha (Enicocephalidae and Aenictopecheidae) (Table 9.1). We follow Sweet (1996), who proposed Aradomorpha (renamed to Aradimorpha in 2006 to avoid homonomy; Sweet 2006) as infraorder, although this is not generally accepted, as recent cladistic analyses and studies on extant and fossil material support its rank as superfamily Aradoidea within the Pentatomomorpha (Cassis and Schuh 2010; Yao et al. 2012).

Saproxylic Hemiptera are geologically a very ancient group. Fossil records date back to the Lower Cretaceous, found in the fossils of the Santana Formations (Grimaldi 1990) and the Crato fossil beds (Martill et al. 2007) in Brazil (Achilidae: 100–140 Mya; Popov and Bechly 2007; Szwedo 2007; Asche 2015; Heiss 2016b) and in Neocomian amber from Lebanon (120 Mya, e.g., Enicocephalidae; Grimaldi et al. 1993; Azar et al. 1999), but some might have evolved much earlier in the Lower Triassic to Upper Permian (ca. 250 Mya; e.g., Enicocephalidae) (Grimaldi et al. 2002; Grimaldi and Engel 2005). In the Upper Cretaceous, many records are known from Burmese and Siberian amber (90–100 Mya, e.g., Enicocephalidae, Aradidae, Achilidae; Kormilev and Popov 1986; Ross et al. 2010; Heiss and Poinar 2012b). Many more species were found in younger Eocene (45 Mya) and Miocene Baltic and Saxonic (22 Mya) amber (Heiss 2013c, 2014a, 2016d) and the Miocene Dominican (15–20 Mya; Aradidae, Termitaphididae; Heiss 2000a; Heiss and Poinar 2012a) and Mexican amber (15–26 Mya; Aradidae, Termitaphididae; Poinar and Heiss 2011; Heiss 2016a). Beside amber inclusions, Aradidae also occur in sediments of Middle Eocene Messel Maar (48 Mya) (Wappler et al. 2015). Specimens enclosed in amber and sediments illustrate that the general habitus of these species have not change substantially since then (see, e.g., Heiss and Poinar 2012b) (Fig. 9.2).

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Fig. 9.1 (continued) (E) Medocostidae *Medocostes lestoni* Štys, 1967 (Ghana) ♀ 8.3 mm; (F) Lasiochilidae *Lasiochilus fusculus* (Reuter 1871) (USA), ♀ 2.9 mm; (G) Anthocoridae *Scoloposcelis pulchella* (Zetterstedt 1838) (Germany), ♂ 3.5 mm; (H) Lyctocoridae *Lyctocoris variegatus* Péricart, 1969 (Iran), ♀ 3.5 mm. Aradimorpha: (I) Aradidae *Aradus obtectus* Vásárhelyi, 1988 (Germany), ♂ 7.2 mm; (J) Termitaphididae *Termitaradus australiensis* (Mjöberg, 1914) (Australia), sex unknown, ca. 4 mm. Dipsocoromorpha: (K) Schizopteridae sp. (Brunei), sex unknown, 0.9 mm. Enicocephalomorpha: (L) Enicocephalidae *Oncylocotis* Stål sp. (Brunei), ♂ 7.1 mm. Fulgoromorpha: (M) Achilidae *Plectoderes* (*Plectoderes*) *collaris* Coquebert de Montbret, 1801 (Costa Rica), ♂ 5.6 mm; (N) Derbidae *Malenia bosnica* (Horváth, 1907) (Albania), ♂ 4.7 mm. Tree adapted from Aguin Pombo and Bourgoin (2014). Photo credits: Claas Damken (A, D, K, L), Gerhard Strauss (B, G, I), Martin M. Gossner (C, H), Laurent Fauvre (E), Scott Horn (F), Mauricio García (J), Gernot Kunz (M, N)

Table 9.1 Overview of saproxylic taxa within the Order Hemiptera

	Total				Zoogeographic regions—broad-scale realms[4]			
	Guild	Genera	Species	Saproxylic species	Nearctic	Palaearctic	Panamanian	Saharo-Arabian
Heteroptera								
Pentatomomorpha								
Rhyparochromidae (genus *Trapezonotus*)	M, C	1	14^{15}	Very few	x	x	–	x
Pyrrhocoridae (genus *Ectatops*)	?	1	28^{16}	Unknown	–	–	–	–
Cimicomorpha								
Reduviidae[2, c]	Pr	>975	Ca. 7000	Few		x	x	x
Elasmodeminae	Pr	1	3	Unknown	–	–	–	–
Physoderinae	Pr	Ca. 15	Ca. 65	Unknown	–	–	x	–
Reduviinae	Pr	140	>1000	Unknown	x	x	x	x
Miridae		1300^{10}	$10{,}400^{10}$	Few	x	x	x	x
Cylapinae	M/Pr	$>100^{11}$	$>457^{11}$	Most	x	x	x	x
Medocostidae	Pr	1^{10}	1^{10}	Unknown	–	–	–	–
Lasiochilidae	Pr	$10^{10,13}$	$62^{10,13}$	Some	x	–	x	–
Lyctocoridae	Pr	1^{10}	27^{10}	Some	x	x	x	x
Anthocoridae	Pr	71^{10}	445^{10}	Some	x	x	x	x
Dufouriellini	Pr	8	50	Some	x	x	x	x
Scolopini	Pr	13	Ca. 50	Some	x	x	x	–
Xylocorini	Pr	1	40	Some	x	x	x	x
Orinii	Pr/Ph	?	?	Few	x	x	x	x

Aradimorpha								
Aradidae	M	294[1]	2078[1]	Most	x	x	x	x
Aneurinae		9[6]	158[6]	Most	x	x	x	x
Aradinae		4[6]	234[6]	Most	x	x	x	x
Calisiinae	M, Ph?[14]	10[6]	106[6]	Many	x	x	x	x
Carventinae		105[6]	341[6]	Most	x	–	x	–
Chinamyersiinae		4[6]	7[6]	All	–	–	–	–
Isoderminae		1[6]	6[6]	All	–	–	–	–
Mezirinae		156[6]	1212[6]	Most	x	x	x	x
Prosympiestinae		5[6]	14[6]	All	–	–	–	–
Termitaphididae		2[2]	11[2,12]	All	x	–	x	–
Dipsocoromorpha	Pr							
Ceratocombidae	Pr	7	>50	Unknown	x	x	x	x
Hypsipterygidae	Pr	1[10]	4[10]	Unknown	–	–	–	–
Schizopteridae	Pr	56	>300	Unknown	x	x	x	x
Enicocephalomorpha	Pr							
Enicocephalidae	Pr	55[10]	304[9]	Unknown	x	x	x	x
Aenictopecheidae	Pr	10[10]	21[9]	Unknown	x	x	x	–
Auchenorrhyncha								
Fulgoromorpha								
Achilidae	M[b]	145[3]	465[3]	Most	x	x	x	x
Derbidae	M[b]	152[3]	1552[3]	Most	x	x	x	x

(continued)

Table 9.1 (continued)

	Zoogeographic regions—broad-scale realms[4]							
	Sino-Japanese	Neotropical	Afrotropical	Madagascan	Oriental	Australian	Oceanian	Highest species diversity
Heteroptera								
Pentatomomorpha								
Rhyparochromidae (genus *Trapezonotus*)	x	–	–	–	–	–	–	Palaearctic
Pyrrhocoridae (genus *Ectatops*)	x	–	–	–	x	–	x	Southeast Asia
Cimicomorpha								
Reduviidae[2, c]	x	x	x	x	x	x	x	Tropics
Elasmodeminae	–	x	–	–	–	–	–	Neotropical
Physoderinae	–	x	x	x	x	–	–	Madagascan, Oriental
Reduviinae	x	x	x	x	x	x	x	Tropics
Miridae	x	x	x	x	x	x	x	
Cylapinae	x	x	x	x	x	x	x	Tropics
Medocostidae	–	–	x	–	–	–	–	Afrotropical
Lasiochilidae	x	x	x	x	x	x	x	Neotropical, Oceanian
Lyctocoridae	x	x	x	?	x	x	x	Mainly Palearctic
Anthocoridae	x	x	x	x	x	x	x	Tropics
Dufouriellini	x	x	x	x	x	x	x	Mainly tropical
Scolopini	x	x	x	?	x	x	x	Neotropical
Xylocorini	x	x	x	x	x	x	x	Palearctic, Nearctic
Orinii	x	x	x	x	x	x	x	Tropics
Aradimorpha								
Aradidae	x	x	x	x	x	x	x	Tropics
Aneurinae	x	x	x	x	x	x	x	
Aradinae	x	x	x	x	x	x	x	Palearctic, Nearctic

Calisiinae	x	x	x	–	x	x	x	Australian, Neotropical, Afrotropical
Carventinae	x	x	x	x	x	x	x	Tropics
Chinamyersiinae	–	–	–	–	–	x	x	Australian, New Zealand
Isoderminae	–	x	–	–	–	x	–	New Zealand
Mezirinae	x	x	x	x	x	x	x	Neotropical, Oriental, Australian
Prosympiestinae	–	x	–	–	–	x	–	New Zealand[8]
Termitaphididae	–	x	x	–	x	x	–	Neotropical, Panamanian
Dipsocoromorpha								
Ceratocombidae	x	x	x	x	x	x	x	Old world tropics
Hypsipterygidae	–	–	x	–	x	–	–	Old world tropics
Schizopteridae	x	x	x	x	x	x	x	Tropics
Enicocephalomorpha								
Enicocephalidae	x	x	x	x	x	x	x	Oriental, Oceanian, Afrotropical, Madagascan
Aenictopecheidae	–	x	x	x	x	x	x	New Zealand, Neotropical, Oriental
Auchenorrhyncha								
Fulgoromorpha								
Achilidae	x	x	x	x	x	x	x	Northern subtropical region
Derbidae	x	x	x	x	x	x	x	Tropical to south temperate region

Only extant taxa are considered. Guild designations are as follows: *M* mycetophagous, *Pr* predacious, *C* carpophagous, and *Ph* phytophagous

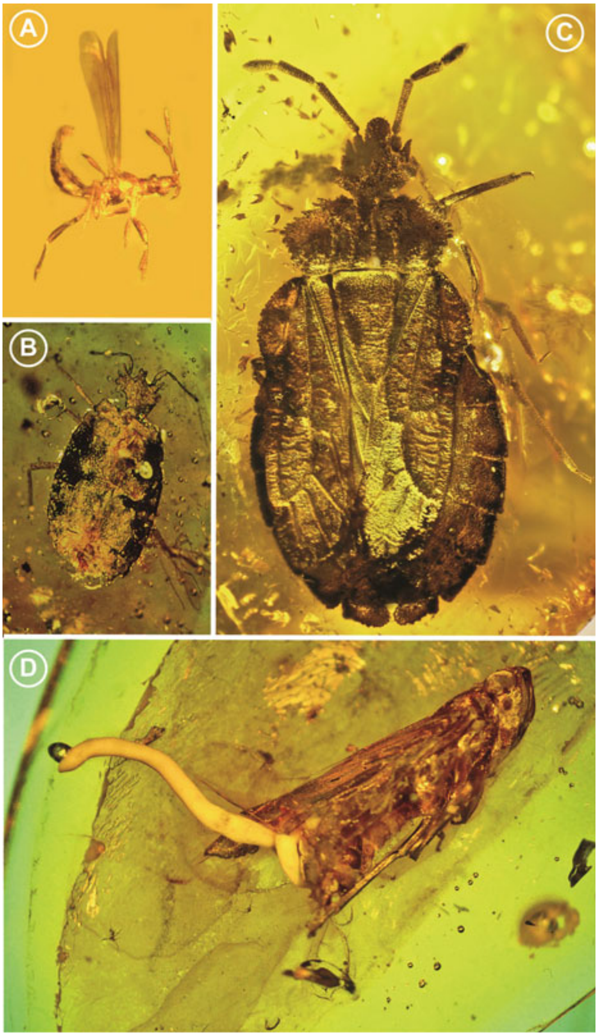
[1] Kormilev and Froeschner (1987), Zoological Record (2017); [2] Schuh and Slater (1995); Weirauch et al. (2014); [3] Bourgoin (2017); [4] Holt et al. (2013); [5] Wachmann et al. (2006); [6] Heiss and Péricart (2007); [7] Metcalf (1948); [8] Larivière and Larochelle (2006); [9] Štys (2008); [10] Henry (2009); [11] Gorczyca (2006a), Zoological Record (2017); [12] García et al. (2016); [13] Ford (1979); [14] Jacobs (2006); [15] Dellapé and Henry (2017); [16] Stehlík and Kment (2017)

[a] Very few species such as *Trapezonotus dispar* from the Palaearctic are thought to feed on fungal hyphae on or under deadwood logs (Wachmann et al. 2007)

[b] Only nymphs

[c] Of this family only a few species are expected to be saproxylic

Fig. 9.2 Examples of saproxylic Hemiptera from fossil records. (A) *Paralienates hyalinus* Maldonado-Capriles, Santiago-Blay & Poinar, 1996 (Heteroptera: Enicocephalidae), from lower Oligocene—upper Eocene Dominican amber, 25–40 million years old (Maldonado-Capriles et al. 1996). (B) *Acaricoris robertae* Heiss & Poinar, 2012 (Heteroptera: Aradidae, Carventinae), from Miocene Dominican amber, 15–20 million years ago (Heiss and Poinar 2012b). (C) *Aradus hoffmannii* Heiss, 2016, Holotype ♀ from Miocene Baltic Amber 22 million years ago (Heiss 2016d). (D) Achilidae (Fulgomorpha) parasitized by *Heydenius brownii* Poinar, 2001 (Nematoda: Mermithidae), from Eocene Baltic amber, 40 million years ago (Poinar 2001). Photo credits: George Poinar (A, B, D), Stefan Heim (C)



9.2 Diversity of Saproxylic Hemiptera

In saproxylic Auchenorrhyncha, more than 2000 species of Achilidae and Derbidae are recorded worldwide, but it is expected that many species are still undiscovered (Emeljanov 2009; Kunz 2011; Asche 2015) (Figs. 9.3A–E and 9.4C, D). Both families occur in all main zoogeographic regions but show the highest diversity in south temperate to tropical regions (Bourgoin 2017). Only immatures are saproxylic (O'Brien 1971; Holzinger et al. 2003; Nickel 2003). Adults of both families are only rarely found in deadwood, but single observations are documented, such as in Achilidae, *Cixidia lapponica* Zetterstedt, 1840, in Austria (Holzinger and Friess 2014).

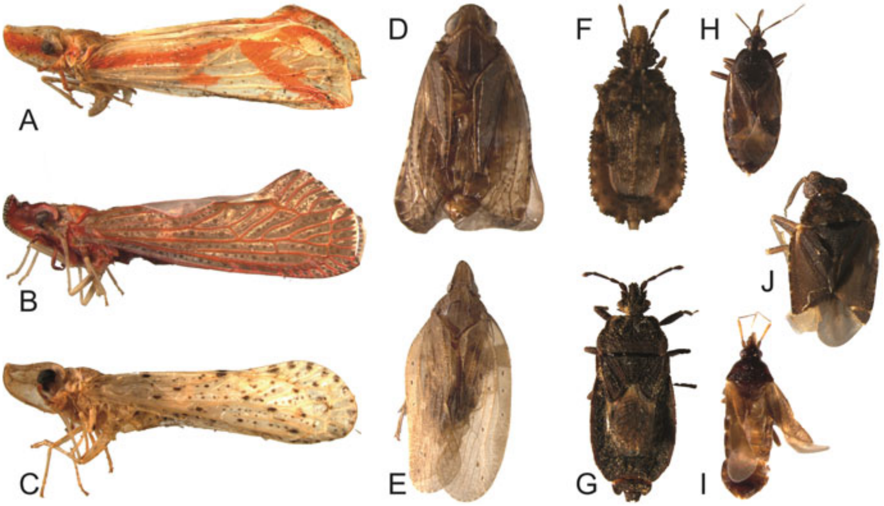


Fig. 9.3 Examples of saproxylic Hemiptera from North America. Auchenorrhyncha—Derbidae: (A) *Otiocerus coquebertii* Kirby, 1821, sex unknown 10.1 mm; (B) *Apache degeeri* (Kirby, 1821), sex unknown 10.2 mm; (C) *Otiocerus abbotii* Kirby, 1821, sex unknown 8.9 mm. Achilidae: (D) *Catonia* Uhler, 1895, sp., sex unknown 4.4 mm; (E) *Cixidia* Fieber, 1866, sp., sex unknown 8.6 mm. Heteroptera—Aradidae: (F) *Calisius contubernalis* Bergroth, 1913, ♀ 3.2 mm; (G) *Mezira granulata* (Say, 1832) , ♀ 5.5 mm. Lyctocoridae: (H) *Lyctocoris stalii* (Reuter, 1871), ♀ 4.2 mm. Lasiochilidae: (I) *Lasiochilus fusculus* (Reuter 1871), ♀ 2.9 mm. Miridae: (J) *Peritropis saldaeformis* Uhler, 1891, sex unknown 2.2 mm. Species D–J were reared from deadwood in the study of Ulyshen et al. (2012). Please note that the size of the species is not scaled. Photo credits: Scott Horn

In saproxylic Heteroptera, nymphs as well as adults have common feeding resource (see below). It can be estimated that within this suborder more than 3000 saproxylic species occur worldwide, but lists are probably far from being complete, in particular because of their cryptic lifestyle.

The importance of saproxylic behavior greatly differs among families within the Heteroptera. Almost all flat bugs (Aradimorpha: Aradidae) are saproxylic (>90%, approx. 2000), feeding on fungal hyphae. Only a few are recorded from nests or burrows of termites, bark beetles, birds, and rodents. However, it is likely that again fungal hyphae are the food source for aradids in those habitats (Kormilev and Froeschner 1987). They rarely become economic pests on cultivated mushrooms as reported for *Brachyrhynchus membranaceus* (Fabricius, 1798) by Meisong et al. (1998). Exceptions are a few phytophagous species such as the Palaearctic *Aradus cinnamomeus* Panzer, 1806, feeding on living pine and *Aradus pallescens frigidus* Kiritshenko, 1913, sucking on roots of herbaceous plants (Cistaceae: *Helianthemum*) (Heiss and Péricart 2007). There are eight subfamilies of flat bugs, with the Mezirinae being by far the most species-rich, accounting for about 60% of all described species with the highest diversity found in the tropics and subtropics (Table 9.1; Fig. 9.4a).

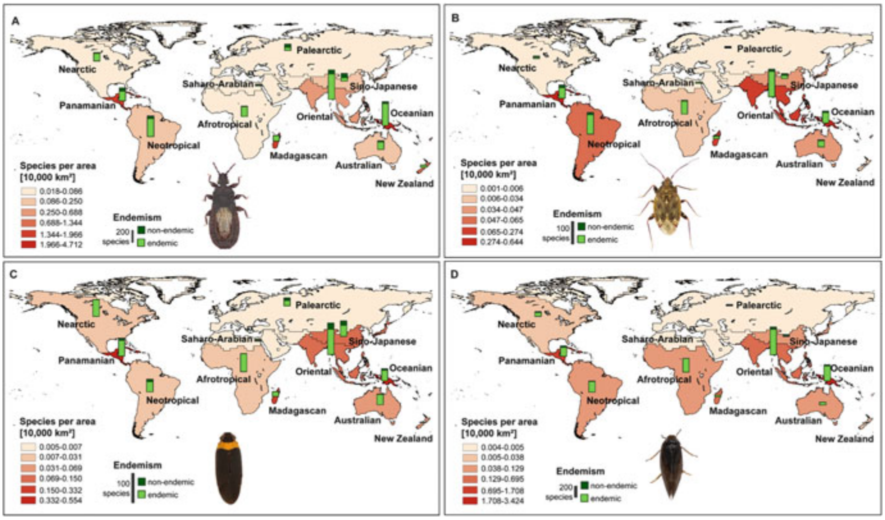


Fig. 9.4 Global distribution of saproxylic Hemiptera diversity illustrated for the Heteroptera families Aradidae (total, 2078 species, realm endemics, 91%) (**A**) and Miridae (Cylapinae only; total, 457 species, realm endemics, 93%) (**B**) and the Fulgoromorpha families Achilidae (total, 465 species, realm endemics, 93%) (**C**) and Derbidae (total, 1552 species, realm endemics, 95%) (**D**). The main zoogeographical realms identified by Holt et al. (2013) are distinguished. In deviation from this publication New Zealand is separated from Australia due to its exceptionally high endemism and suprageneric diversity in saproxylic Aradidae. The colors reflect the diversity corrected for the size of the realm from pale red (low diversity) to dark red (high diversity). The stacked bars show the total number of species and the proportion of endemics for the respective realm. Please note that the state of species recording differs among realms. Images: (**A**) Aradidae *Neuroctenus serrulatus* Stal, 1870 (Brunei), ♀ 5.4 mm; (**B**) Miridae Cylapinae *Peritropis javanica* Poppius 1909 (Brunei), ♀ 3.7 mm; (**C**) Achilidae *Plectoderes* (*Plectoderes*) *collaris* Coquebert de Montbret, 1801 (Costa Rica), ♂ 5.6 mm; (**D**) Derbidae *Malenia bosnica* (Horváth, 1907) (Albania), ♂ 4.7 mm. Only extant taxa including subspecies are considered.

References Used All data on Achilidae and Derbidae were extracted from Bourgoin (2017). Worldwide data on Aradidae and Cylapinae were extracted from Kormilev and Froeschner (1987) (Aradidae) and from Gorczyca (2006a) (Cylapinae). Additionally the following references were used:

Nearctic: Aradidae—Taylot (2009), Coscarón and Contreras (2015)

Panamanian, Neotropical: Aradidae—Heiss (1994a, 1999a, c, 2009b, 2012c, 2013d, 2014b, 2015b, 2016c, 2017), Contreras (2014), Coscarón and Contreras (2015), Heiss and Moragues (2015), Cylapinae: Wolski and Henry (2012); Wolski (2013, 2014), Carpintero and Cherot (2014)

Palearctic, Saharo-Arabian: Aradidae—Heiss (2001d), Ghahari and Heiss (2012), Cylapinae: Chêrot et al. (2006)

Afrotropical: Aradidae—Heiss (1986, 1988, 1989b, 1994b, 1999c, 2001c, 2004b, 2013a, 2015c), Jacobs (1986, 1990, 1996a, b, 2002, 2006), Kormilev (1986), Hoberlandt (1987), Heiss and Jacobs (1989), Heiss and Grebennikov (2015, 2016), Heiss and Baňař (2016); Cylapinae: Gorczyca (2006b, 2012, 2015), Gorczyca et al. (2016)

Madagascar: Aradidae— Heiss (2004c, 2010e, 2011e, f, 2012a, b), Heiss et al. (2012), Heiss and Marchal (2012), Heiss and Baňař (2013a), Baňař et al. (2016), Legros et al. (2016); Cylapinae: Gorczyca (2011, 2012)

Sino-Japanese: Aradidae—Heiss (2001d), Bai et al. (2006a), Heiss and Nagashima (2008), Nagashina and Shono (2012), Cui et al. (2015), Heiss and Baňař (2015), Ito (2016); Cylapinae: Yasunaga and Miyamoto (2006), Yasunaga and Wolski (2017)

The second family in the Aradimorpha are the circumtropical Termitaphididae (Fig. 9.1, image J), a small group of 2–4 mm large scale-like inquilines living in termite nests of the families Termitidae and Rhinotermitidae. There is currently no evidence to believe that any of the 11 extant species prey upon termites; rather it is suspected they have a mycetophagous lifestyle similar to the Aradidae (Sweet 2006). Marchal and Guilbert (2016) conducted a cladistic analysis using molecular and morphological characters and found that the Termitaphididae are not the sister group to the Aradidae and should be transferred into the Pentatomomorpha. However, for the purpose of this review, we keep the Termitaphididae in the Aradimorpha.

Within the Cimicomorpha, the family Lyctocoridae is currently comprised of 27 species in the genus *Lyctocoris* Hahn (Henry 2009), of which some species appear to be very common in deadwood of temperate forests, such as *Lyctocoris stalii* (Reuter, 1871) in North America (Ulyshen et al. 2012; Fig. 9.3) or *Lyctocoris variegatus* Pericart, 1969, in the Hyrcanian beech forests (*Fagus orientalis* Lipsky) of Iran (Müller et al. 2016) (Fig. 9.1, image H). Most Lyctocoridae occur in the Palearctic (Schuh and Slater 1995) and are subcortical predators of bark beetles and other small arthropods (Kelton 1967; Schuh and Slater 1995). In the family Anthocoridae, saproxylic species are found in several tribes. In the Xylocorini, members of the genus *Xylocoris* Dufour, 1831, are commonly collected under the bark (Schaefer and Panizzi 2000; Yamada et al. 2013), for example, *Xylocoris cursitans* (Fallen 1807) in beech forests (*Fagus sylvatica* L.) but also other forest types of Germany (pers. obs.) and *Xylocoris* cf. *ampoli* Yamada et al., 2013, under the bark of felled trees in a mixed dipterocarp forest in Brunei (pers. obs.). Among the tribe Scolopini, *Calliodis temnostethoides* (Reuter, 1884) was reared from deadwood logs in North America (Ulyshen et al. 2012). *Scoloposcelis pulchella* (Zetterstedt 1838) was observed in bark beetle galleries created in conifers of Central Europe (Kenis et al. 2004) (Fig. 9.1, image G), and the Australasian *Scoloposcelis parallelus* (Motschulsky, 1863) was collected under the bark and dead bark, feeding

◄

Fig. 9.4 (continued) ***Oriental, Oceanian***: Aradidae—Kormilev (1968, 1977, 1983, 1986), Vásárhelyi (1979, 1986, 1988, 1990), Heiss (1982, 1989a, 1992, 1993, 1994b, 1997, 1999b, 2000b, c, 2001b, 2003, 2007, 2009a, 2010a, b, c, d, f, g, 2011a, b, c, d, 2013b, e, 2015a), Monteith (1982), Heiss and Hoberlandt (1988), Bai et al. (2006b, 2007a, b, 2009, 2010, 2011a, b, 2012, 2017), Yan et al. (2007), Heiss and Nagashima (2008), Zhang et al. (2010a, b), Pham et al. (2011, 2013, 2014), Heiss and Baňař (2013b, c, d, 2015), Yang (2013), Heiss et al. (2014), Shi et al. (2016); Cylapinae: Gorczyca (2006c), Gorczyca and Wolski (2006, 2007), Moulds and Cassis (2006), Wolski and Gorczyca (2006, 2007, 2012, 2014a, b), Chêrot and Gorczyca (2008), Gorczyca (2008, 2014), Gorczyca and Chêrot (2008), Sadowska-Woda and Gorczyca (2008), Wolski (2010, 2012), Konstantinov (2012), Murphy and Polhemus (2012), Mu and Liu (2014), Yasunaga et al. (2015), Yeshwanth et al. (2016) Yeshwanth and Cherot (2015), Wolski et al. (2016), Wolski and Yasunaga (2016)

Australian: Aradidae—Kormilev (1977), Monteith (1997), Cassis and Gross (2002); Cylapinae: Cassis and Monteith (2006), Moulds and Cassis (2006), Wolski and Gorczyca (2014b), Namyatova and Cassis (2016)

New Zealand: Aradidae—Larivière and Larochelle (2006, 2014); Cylapinae: Larivière and Larochelle (2014)

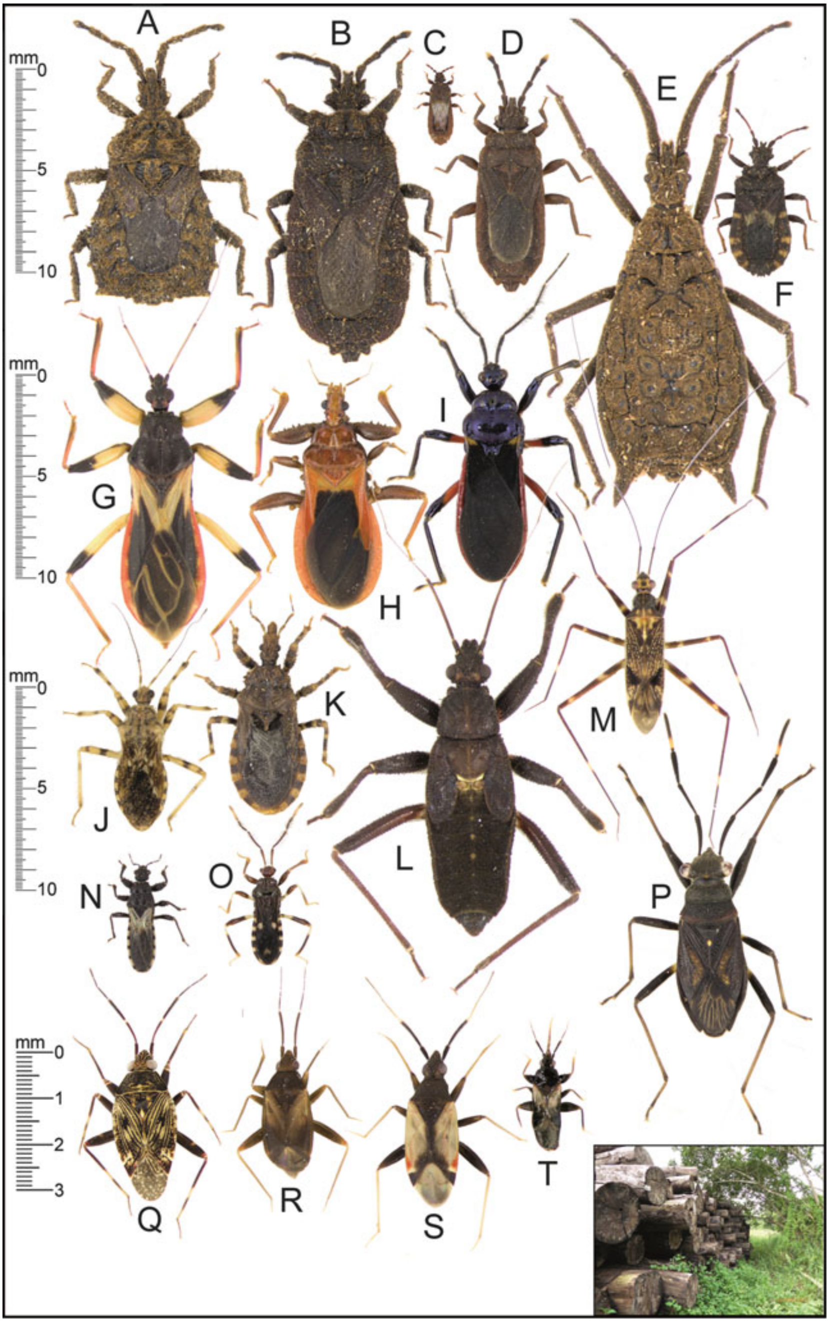


Fig. 9.5 Illustration of the diversity saproxylic Heteroptera found on a single wood pile at a sawmill property adjacent to a peat forest fragment near Labi (Brunei Darussalam, Borneo) during 4 days and nights in October 2014 and 1 day and night in January 2015. The ca. 20 m wide and up to 2 m tall pile of felled logs comprised mostly of *Shorea albida* (Dipterocarpaceae) with partially

on beetle larvae (Cassis and Gross 1996). The New Zealand endemic *Maoricoris benefactor* China 1933 is frequently observed on dying or dead trees of *Pittosporum crassifolium* Banks & Sol. ex A.Cunn. and *Pseudopanax* K. Koch spp. (Larivière and Larochelle 2004; Thorpe 2014a). In the tribe Dufouriellini, several members of the cosmopolitan genus *Cardiastethus* Fieber 1860 are presumably saproxylic. *Cardiastethus assimilis* (Reuter, 1871) and, in Australia, *C. aridimpressus* Gross, 1955; *C. lincolnensis* Gross, 1955; and *C. minutus* Poppius, 1909, are frequently collected under the bark (Cassis and Gross 1996). *Dufouriellus ater* (Dufour, 1833) is widespread in the western Palearctic Region and feeds on bark beetles (Scolytidae) under the bark (Schaefer and Panizzi 2000). In the tribe Oriini, *Orius insidiosus* (Say, 1832) was reared from deadwood logs in North America (Ulyshen et al. 2012), but this species and most members of Oriini are usually associated with living forbs, shrubs, and trees, where they feed both on small invertebrates and plant material such as pollen (Schuh and Slater 1995; Schaefer and Panizzi 2000). Species of Lasiochilidae mainly occur in the tropics with about 100 species but are nearly absent from the Palaearctic (Schuh and Slater 1995). In North America, *Lasiochilus fusculus* (Reuter 1871) was reared from deadwood logs (Ulyshen et al. 2012; Fig. 9.3).

Specimens of *Medocostes lestoni* Štys, 1967, in the monotypic family Medocostidae have been collected from under the bark in Africa (Kerzhner 1989; Schuh and Slater 1995). Almost nothing is known about the natural history of this family.

In the tropics, some Reduviidae of the subfamilies Elasmodeminae, Physoderinae (Fig. 9.1, image C), and Reduviinae (Fig. 9.5, image G, H) might be classified as

Fig. 9.5 (continued) loose bark and fungal growth (inset). *S. albida* trunks harvested from the edge of a peat dome often have a hollow heart, thereby creating additional microhabitats for saproxylic species. Specimens Q–T are shown at a different scale. Additional species with known or suspected deadwood association but collected by light trapping near the old log pile are not shown here (e.g., Miridae: Cylapinae). Insects were not collected deep inside and on the top of the log pile due to health and safety issues. Also, species, collected at the old log pile but for which an association to deadwood is doubtful, are not shown here (e.g., diurnal foliage-living *Eulyes* Amyot & Serville, 1843 sp. (Reduviidae: Harpactorinae); granivore *Horridipamera nietneri* (Dohrn, 1860) (Rhyparochromidae); Cydnidae spp.). Species list: (A) *Crimia tuberculata* (Amyot & Serville, 1843) (Aradidae: Mezirinae) (♀), in litter at base of pile; (B) *Brachyrhynchus* sp. (Aradidae: Mezirinae) (♀), on bark; (C) cf. *Neuroctenus* Fiber sp. (Aradidae: Mezirinae) (♂), under bark; (D) *Brachyrhynchus membranaceus* (Fabricius) (Aradidae: Mezirinae) (♀), on fungi; (E) *Chelonocoris acuminatus* Miller (Aradidae: Mezirinae) (♀), on fungi/bark; (F) *Artabanus bilobiceps* (Lethierry, 1888) (Aradidae: Mezirinae) (♀), on fungi/bark; (G) *Tapeinus* cf. *singularis* (Walker, 1873) (Reduviidae: Reduviinae) (♂), under bark; (H) Reduviinae (Reduviidae) (♂), under bark; (I) Ectrichodiinae indet. (Reduviidae) (♂), in litter at base of pile; (J) Reduviinae Reduviidae) (♂), under bark; (K) Physoderinae (Reduviidae) (♂), in litter at base of pile; (L) Reduviidae nymph, in litter at base of pile; (M) *Rhinomiris* Poppius sp. (Miridae: Cylapinae) (♀), on fungi/bark; (N) *Neostachyogenys tristis* Miller, 1953 (Reduviidae: Reduviinae) (♂), under bark; (O) Ectrichodiinae (Reduviidae) (♂), in litter at base of pile; (P) *Ectatops* Amyot & Serville 1843 sp. (Pyrrhocoridae) (♂), in litter at base of pile; (Q) *Peritropis* Uhler 1891 sp. (Miridae: Cylapinae) (♂), on bark; (R) *Fulvius* Stål 1862 sp. 1 (Miridae: Cylapinae) (♂), under bark; (S) *Fulvius* Stål 1862 sp. 2 (Miridae: Cylapinae) (♀), on bark; (T) Anthocoridae sp. (♂), under bark. Photo credits: Claas Damken

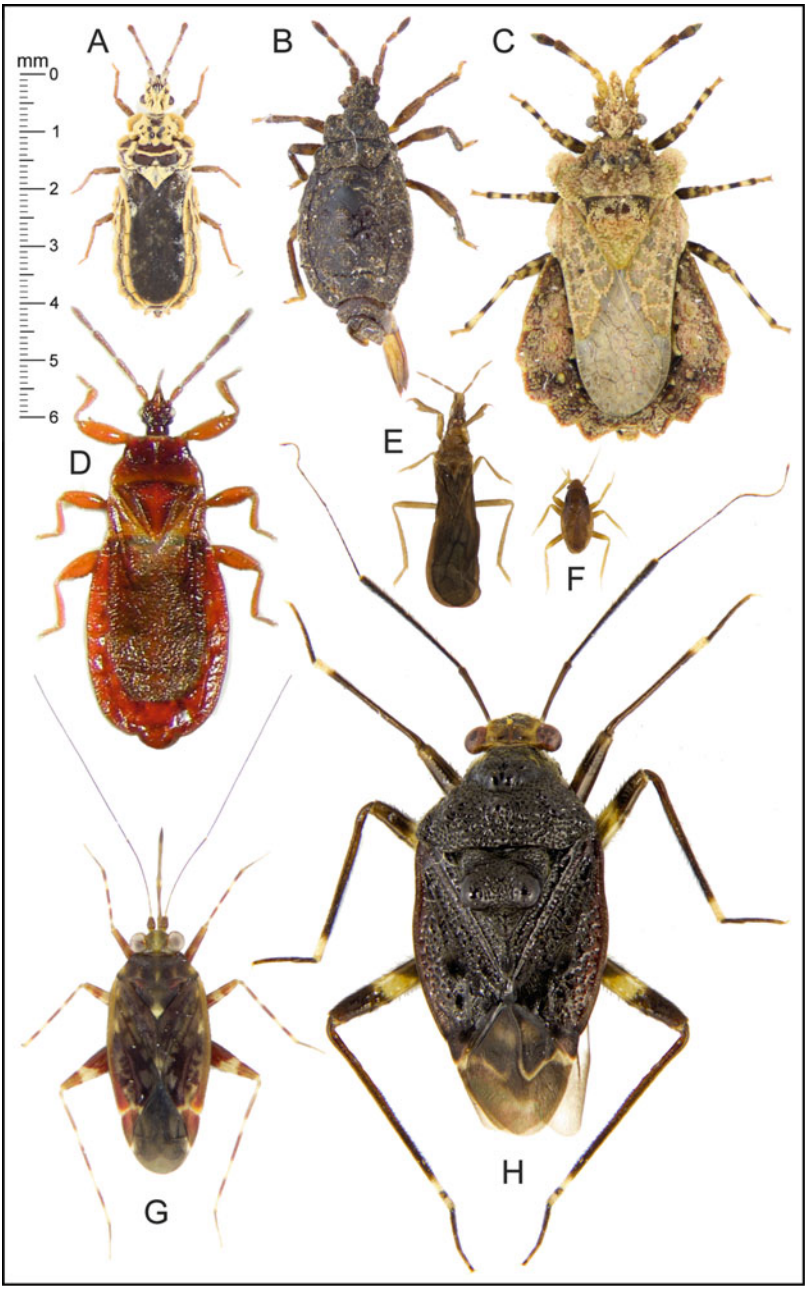


Fig. 9.6 Selection of species illustrating different saproxylic Heteroptera groups: (A) Aradidae, Carventinae, *Drakeida* sp. Kormilev, 1958 (♀), mixed peat forest, dead lying tree, DBH 15 cm, on bark, Badas Forest Reserve, Brunei 2014; (B) Aradidae, Prosympiestinae, *Neadenocoris* cf. *ovatus* Usinger and Matsuda 1959 (♀), *Pinus radiata* plantation, reared from dead pine log, Tarawera Forest, North Island, New Zealand 2010; (C) Aradidae, Chinamyersiinae, *Chinamyersia cinerea*

saproxylic (Schuh and Slater 1995). There are several observations of both juveniles and adults predating under the bark of deadwood logs or in tree hollows (Schuh and Slater 1995; Hwang and Weirauch 2012; pers. observ.). While the specific degree of deadwood dependence of any of these species is hitherto understudied, dorsally flattened Elasmodeminae and Reduviinae are also found under loose bark of living trees, and Physoderinae are frequently encountered in non-wood dead plant matter such as rotten banana leaves. We are thus convinced that deadwood habitat niches contribute to the high biodiversity observed in these taxa.

In the most species-rich Heteroptera family, Miridae, saproxylic species are known to occur only in the subfamily Cylapinae (Fig. 9.6, images G, H; Fig. 9.5, images M, Q, R, S; Fig. 9.7, image A), a primarily tropical group (Schuh and Slater 1995; Wheeler 2001; Gorczyca 2006a) (Fig. 9.4b). Several species have, however, also been reared from dead snags in North America (Ulyshen et al. 2012). While most specimens have been collected from deadwood or deadwood fungi and are presumably fungivorous (Wheeler and Wheeler 1994; Yasunaga 2000), there is evidence for a predatory lifestyle among some Cylapinae (Pluot-Sigwalt and Chérot 2013).

Within the predacious Dipsocoromorpha, members of the families Ceratocombidae (Fig. 9.6, image F), Hypsipterygidae, and Schizopteridae (Fig. 9.1, image K) have been extracted from deadwood (Schuh and Slater 1995) and reared from non-native deadwood in *Pinus radiata* plantations in New Zealand (Damken et al. in prep). However, more specimens have been collected in humid forests and near streams, by litter sifting, light trapping, as well as flight interception traps (Weirauch and Fernandes 2015). Due to their small size, a lack of sampling in many regions, and the taxonomic impediment, many species remain undescribed, and no studies have so far investigated if any of the species are truly saproxylic or just utilize suitable microhabitats such as the subcortical space.

In the Enicocephalomorpha, which consist of Enicocephalidae (ca. 400 species) and Aenictopecheidae (ca. 20 species), some species have been reared from deadwood, such as *Systelloderes inusitatus* Drake & Harris 1927 (Enicocephalidae) in North America (Ulyshen et al. 2012) and *Maoristolus tonnoiri* (Bergroth, 1927) in exotic *Pinus radiata* plantations in New Zealand (Damken et al. in prep) (Fig. 9.6,

Fig. 9.6 (continued) (Myers & China, 1928) (♀), Manuka (*Leptospermum scoparium*) forest, fine woody debris, under bark, Dunedin, New Zealand 2015; (D) Aradidae, Isoderminae, *Isodermus gayi* (Spinola, 1852) (♂), Chile; (E) Aenictopecheidae, Maoristolinae, *Maoristolus tonnoiri* (Bergroth, 1927) (sex unknown), *Pinus radiata* plantation, reared from dead pine log, Tarawera Forest, North Island, New Zealand 2010; (F) Ceratocombidae, Ceratocombinae, *Ceratocombus novaezelandiae*, Larivière and Larochelle 2004 (♂), *Pinus radiata* plantation, reared from dead pine log, Tarawera Forest, North Island, New Zealand 2010; (G) Miridae, Cylapinae, Cylapini, Cylapomorpha Poppius 1914 sp. (♀), mixed dipterocarp forest, dead lying tree, DBH 15 cm, on bark with fungi, Temburong National Park, Brunei 2014; (H) Miridae, Cylapinae, Bothriomirini, *Leprocapsus scutellaris* Poppius 1914 (♀), mixed dipterocarp forest, dead lying tree, DBH 60 cm, on bark, Temburong National Park, Brunei 2014. Photo credits: Claas Damken, Ernst Heiss (D)

Fig. 9.7 Selection of tropical saproxylic Hemiptera in their habitat. (A) Miridae, Cylapinae, *Rhinocylapus* Poppius 1909 sp. ♂ ca. 4–5 mm & ♀ ca. 6–7 mm, found on a dead lying tree in a lowland mixed dipterocarp forest, Temburong National Park, Brunei 2014. (B) Reduviidae, Centrocnemidinae, *Neocentrocnemis* Miller, 1956 sp. ♂, ca. 25–30 mm, found on bark in a lowland mixed dipterocarp forest, Temburong National Park, Brunei 2014. (C, D) Deadwood habitats of saproxylic Heteroptera in the Marojey National Park, North-East Madagascar (30.09.2012). Under the bark of downed tree (10 m long, 20 cm diameter; C, top) with white fungi fruiting bodies (inset) one female of Aradidae, Mezirinae, *Neuroctenus* Fieber (1860) sp. 1 ♀ 5.7 mm (C, bottom left) and one

image E). Similar to the Dipsocoromorpha, numerous species await description (Štys 2008), and research is needed to assess how strong members of the Aenictopecheidae and Enicocephalidae are linked to the deadwood food web. The insular part of Southeast Asia is a hotspot of generic and species diversity with diversity and endemism comparable to Madagascar, New Zealand, New Caledonia, and Fiji, which contrasts with the paucity in species and genera described for New Guinea and Australia (Štys 2008).

Within the Pentatomomorpha family Rhyparochromidae, only a few species are suggested to be saproxylic such as the Palaearctic *Trapezonotus dispar* Stål, 1872 (Wachmann et al. 2007) (Fig. 9.1, image B). Species of this family are occasionally collected from deadwood in the tropics (pers. oberserv.), but details of their biology remain largely unknown. The family Pyrrhocoridae might also include some saproxylic species in the genus *Ectatops* Amyot & Serville, 1843 (Fig. 9.5, image P). Although there is very little information published on bionomics of *Ectatops*, specimens have been found in deadwood in the Cameron Highlands (Peninsular Malaysia) (Kment, pers. comm) and in Borneo (Brunei) in an old log pile (Fig. 9.5, inset), on the bark of dead trees as well as on fruiting bodies of deadwood fungi at night (pers. observ.).

9.2.1 Global Gradients in Diversity

By far the highest diversity of saproxylic Hemiptera can be found in the tropics and subtropics (Fig. 9.4). The highest numbers of species relative to area occur in the Panamanian (all groups), Oriental (Cylapinae), Oceanian (all groups), as well as Madagascan (all groups except Derbidae) realms. In contrast, the Nearctic (Aradidae and Cylapinae), Palaearctic (all groups), Saharo-Arabian (all groups), and Afrotropical (Aradidae) realms appear to be species-poor relative to their respective areas. It must be emphasized that for the Aradidae in the Afrotropical realm, further sampling and taxonomic work are needed to fully incorporate, for example, the presumably high number of yet unknown species from the Eastern Afromontane region and coastal forests of Eastern Africa into our findings (Štys and Baňař 2013).

In all zoogeographic realms, we found a very high percentage of endemism in all saproxylic Hemiptera (total percentage: Aradidae, 91%; Miridae Cylapinae, 93%;

Fig. 9.7 (continued) larvae of Reduviidae, Physoderinae sp. juv. 5.5 mm (C, bottom right) was found. Under the bark of a downed log in a small canopy gap (D) with many orange fungi fruiting bodies (inset), many larvae, females and males of Aradidae, Mezirinae, *Neuroctenus* cf. *caffer* or *spiniceps* ♂ 5.9 mm + ♀ 6.9 mm (D, bottom, one male, one female) were found. (E) Aradidae, Mezirinae, *Mezira* Amyot & Serville 1843 sp. ♀ 8.8 mm found under the bark of a dying standing tree of >60 cm dbh, 50 cm above ground next to a fungi sporocarp in a restoration site of the Brazilian Atlantic forest near Assis (03.09.2012). Photo credits: A, B: Hanyrol H. Ahmad Sah, C, D, E: Martin M. Gossner

Achilidae, 93%; Debidae, 95%). This supports the classification of Holt et al. (2013), who classified the realms based on global distribution data for amphibians, non-pelagic birds, and nonmarine mammals. Across groups the highest percentages of endemics are found in the Afrotropical (mean 97% ± 2.5 SD), Madagascan (93 ± 4.8), Oceanian (90 ± 3.2), Neotropical (88 ± 6.4), Australian (88 ± 4.9), and Oriental (88 ± 5.5) realms, while the Saharo-Arabian (51 ± 27.9), Palearctic (51 ± 6.3), and Sino-Japanese (52 ± 20.2) realms show the lowest percentages. Some regions show high endemism rates only in particular groups, such as the Nearctic in Achilidae (98%). Apart from the Aradidae (39 species, 97% endemics), New Zealand as part of but in contrast to the Australian realm has a depauperate saproxylic Hemiptera fauna, with only one or two described species in each the Derbidae, Achilidae, and Cylapinae.

In general, neighboring realms which are connected by land often have a higher proportion of shared species, such as the Panamanian and the Neotropical realm [Aradidae, 44 shared species out of 510 species (8.6%); Cylapinae, 10/149 (6.7%); Achilidae, 7/34 (20.6%); Derbidae, 7/75 (9.3%)], the Palearctic and the Sino-Japanese realms [Aradidae, 31/202 (15.3%); Cylapinae, 3/26 (11.5%); Achilidae, 5/34 (15%); Derbidae, 12/75 (16%)], and the Oriental and Sino-Japanese realms [Aradidae, 44/565 (7.8%); Cylapinae, 6/142 (4.2%); Achilidae, 13/34 (38%); Derbidae, 21/75 (28%)].

9.3 Morphological Adaptations

Body size of saproxylic Hemiptera varies greatly. In Achilidae, species range from a few millimeters (e.g., Plectoderini Fennah; Fennah 1950; Asche 2015) to up to 15 mm, such as *Emeljanocarinus gargantuan* Bourgoin and Soulier-Perkins (2006), from Madagascar, which is regarded as an example of island gigantism (Bourgoin and Soulier-Perkins 2006; Asche 2015). In saproxylic Heteroptera, the largest variation in body size can be observed in the family Aradidae. Schuh and Slater (1995) note a range of 3–11 mm for Aradidae, but a recent survey by one of us in Northern Borneo yielded specimens ranging from 2 mm to nearly 20 mm.

Saproxylic Hemiptera species show numerous morphological adaptations to the cryptic life in deadwood. Most species are extremely dorsoventrally flattened, an adaptation for movement under the bark and in small crevices in wood (Fig. 9.8, image B) (Weber 1930). With their brownish to blackish color, they are well camouflaged in their habitat and thus difficult to detect. Pyrophilous species are all very dark, an adaptation to burned wood. Many apterous species of the flat bug subfamilies Carventinae (Fig. 9.8, image C) and Mezirinae (Fig. 9.5, image E) have waxy surface incrustations or are covered in debris, which might act as a form of camouflage when feeding in litter and on bark of rotten branches on the forest floor (Larivière and Larochelle 2006). In the wet tropics, where fallen dead trees do not offer much subcortical space but provide a rather stable habitat for aradids feeding on late succession stages, some larger species are remarkably tubercular bark mimics

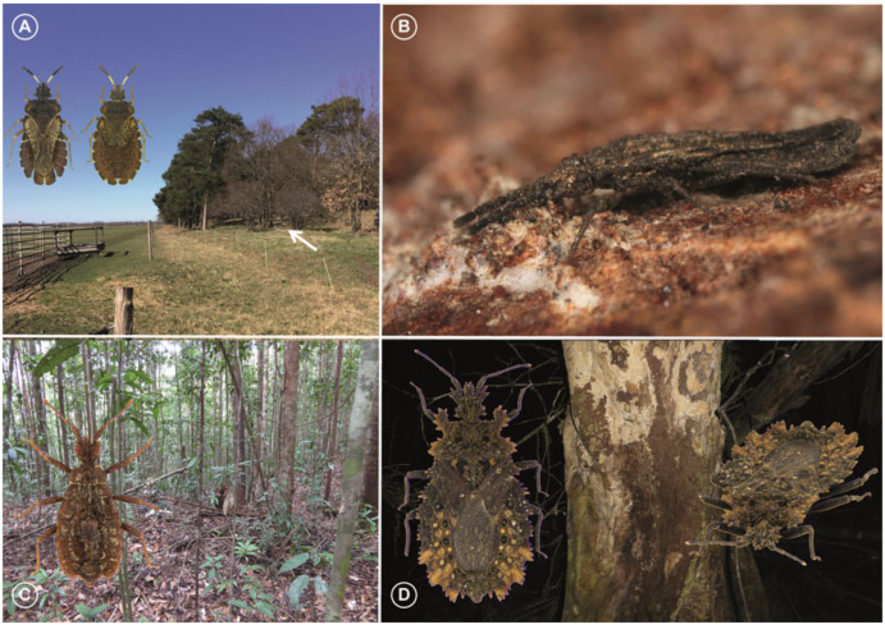


Fig. 9.8 Morphological adaptations of Aradidae. Many species that live in the deadwood-litter interface show wing reduction. (A) In Southeast European *Aradus distinctus* Fieber, 1860, females are mainly brachypterous and males macropterous (♂ 6.0 mm ♀ 6.8 mm). The white arrow shows the leaf litter microsite beyond a *Corylus avellana* L. shrub where the species was found in Brandenburg, Germany (Esser 2013). (B) Saproxylic Hemiptera that live under the bark are mostly dorsoventrally flattened, such as European *Quilnus marcosi* Heiss & Baena, 2006 (♂ 5.6 mm), found under the bark of a burned pine tree in the Valais, Switzerland. (C) Apterous Aradidae are commonly encountered in fine woody debris in tropical forests, where suitable habitats in close proximity reduce the need for dispersal. Carventinae sp. (♂ 3.0 mm), mixed dipterocarp forest, Andulau Forest Reserve, Brunei 2015. (D) Supracorticolous species in the tropics often show grotesque, tubercular form of bark mimics, adapted to exposed habitats such as dry snags. *Acantharadus quaternarius* (Bergroth, 1886), mixed peat swamp forest, Labu Forest Reserve, Brunei 2013 (♂ 17 mm). Photo credits: (A) habitat, Tobias Mainda; insets, Gerhard Strauss; (B) Martin M. Gossner; (C, D) Claas Damken

(Monteith 1982; see also below), such as the oriental *Acantharadus quaternarius* (Bergroth, 1886) (Fig. 9.8, image D). Apterous aradids living in wet litter beneath deadwood might use a secretion emitted from the dorsal abdominal scent glands as repellent (Aldrich 1988; Davidová-Vilímová 2006). Termitaphididae (Fig. 9.1, image J) living in termite nests are dorsoventrally flattened with flexible abdominal connexiva which are compressed to the ground when disturbed by the host termites (Myers 1924; Sweet 2006). They are completely lacking wings, eyes, and ovipositors and thus show extreme adaptations to their life in termite nests (Miller 1971; Schuh and Slater 1995). Also Achilidae are dorsoventrally depressed, and most species are brownish-white in color and well camouflaged. Immatures of Achilidae and Derbidae are coated with a waxy material which protects them from predators (Fig. 9.9) (Hepburn 1967; Liang and O'Brien 2002; Emeljanov 2009).

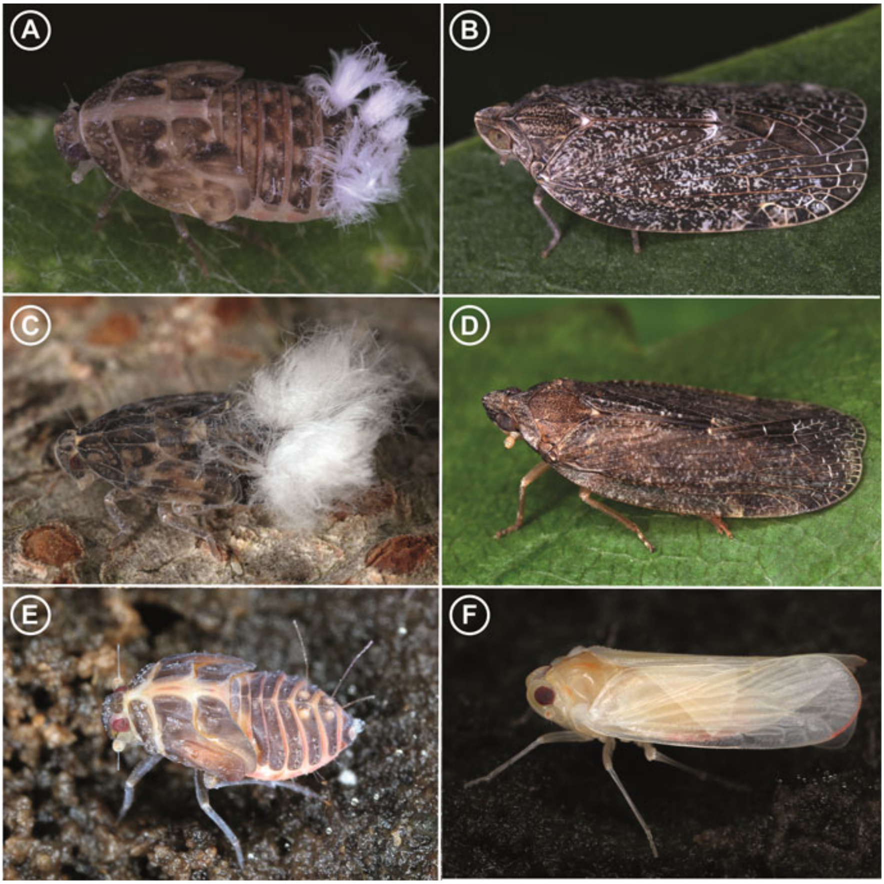


Fig. 9.9 Examples of Palaearctic saproxylic Auchenorrhyncha in their habitat (left nymphs, right adults). (A, B) Achilidae, *Cixidia pilatoi* D'Urso and Guglielmino 1995, 7.2 mm, Germany; (C, D) Achilidae, *Cixidia (Epiptera) lapponica* (Zetterstedt, 1840), 7.4 mm, France; (E, F) Derbidae, *Omolicna* Fennah, 1945, sp., 4.3 mm, Costa Rica. The nymphs are coated with a waxy material which protects them from predators. Photo credits: Gernot Kunz

Species that live subcortically under the bark of deadwood and feed on ephemeral food resources have well developed wings and show high dispersal propensities. This allows them to quickly colonize new wood sources (Heiss and Péricart 2007; Seibold et al. 2014). Flat bugs that inhabit the wet forest floor and feed there on fungi growing on small branches or in the log-soil interface are especially diverse in the tropical rainforests (Monteith 1982). They use more predictable resources which have resulted in wing reductions in many species (dispersal capability-reproduction trade-off; Guerra 2011). Many of the tropical species in this guild have evolved a more sedentary life on the outside of the bark. As flight ability and flat shape are not a constraint for this species, but camouflage becomes even more important, these rainforest Aradidae lost their wings and evolved into grotesque, tubercular forms that resemble bark (Usinger and Matsuda 1959; Monteith 1982). According to Monteith (1982), tropical Aradidae exhibit an evolutionary stable stage in which subcortical species coexist with a complement of totally apterous, supracorticolous species. Apterous and micropterous species living in leaf litter are exceptionally species-rich in the subfamilies Carventinae and Mezirinae (Heiss 2001a, 2012b; Heiss and Grebennikov 2016) in all tropical regions. They show a high degree of endemism, e.g., all apterous Mezirinae from Madagascar are considered to be endemic (Heiss 2012b). Wing reductions, however, occur in over 50% of all known genera and in seven of the eight subfamilies of Aradidae (Schuh and Slater 1995). Although wing reductions are rare in the subfamily Aradinae, females of species living in leaf litter, such as *Aradus distinctus* Fieber, 1860, from Southeastern Europe (Fig. 9.5; Wachmann et al. 2007) and *Aradus safavii* Hoberlandt, 1974, from Iran (considered as an endemic species of the northeastern mountain range; Heiss 2004a) are mostly brachypterous (at least in one sex).

Within the Heteroptera, elongations of stylet bundles independently evolved as an adaptation to the mycetophagous feeding behavior at least four times (Cobben 1978). In Aradidae, which live under the bark of deadwood, and in Termitaphididae living in termite nests, the bundles are much longer than the rostrum and coiled within the clypeus region (Miller 1971). The bundles can be up to five to six times the lengths of their bodies (Weber 1930) and allow them to pierce fungal hyphae deep in the wood. Similarly very elongated coiled mouthparts have been described in Achilidae (O'Brien 2002). Additionally adaptations of the gut systems to the mycetophagous feeding behavior have been observed in Aradidae (Nardi et al. 2009).

9.4 Ecology

While many studies have focused on saproxylic beetles, the ecology of saproxylic Hemiptera remains largely unexplored, especially in tropical and subtropical regions. Many saproxylic Hemiptera, such as all Aradidae, show acyclic generations, meaning that different juvenile stages and adults can be observed all year round (Fig. 9.13a; Heiss and Péricart 2007; Wachmann et al. 2007). Achilidae may exhibit a single generation per year (Bartlett et al. 2011), but adults are not closely synchronous (O'Brien 1971). Species might avoid extreme climatic conditions by moving to microsites with favorable microclimatic conditions. In temperate regions, some species have been observed overwintering in the litter close to their host trees (Heliovaara 1982; Leschen and Taylor 1987), and in tropical regions during dry spells, species presumably outlast unfavorable periods in the litter or topsoil. In Aradidae, parental care has been observed, during which the male is safeguarding the egg mass for several weeks and parental care might be extended to nymphal stage (McClure 1932; Taylor 1988a). This might have evolved to reduce mortality of offsprings due to high predation pressure or pathogenic fungi (Klug and Bonsall

2014). Stridulatory structures have evolved several times within the Aradidae (Heteroptera) (Usinger 1954; Heiss and Baňař 2016) and also in Achilidae and Derbidae (Fulgoromorpha) (Tishechkin 2008; Cocroft et al. 2014). These structures produce sound and vibration and most likely play an important role in mating but might also be used in other behavioral and ecological contexts (Cocroft et al. 2014).

9.4.1 Trophic Level and Host Specialization

Among the saproxylic Hemiptera, none of the known species is able to utilize nutrients from the wood itself. Most are fungivores, feeding on fungal hyphae by using their piercing-sucking mouthparts to suck the cell contents (Miller 1971). Some species are predators (only Heteroptera).

In Auchenorrhyncha, most adults feed on living woody plants. Achilidae are mainly polyphagous but are more often associated with gymnosperms than other planthopper families, whereas Derbidae are mainly host-specific (Wilson et al. 1994) and comprise some economic pest species (Wilson and O'Brien 1987). Nymphs of both families are fungivores, feeding on fungi under the bark of dead logs or decaying organic debris near the adult host plant, but little is known about the habitat association of these species, even in Europe where the autecology of insects is comparably well studied (Willis 1982; Wheeler and Wilson 1996; Howard et al. 2001; Emeljanov 2009; Asche 2015). Nymphs of Achilidae have often been observed on patches of fungus under the bark of pine and oak trees (Asche 2015). To give a few examples, species of the genus *Catonia* are known to be associated with dead pines (O'Brien 1971); others are reported from pines and spruce, e.g., *Cixidia lapponica* (Zetterstedt, 1840) (Nickel 2010; Holzinger and Friess 2014), and oak, e.g., *Cixidia pilatoi* (D'Urso and Guglielmino 1995) (Nickel 2003). In Derbidae, many tropical species seem to be associated with palms (Howard et al. 2001) but are known from broad-leaved trees, e.g., *Quercus* and *Ulmus*, in temperate forests (Willis 1982; Wheeler and Wilson 1996). The ecology of both families is largely unknown.

Saproxylic Heteroptera depend on deadwood as both larvae and adults. Most species are fungivores, sucking on fungal hyphae on or under the bark (Aradidae, Miridae: Cylapinae) or at the log-litter interface (Aradidae, Rhyparochromidae: *Trapezonotus dispar* Stål, 1872) (Wachmann et al. 2007). Sometimes, preferably in the evening and at night, they can be found on fungal fruiting bodies (Fig. 9.10). Some species seem to be specialized on particular fungi, for instance, the Palaearctic *Aradus betulae* (Linnaeus, 1758) on *Fomes fomentarius* (L.: Fr.) J.J. Kickx (Fig. 9.10) or *Aradus obtectus* Vásárhelyi (1988), on *Fomitopsis pinicola* (Sw.: Fr.) P. Karst., but still little is known about the fungal host associations of most species. Even for Europe where we have the most comprehensive knowledge, the preference for particular fungi is far from clear (Gossner et al. 2007; Heiss and Péricart 2007) and often anecdotal (e.g., Förster 1953; Gyllensvard 1958).

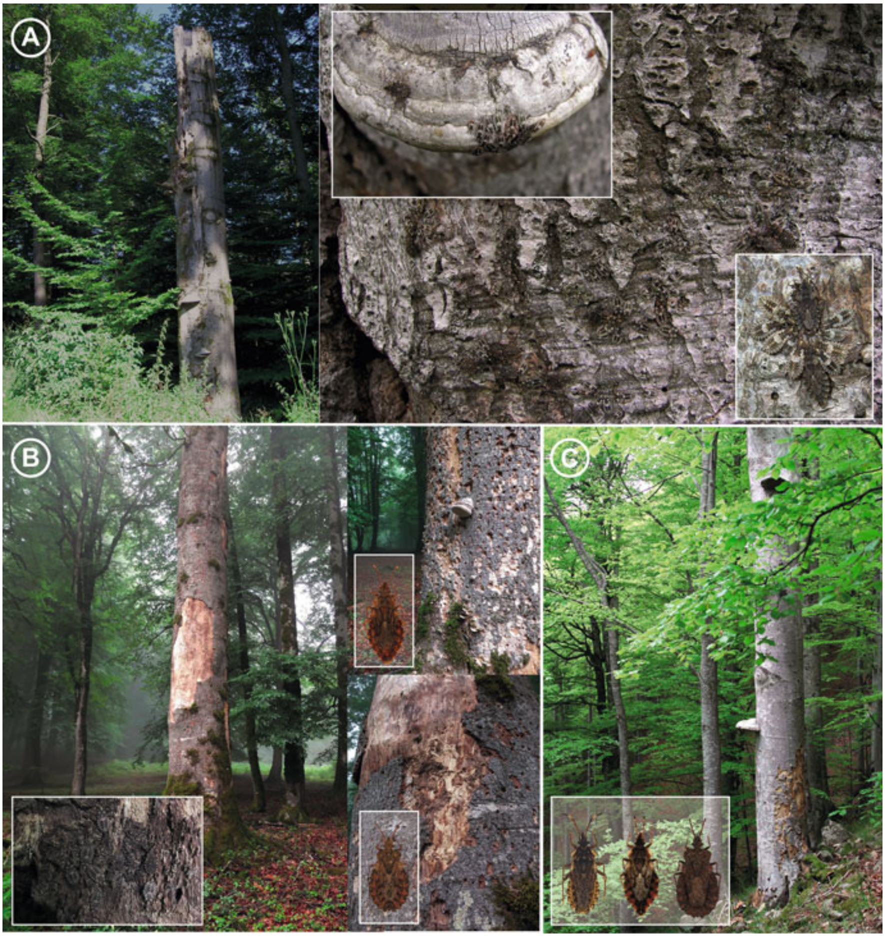


Fig. 9.10 Examples of snags that are colonized by Aradidae. Some species of the *Aradus betulae* group use similar niches in different regions. *Aradus betulae* (Linnaeus, 1758) preferably colonizes snags that are colonized by *Fomes fomentarius* (L.: Fr.) J.J. Kickx, i.e., *Fagus sylvatica* L. in the Spessart, Germany (A) and in the Central Balkan mountains, Bulgaria (C). It uses the drier part of the snags. The same is true for *Aradus brenskei* Reuter, 1884, which was found on the same snag in Bulgaria (C) and *Aradus elburzanus* Heiss 2004 on *Fagus orientalis* Lipsky in the Caspian beech forest of Iran (B, top right). These species are often aggregated in groups with adults and different larval stages (A right, B inset bottom left), and *A. betulae* can be observed frequently during dawn on the fruiting bodies of *F. fomentarius* and on the bark (A right). On the wetter part of the snags *Aradus conspicuus* Herrich-Schäffer, 1835 (observed on the snag in Bulgaria), and *Aradus inopinus* Kiritshenko, 1955 (observed on the snag in Iran; B bottom right), can be found. The latter two species are, however, more frequently observed under the bark of logs of different diameter. Images: *A. elburzanus*, ♀ 10.0 mm, *A. inopinus* ♀ 9.8 mm, *A. brenskei* ♂ 8.0 mm, *A. betulae* ♀ 9.8 mm, *A. conspicuus* ♀ 10.2 mm. Photo credits: Martin M. Gossner, except *A. brenskei* (Gerhard Strauss)

Predators among saproxylic species occur in the Heteroptera families Anthocoridae, Lyctocoridae, Lasiochilidae, Miridae, Medocostidae, Reduviidae (all Cimicomorpha), Ceratocombidae, Hypsipterygidae, Schizopteridae (Dipsocoromorpha), Enicocephalidae, and Aenictopecheidae (Enicocephalomorpha). Most of them feed on eggs, larvae, and pupae of other arthropods, such as bark beetles in the case of subcorticolous Cimicomorpha (Wegensteiner et al. 2015). While most species are supposed to be generalist feeders, specialization can also be observed. The genus *Scoloposcelis* Fieber, 1864, for instance, is specialized on bark beetles. These species live in the galleries of bark beetles and larvae and adults feed on their brood. Developing larvae of *Scoloposcelis pulchella* (Zetterstedt 1838) (Fig. 9.1, image G), an important predator of *Pityogenes chalcographus* Linnaeus 1758 (Dippel et al. 1997), have been reported to kill 39–144 bark beetle larvae per individual (Kenis et al. 2004). This species as well as *Xylocoris cursitans* (Fallén, 1807), another Palaearctic anthocorid species, is known to kill more prey than they consume (Herard and Mercadier 1996), underscoring the importance of these species for bark beetle control (Heidger 1994; Dippel et al. 1997). In New Zealand, *Maoricoris benefactor* China 1933 might be an effective predator on the wood-boring weevil *Torostoma apicale* Broun, and the bark beetles *Chaetoptelius mundulus* (Broun, 1881) and *Acrantus opacus* Broun, 1895, on *Pittosporum crassifolium* Banks & Sol. ex A. Cunn. and *Pseudopanax* K. Koch spp. trees (Larivière and Larochelle 2004; Thorpe 2014a, b).

Some subfamilies of Reduviidae have morphological adaptations for a supracorticolous or subcorticolous habitat. For example, members of the oriental Centrocnemidinae are ambush predators on bark and are well camouflaged with their tuberculate body and widely flattened humeral extensions (Fig. 9.7, image B). Some genera in the subfamily Reduviinae (e.g., *Staliastes*, *Tapeinus*) and the neotropical Elasmodeminae are dorsally flattened and are subcortical predators (Forero et al. 2011) (Fig. 9.5, images G, H). Other Reduviidae such as Physoderinae (Fig. 9.1, image C, Fig. 9.7) have a cryptic lifestyle, hiding in tree holes, under rotten trunks, or in dead plant matter (Schuh and Slater 1995; Weirauch et al. 2014)

For saproxylic Miridae of the subfamily Cylapinae (Cimicomorpha), Wheeler (2001) suggests that predacious as well as mycetophagous saproxylic species occur in different genera of this group and some species might be omnivorous. Further empirical studies are needed to verify this.

Box 9.1 Tree Species Preference of Saproxylic Hemiptera

Methods: To test whether saproxylic Heteroptera show a preference for particular tree species, we used data from a large-scale deadwood experiment conducted within the Biodiversity Exploratories Project in three regions of Germany (for details, see Fischer et al. 2010). In this experiment, a total of 764 logs (length 4 m, mean diameter 31 ± 5.9 SD) of 13 different tree species

(continued)

Box 9.1 (continued)
were exposed in 2 subplots of a total of 30 forests in 3 regions of Germany in spring 2009. Each subplot comprised all 13 tree species that were placed in random order with 1 m distance between each log. Arthropods were sampled by closed emergence eclectors, which were moved 35 cm along the log every year, between 2010 and 2014 (2010 and 2014: 1 subplot, 2011–2013: 2 subplots) (Gossner et al. 2016). *Aradus conspicuus*, an indicator species of international importance for nature conservation (Speight 1989), was the only species that emerged in sufficient number in one region (Biosphere reserve Schorfheide-Chorin, NE of Berlin) to allow tests on differences in frequency between tree species. The data for each tree species was pooled per subplot and year. Differences between tree species were tested using a generalized mixed effects model with Poisson error distribution (lme4 package; Bates et al. 2015) with plot as a random factor. Subsequently, we tested each tree species combination for statistical significance using multiple comparisons of means based on Tukey contrasts (glht function in the multcomp package; Hothorn et al. 2008).

Results and Discussion: Overall, 243 individuals of *Aradus conspicuus* Herrich-Schäffer, 1835, emerged from the 234 logs exposed in 9 forests of the Schorfheide-Chorin Biosphere Reserve. Significant differences were observed between tree species with the highest frequency found on *Carpinus* L., followed by *Betula* L., *Prunus* L., and *Quercus* L. (Fig. 9.11). This suggests that saproxylic Heteroptera can show a strong preference for particular tree species. In line with the results from the same experiment on the diversity of saproxylic beetles (Gossner et al. 2016), we found *Carpinus* to be especially important. This suggests that *Carpinus* favors not only saproxylic beetle diversity but also the occurrence of *A. conspicuus* and probably other saproxylic Heteroptera. This suggests that *Carpinus* should be given high priority in deadwood conservation strategies in Central Europe (Gossner et al. 2016).

9.4.2 Habitat Association

Long habitat tradition, which describes the continuous availability of suitable deadwood structures, is assumed to be crucial for several saproxylic Hemiptera. Gossner et al. (2007), for example, suggested, based on their results from different forest areas in Germany and other studies, that the discontinuity in the availability of suitable breeding substrates is the reason for the absence of *Aradus betulae* (Linnaeus, 1758) in some regions in Germany. Some species, so-called primeval forest relict species (Eckelt et al. 2017), might be even more demanding in their habitat requirements in terms of continuity and habitat amount and thus are only found at a few relict sites in landscapes that are largely shaped by human activity over

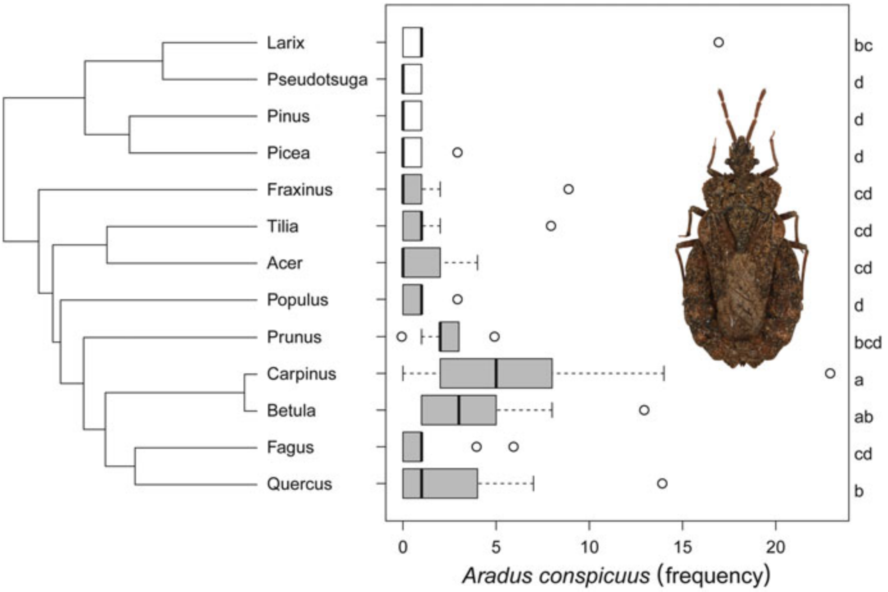


Fig. 9.11 Frequency of *Aradus conspicuus* Herrich-Schäffer, 1835, emerging from logs of 13 different tree species in a deadwood experiment conducted in the Biosphere reserve Schorfheide-Chorin (234 logs on 2 subplots in 9 forests). The frequency of emergence showed significant differences between tree species. Proposed phylogeny of tree genera (see Kahl et al. 2017) is shown for illustrative purpose only. Significant differences between tree species are shown by letters at the right plot margin (GLMER followed by multiple comparisons of means based on Tukey contrasts). Image: ♀ 10.2 mm, *Carpinus*, Schorfheide-Chorin. Photo credits: Martin M. Gossner

centuries, such as Central Europe. The Palaearctic species *Mezira tremulae* (Germar, 1822) (Möller 2009); *Aradus serbicus* Horváth, 1888 (Morkel 2010); and *Cixidia lapponica* (Zetterstedt, 1840) (Holzinger and Friess 2014) may be classified as such primeval forest relict species among Hemiptera.

Other species show very low population sizes, until a large-scale disturbance event provides a surplus supply of suitable habitats. This has been shown for the Bavarian Forest National Park in Southeast Germany where large-scale wind throws and bark beetle attacks exponentially increased the availability of spruce snags (Müller et al. 2008) that were intensively colonized by *Fomitopsis pinicola* (Sw.: Fr.) P. Karst and thus provided an optimal habitat for *Aradus obtectus* Vásárhelyi 1988 (Gossner 2011; Seibold et al. 2014). High deadwood amount has been shown to be crucial for saproxylic insects in general (Gossner et al. 2013a; Seibold et al. 2015a, 2017) but also for saproxylic Heteroptera (Seibold et al. 2014). High deadwood amount in forests is often correlated with high deadwood microhabitat diversity which might additionally increase saproxylic species diversity (Gossner et al. 2013b).

It is commonly accepted that habitat heterogeneity increases diversity, because it promotes a high diversity of microhabitats and niches and simultaneously limits intraspecific competition (heterogeneity-diversity hypothesis; MacArthur and MacArthur 1961; Wilson 2000). The scale of optimal heterogeneity might, however, differ between different organisms (Schall et al. 2017). Saproxylic species colonize a high diversity of microhabitats, and thus a high diversity of these small-scale structures might be crucial to sustain high diversity (Stokland et al. 2012).

Little is known about the microhabitat preferences of saproxylic Hemiptera. Boreal and temperate forests of Europe and some temperate forests in North America are best studied in this respect. These studies indicate a great variety of microhabitats are used by saproxylic Hemiptera. Deadwood diameter, decay stage, and canopy openness have shown to be crucial microhabitat niches for saproxylic insects (Gossner et al. 2013b; Seibold et al. 2015b). Regarding the *deadwood diameter niche*, a variety of diameter classes are colonized by saproxylic Hemiptera, but large-diameter deadwood and in particular snags are most important for sustaining a high species diversity (Gossner et al. 2007; Möller 2009; Ulyshen et al. 2012; Marchal et al. 2013). Only a few species seem to occur in [e.g., *Aradus depressus* (Fabricius, 1794), *A. versicolor* Herrich-Schäffer, 1835, *Aneurus laevis* (Fabricius, 1775)] or even prefer [*Aneurus avenius* (Dufour, 1833)] branches and twigs of small diameters (Fig. 9.12), where fungi are generally more diversified (Heilmann-Clausen and Christensen 2004). Regarding the *deadwood decay niche*, early decay stages are clearly preferred by

Fig. 9.12 Species of the genus *Aneurus* Curtis 1825 are mostly found in small-diameter deadwood including dead branches of living trees (*Aneurus avenius* (Dufour, 1833) on *Carpinus betulae* L., Germany; A), under the bark of small-diameter snags or small-diameter branches on the forest floor (*Aneurus laevis* on *Fagus orientalis* Lipsky, Iran; B). In Iran, *A. laevis* (Fabricius, 1775) seems to occur more often under the bark of larger diameter deadwood (C) and therefore has a higher diameter niche position compared to other regions (see Box 9.2)

most species, and only a few species might be present in highly decayed deadwood (e.g., *Mezira tremulae* (Germar, 1822), *Aradus betulinus* Fallen, 1807). Most species depend on at least partly remaining bark. Regarding the *deadwood canopy niche*, most saproxylic Hemiptera species prefer sun-exposed but still moist deadwood. Significant positive effects of sun exposure of deadwood on saproxylic Heteroptera have been shown in an experimental study in the Bavarian Forest National Park in Southern Germany (Seibold et al. 2014). In boreal forests, Aradidae seemed to be favored by clear-cuts and forest fire [also non-pyrophilous species such as *A. betulae* (Linnaeus, 1758)] (Johansson et al. 2010), provided that sufficient deadwood is left in the forest. This is most likely also because of the open character of these "forests". In addition, the observation that anthropogenic stacks of wood that are exposed under sunny conditions provide suitable habitats for saproxylic Hemiptera (Fig. 9.5) support the idea that high amounts of deadwood of suitable decay stages under sun-exposed conditions promote saproxylic Hemiptera diversity. Figure 9.13 illustrates the microhabitat niches of some European species based on the few systematic studies available. It shows differences in niche positions among species but suggests a lack of species preferring shady conditions and very late decay stages.

Independent of their diameter, decay and canopy niche, several species show a preference for particular deadwood types. Large senescent trees and snags are preferred by *Aradus betulae* (Linnaeus, 1758), *Mezira tremulae* (Germar, 1822) (both large diameter), and *Aradus bimaculatus* Reuter, 1872 (also dead branches on living trees), in European broad-leaved forests (Gossner et al. 2007, 2014; Möller 2009). Other examples from European conifer forests include *Aradus obtectus* Vásárhelyi 1988, and *Aradus betulinus* Fallen, 1807 (Wachmann et al. 2007; pers. observation; Möller 2009), and an example from Oriental beech forests is *Aradus elburzanus* Heiss 2004 (Heiss 2004a; Müller et al. 2016; pers. observation). The importance of snags for saproxylic aradids has been shown for boreal conifer forests (Jonsell et al. 2005). Some species are known to prefer downed logs (e.g., *Aradus brevicollis* Fallen, 1807; Wachmann et al. 2007; Möller 2009), among those species that show associations with leaf litter and live under the bark of small branches or logs. Examples are *Systelloderes inusitatus* Drake and Harris, 1927 (Enicocephalidae), from North America (Ulyshen et al. 2012), the flat bugs *Aradus safavii* Hoberlandt, 1974 (♂ stenopterous, ♀ brachypterous), from Oriental beech forests (Heiss 2004a), and *Aradus distinctus* Fieber, 1968 (Fig. 9.8), and *Aradus graecus* Heiss 1997 (♂ macropterous, ♀ mostly brachypterous), from Europe (Wachmann et al. 2007; Schäfer 2014; Winkelmann and Heiss 2016). These species often have reduced wings and thus low dispersal propensities. Other species might be less specialized, occurring in snags and downed logs equally, e.g., the lasiochilid *Lasiochilus fusculus* (Reuter, 1871) and the lyctocorid *Lyctocoris stalii* (Reuter, 1871) in North America (Ulyshen et al. 2012); the flat bugs *Aradus corticalis* (Linnaeus, 1758), *Aradus depressus* (Fabricius, 1794), and *Aradus truncatus* Fieber, 1860, in European beech forests (Wachmann et al. 2007; Möller 2009); and *Aradus inopinus* Kiritshenko, 1955, in Oriental beech forests (Müller et al. 2016; pers. observation). In addition, *Aradus conspicuus* Herrich-Schäffer, 1835, and *Aradus*

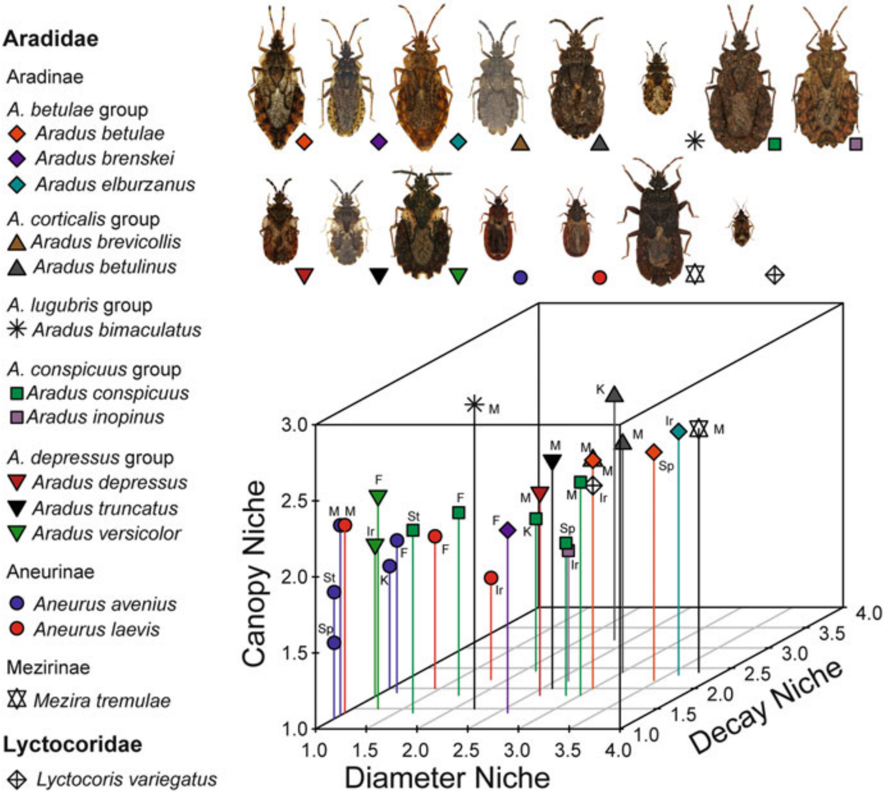


Fig. 9.13 Three-dimensional scatter plot showing the niche position of 15 saproxylic Heteroptera species regarding their microhabitat niche preference (diameter and decay stage of deadwood, canopy openness) in different studies: F: France, Marchal et al. (2013) (N deadwood objects: *A. avenius* 125, *A. laevis* 191, *A. conspicuus* 12, *A. versicolor* 7, *A. brenskei* 10). K: Germany, Kellerwald-Edersee National Park, Morkel (2017) (*A. avenius* 25, *A. conspicuus* 147, *A. betulinus* 32). M: Germany, Möller (2009). I: Iran, Müller et al. (2016) (*A. laevis* 11, *A. versicolor* 7, *A. elburzanus* 11, *A. inopinus* 45, *L. variegatus* 13). Sp: Germany-Spessart (*A. avenius* 10, *A. conspicuus* 39, *A. betulae* 16). St: Germany-Steigerwald (*A. avenius* 51, *A. conspicuus* 22), both Gossner et al. (2007). *Aradus versicolor* Herrich-Schäffer, 1835, is shown as the form "*diversicornis*" from Iran (see Heiss 2004a). For details, see text. Images are scaled according to their size (*A. betulae*, ♀ 9.8 mm, Germany; *A. brenskei*, ♂ 8.0 mm, Greece; *A. elburzanus*, ♀ 10.0 mm, Iran; *A. brevicollis*, ♂ 7.8 mm, Austria; *A. betulinus*, ♀ 8.5 mm, Germany; *A. bimaculatus*, ♀ 5.0 mm, Germany; *A. conspicuous*, ♀ 10.2 mm, Germany; *A. inopinus*, ♀ 9.8 mm, Iran; *A. depressus*, ♀ 5.9 mm, Germany; *A. truncatus*, ♂ 5.8 mm, Austria; *A. versicolor*, ♀ 7.7 mm, Iran; *A. avenius*, ♀ 5.2 mm, Germany; *A. laevis*, ♀ 4.9 mm, Iran; *M. tremulae*, ♂ 8.8 mm, Germany; *L. variegatus*, ♀ 3.5 mm, Iran. Photo credits: Martin M. Gossner, except *A. brenskei*, *A. brevicollis*, and *A. truncatus* (all Gerhard Strauss)

versicolor Herrich-Schäffer, 1835, frequently colonize stumps that remain after harvests (Gossner et al. 2007; Marchal et al. 2013). Species of the genus *Aneurus* Curtis 1925 occur frequently in downed and standing thin deadwood as well as in dead branches on living trees (Gossner et al. 2007; Möller 2009).

Similar to saproxylic beetles (Grove 2002; Gossner et al. 2016), a preference for particular tree species has been shown in saproxylic Hemiptera (O'Brien 1971; Stehlik and Heiss 2001; Nickel 2003; Ulyshen et al. 2012; Marchal et al. 2013) but is less supported by other studies. Broad taxonomic groups such as angiosperms vs. gymnosperms seem to be more important to saproxylic Hemiptera than tree species (Heiss and Péricart 2007; Seibold et al. 2014). The preference for particular tree species might be due to the occurrence of their host fungi (Usinger and Matsuda 1959; Lis 1990). *Aradus betulae* (Linnaeus, 1758), dependent on *Fomes fomentarius* (L.: Fr.) J.J. Kickx, is preferentially found on beech trees in the central to southern European forests but on birch trees in northern European countries (Helioevaara and Vaisanen 1983; Wachmann et al. 2007). Also for *Aneurus* Curtis 1925 species, different tree species preferences were observed in different studies, e.g., *A. avenius* (Dufour, 1833) was preferentially found on oak and hornbeam in a study in France (Marchal et al. 2013), while it was most common on beech in Southern Germany (Gossner et al. 2007). Most likely the occurrence of particular fungi and the abundance of particular tree species (and thus deadwood amount) in a region might be more important than the tree species per se.

Box 9.2 Microhabitat Niches of Saproxylic Palaearctic Heteroptera

Methods: To assess the microhabitat niches of saproxylic Heteroptera, a standardized assessment was conducted in European (*Fagus sylvatica* L.) beech forests in three regions of Germany [Steigerwald, 16.05.–25.05.2005; Spessart, 15.05.–19.05.2006; Gossner et al. (2007), Kellerwald-Edersee National Park including areas dominated by spruce (*Picea abies* (L.) H. Karst.): 2012–2015 (Morkel 2017)], in Oriental (*Fagus orientalis* Lipsky) beech forests in one region of Iran [Kheyrood forest, 28.06.–03.07.2014; Müller et al. (2016)], and in oak forests (*Quercus petraea* (Matt.) and *Q. robur* L.) of France [Rambouillet and Fontainebleau forest, 31.05.–23.06.2010; Marchal et al. (2013)]. Saproxylic Heteroptera were hand-collected within point sample plots (Steigerwald, 69; Spessart, 45; Kellerwald-Edersee, 514; Kheyrood forest, 24; Rambouillet and Fontainebleau forest, 56) of 18 m radius (Kellerwald, 12.6 m) for 45 min by one person (for details, see Gossner et al. 2007; Müller et al. 2016). Information compiled in a long-term study on the habitat and substrate preferences of saproxylic Heteroptera (Möller 2009) was used as an additional dataset. In total, six different datasets were analyzed. The microhabitat niche of each species was defined by the diameter (4 categories, 1, <15 cm; 2, 15–35 cm; 3, 36–70 cm; 4, >70 cm), decay stage (4 categories; 1, freshly dead (1–2 years); 2, initiated decomposition (loose bark, tough sapwood); 3, advanced decomposition (soft sapwood, partly tough hardwood); 4, extremely decomposed and moldered), and canopy cover (3 categories; 1, closed; 2, semi-open; 3, open).

(continued)

Box 9.2 (continued)

We subsequently estimated the niche positions for each Heteroptera species along these three axes on the basis of occurrence of species across these categories and weighting scores (0.5, very rarely used; 1, rarely used; 2, commonly used; 3, preferred). For details on the procedure, see Gossner et al. (2013b).

Results and Discussion: Overall 15 saproxylic Heteroptera species were recorded in the 5 studies. The position of the species in the three-dimensional niche space (Fig. 9.13) shows three main findings:

First, species cover most of the diameter and canopy niche space but only part of the decay niche. This suggests that saproxylic Heteroptera in the studied regions only rarely use extremely decomposed deadwood. As exception, *Mezira tremulae* (Germar, 1822) was once found in a heavily decomposed beech deadwood log (Fig. 9.14).

Second, we observed a conspicuous niche separation from species preferring small deadwood of early decay stage at intermediate canopy openness (Aneurinae, *Aradus versicolor* Herrich-Schäffer, 1835) to species preferring very large (preferentially snags) deadwood pieces of slightly later decay stage at high canopy openness [e.g., *Aradus betulae* (Linnaeus, 1758), *A. elburzanus* Heiss 2004, *A. betulinus* Fallen, 1807, *Mezira tremulae* (Germar, 1822)].

Third, some species show different niche positions in different regions (e.g., *Aneurus laevis* (Fabricius, 1775), *Aradus conspicuus* Herrich-Schäffer, 1835).

Several Heteroptera species are known to be pyrophilous (Fig. 9.15), meaning that they are attracted to recently burned sites by smoke and/or heat using specific sensorial adaptations to detect forest fires (see section on host finding below). Thus, they appear immediately after forest fires where they feed on fungi growing on the burned wood, e.g., *Aradus lugubris* Fallen, 1807, on *Daldinia loculata* (Lév.) Sacc. (*Xylariaceae*) (Wikars 2001). It has been proposed that these fire-related ascomycete fungi quickly colonize competition-free substrates but are rapidly outcompeted by other fungi (Wikars 1997). Thus, both pyrophilous flat bugs and fungi take advantage of high resource availability, more easily attainable nutrients, and low interspecific competition because most species were killed by fire and favorable microclimatic conditions, i.e., high temperature (Wikars 1992, 1997). Moreover, they might use spotfires which occur within several days after the head fires as mating sites (Wikars 1992). These species occur on these sites in high abundance, mostly only in the first to third year, but no longer than about 5 years after fire (Wikars 1992, 1997). This has been observed in many boreal (Lappalainen and Simola 1998; Hjältén et al. 2006; Heikkala et al. 2017) as well as temperate forests (Wyniger et al. 2002; Deyrup and Mosley 2004; Moretti et al. 2004) throughout the

Fig. 9.14 The primeval forest relict species *Mezira tremulae* (Germar, 1822) is a Palaearctic species that prefers large-diameter snags and logs. It is one of the exceptions among Palaearctic Aradidae that prefers deadwood of late decay stages (see picture, Gross-Gerau, Germany). Photo credits: Martin M. Gossner

Fig. 9.15 Examples of pyrophilous (left) and secondary colonizers of burned sites (right) within the flat bug species (Aradidae). (A) Forest fires and associated pyrophilous flat bugs in eastern Finland (municipality of Lieksa). A total of five pyrophilous flat bug species (according to Wikars 1992) were recorded, among others *Aradus laeviusculus* Reuter, 1875 (inset left, ♀ 6.2 mm); *Aradus lugubris* Fallen, 1807 (middle, ♀ 5.5 mm); and *Aradus crenaticollis* R.F. Sahlberg, 1848 (right, ♀ 7.8 mm) (Heikkala et al. 2017). (B) After a forest fire in a pine-dominated forest near Leuk, Valais, Switzerland in 2003, 11 flat bug species were observed, among those 4 pyrophilous species directly after the fire (Moretti & Obrist, Swiss Federal Research Institute WSL, pers. comm. and pers. observ.). Additionally seven secondary colonizers have been recorded, benefitting from the large supply of deadwood resources, among those *Aradus obtectus* Vásárhelyi 1988 (inset top, ♀ 7.9 mm) and *Quilnus marcosi* Heiss and Baena 2006 (inset bottom, ♂ 5.6 mm and nymph 4.4 mm), which we found under the bark of standing fire-killed pine trees 14 years after forest fire (Gossner et al. 2018). The habitat tree of *Aradus obtectus* is shown in the picture. Photo credits: left, Petri Martikainen, except *A. lugubris* (Martin M. Gossner); right, Martin M. Gossner

world. While fire plays also an important role in temperate regions (Attiwill 1994; Pignatti et al. 2002; Tinner et al. 2005), most available information on pyrophilous species comes from boreal forests. Wikars (1992, 1997) lists eight species (one Anthocoridae, seven Aradidae) that are attracted to burning or newly burned areas of which five Aradidae are known to be attracted to ongoing fires. The rapid appearance of these species in recently burned sites raises the question of where and how these taxa survive between forest fires and whether fires are even necessary for their long-term persistence (Saint-Germain et al. 2008). It is undoubted that after fire, a high number of more or less synchronously dying fire-killed trees provide an almost unlimited availability of microhabitats for egg laying and food source for larvae and adults. Thus, reproducing individuals are attracted over large distances and immediately increase populations. Disturbances caused by bark beetle attack and wind throws provide suitable resources for many years and allow several generations to survive and act as a source for colonizing suboptimal habitats in the surrounding area, such as shown for *Aradus obtectus* Vasarhelyi, 1988, in the Bavarian Forest National Park in southern Germany (Seibold et al. 2014, see above). However, pyrophilous species might be unable to produce multiple generations in recently burned forests depending on how quickly the suitability of burned substrates declines over time. Therefore, Saint-Germain et al. (2008) suggested that, considering the low fire frequency and therefore the low connectivity in many regions, recent burns cannot act as important population sources and the suitability of the unburned matrix might be more important for survival than the occurrence of fire events. There are a few indications that at least some of these species are also attracted to the smoke of domestic fires and therefore recorded from human residences, i.e., *Aradus lugubris* Fallen, 1807 (Helioevaara and Vaisanen 1983). Others are, however, described as specialists, being able to breed only in freshly burned trunks and thus vanished due to the suppression of natural forest fires, such as *Aradus annulicornis* Fabricius, 1803, and *A. signaticornis* R.F. Sahlberg, 1848, and maybe also *A. aterrimus* Fieber, 1864; *A. laeviusculus* Reuter, 1875 (rediscovered in 1996; Viiri and Eerikäinen 2012); and *A. angularis* J. Sahlberg, 1886, from the Finnish fauna (Helioevaara and Vaisanen 1983). Despite their strong dispersal abilities, these species might depend on frequently occurring forest fires. Whether and to what extent they can maintain viable populations in the forest matrix between forest fire events remains unclear.

After initial colonization by pyrophilous species, a second wave of non-fire-adapted species could be expected, as the availability of deadwood is still high. This has been observed in saproxylic beetles by Boulanger and Sirois (2007), but not earlier than the snags broke down which triggered fungal colonization and accessibility for soil-dwelling organism. Observations of non-pyrophilous Aradidae (*Aradus obtectus* Vásárhelyi 1988, *Quilnus marcosi* Heiss and Baena 2006) in pine snags on a burned site in Switzerland 14 years after a forest fire suggest that colonization by this group might not necessarily depend on the breakdown of snags (Fig. 9.15; Gossner et al. 2018). Other studies also found an increase in saproxylic Hemiptera along a post-fire succession gradient with *Cixidia confinis* (Zetterstedt, 1828) and *C. lapponica* (Zetterstedt, 1838) among Auchenorrhyncha and *Aradus brevicollis* Fallen, 1807; *A. erosus* Fallen, 1807; *A. corticalis* (Linnaeus, 1758); and *A. betulinus* Fallen, 1807, among Heteroptera showing their main occurrence 5–25 years after forest fires and *Aradus truncatus* Fieber, 1860, even in later successional stages in Sweden (Wikars 1992).

9.4.3 Host Finding

The host-finding mechanisms in saproxylic insects are not well studied, except for bark beetles and longhorn beetles. Most previous studies have concentrated on pyrophilous species. These species evolved specific sensorial adaptations, i.e., infrared receptors, to detect forest fires and have been first described in buprestid beetles of the genus *Melanophila* Eschscholtz, 1829 (Evans 1964; Schmitz et al. 1997). Schmitz et al. (2008) discovered such structures in the pyrophilous Australian flat bug *Aradus albicornis* (Walker, 1873) and later also found similar structures in *Aradus lugubris* Fallen, 1807; *Aradus fuscicornis* Kormilev, 1966 (all three prothoracic and mesothoracic IR); and *Aradus flavicornis* Dalman, 1823 (only prothoracic IR) (Schmitz et al. 2010). The structure of these receptors appears to be similar in all of these species and can be classified as photomechanic IR receptors. The warming of each sensillum causes an expansion of a fluid-filled annular channel below a cup-shaped plug of cuticle and evokes a fast phasic response of the dendrite tip of a mechanosensitive neuron which is inserted in the center. The less packed sensilla in comparison to *Melanophila* Eschscholtz, 1829, beetles, however, suggests that they might be less sensitive and may serve only to prevent *Aradus* species from coming too close to a fire hotspot (Schmitz et al. 2010). Additional olfactory sensors in the antennae might serve for long-term navigation toward fire as shown for pyrophilous buprestid beetles (Schutz et al. 1999). Both information converge on descending brain neurons and enable directed flight toward forest fires.

The importance of different cues involved in host finding by non-pyrophilous fungivorous species is less well studied. It can be assumed that ephemeral deadwood structures can be detected from long distance. Skototaxis, the orientation to dark objects, has been proposed as important mechanism in aradid dispersal and habitat selection of litter—as well as dead tree-inhabiting species (Taylor 1988b). However, the relative importance of skototactic response in the orientation and host finding of species with different habitat requirements is unclear. Macropterous aradids are occasionally encountered at lights (Miller 1971) or observed to orient toward the sun (latter in the phytophagous *Aradus cinnamomeus* (Dufour, 1833); Brammanis 1975). In contrast, achilids, which are all macropterous, were most readily collected at lights (Bartlett 2016). Whether this behavior occurs only in the absence of dark object, as suggested for *A. cinnamomeus* by Heliovaara and Terho (1981), needs further investigation. Based on a field experiment, in which they exposed different amounts of deadwood in beech forests, Seibold et al. (2014) showed that saproxylic Heteroptera use wood-borne rather than fungal volatiles to locate suitable habitats at long distances during dispersion flights in May. With higher deadwood amounts, and thus higher surface areas, the emission of volatiles and therefore the attraction of flat bugs were increased. A subsequent olfactometer test suggested that in contrast to long-distance orientation, *Aradus obtectus* Vásárhelyi 1988, relies on olfactory cues emitted by the mycelia of its host species to locate microhabitats at short distances (Koban et al. 2016). Additionally pheromonal secretions emitted by dorsal abdominal scent glands might be used to attract the opposite sex of conspecifics and cause aggregation and thereby prevent inbreeding in gregarious species as suggested by Davidová-Vilímová (2006) for the Palaearctic species, *Aradus betulae* (Linnaeus 1758).

For a few predatory species that are strongly associated with bark beetles, the use of beetle aggregation pheromones to locate their prey has been shown. Several studies observed high abundances of *Scoloposcelis pulchella* (Zetterstedt, 1838) in pheromone traps for bark beetles, with pheromones for *Pityogenes chalcographus* (Linnaeus, 1761) being most attractive (Heidger 1994; Wachmann et al. 2006).

9.5 Management and Conservation

There are several indications that past and present management affects saproxylic insects (Siitonen 2001). Studies on saproxylic beetles in European forests have revealed that large species that depend on large-diameter and sun-exposed deadwood are most severely affected by management (Gossner et al. 2013b) and thus face high extinction risk (Seibold et al. 2015b). This reflects the degradation of forests due to intensified management during the last centuries, i.e., conversion of broad-leaved to conifer forests (Grove 2002), increased canopy cover (Schall et al. 2017), and a loss of old growth forest attributes (Bauhus et al. 2009). As many saproxylic Hemiptera depend on large-diameter deadwood of broad-leaved trees, an increasing extinction risk for many species can be expected. Therefore, many of these species are classified as threatened on national species Red lists (Friess et al. 1999; Rabitsch 2007; Holzinger 2009; Nickel et al. 2016; Simon et al. 2018). Moreover, increasing demands for fuelwood have additionally increased the pressure on logging residues, even of small diameter (Bouget et al. 2012; Lassauce et al. 2012). This might even affect species that are still abundant and less specialized such as *Aradus conspicuus* Herrich-Schäffer, 1835 (e.g., use stumps after tree harvests as surrogate habitat; Gossner et al. 2007; Marchal et al. 2013), or *Aneurus* species that preferably occur in small-diameter deadwood (Gossner et al. 2007; Marchal et al. 2013), which is the most common deadwood resource in managed forest and sometimes even favored by management (Schiegg 2001; Gibb et al. 2005).

Efforts to suppress fire are widespread, even in regions where fire was historically a common event such as in boreal forests (McCullough et al. 1998; Granström 2001). For forests of east-central Canada, for instance, a decrease of forest fire frequency from 60–100 years before European settlement to 500–1000 years after fire suppression was implemented in the early twentieth century (McCullough et al. 1998). Fire suppression is thought to be a major cause for the disappearance of pyrophilous species in Finland and Sweden since the nineteenth century (Helioevaara and Vaisanen 1983; Ahnlund and Lindhe 1992) and for the population declines of other species that are classified as threatened in the Finnish and Swedish Red Lists (Gärdenfors 2000; Rassi et al. 2001). Species which are secondary colonizers of burned sites due to the high resource availability are additionally affected negatively by fire suppression. Granström (2001) suggests that the combination of intensive forest management and fire suppression programs threatens many flat bugs in Fennoscandia. This is supported by the study of Siitonen and Martikainen (1994) who showed that in adjacent Russian Karelia, where forest management has been much less intensive, many of the species threatened or extinct in Finland and Sweden still occur at high population densities. Moreover, in Alaska, lower levels of anthropogenic impact and higher fire frequency might sustain higher populations of endangered flat bug species, as shown for *Aradus signaticornis* R.F. Sahlberg, 1848, which is endangered in Finland and Sweden, by Hjältén et al. (2006).

In tropical ecosystems, the taxonomic impediment, a lack of comprehensive species inventories, and unknown habitat requirements of most species are hindering an effective conservation management for saproxylic hemipterans. While there were a few attempts to document the Heteroptera fauna of tropical forests (Hodkinson and Casson 1991; Lucas et al. 2016), to our knowledge no study has looked at the importance of deadwood availability or forest management on tropical saproxylic species, apart from occasional observations of single species (Wolski and Yasunaga 2016).

Edwards et al. (2014) studied the effect of selective logging and land conversion on Heteroptera in Northern Borneo. They found that (i) a large proportion of species occurring in primary forests can also be detected in once- and twice-logged forests and (ii) twice-logged forests contained an even significantly higher species diversity than primary forests (229 vs. 174 species, respectively). Although the study detected an impressive total number of 401 Heteroptera species and emphasizes the potential conservation value of selectively logged tropical forests for biodiversity, we argue that the study falls short of providing strong data of the effects of logging and land conversion of tropical Heteroptera communities and in particular saproxylic species. Firstly, specimens for this study were sampled using Malaise traps; hence, mostly flying species were collected but presumably none of the flightless species. Secondly, species numbers were obtained using metabarcoding without assigning any DNA sequences to database-recorded species. The species pool detected in the primary forest might contain transient or generalist species without any true ecological relationship to pristine forest habitats, and species number in heavily disturbed forests might be inflated by further non-forest species feeding on grasses or forbs in the more open understory. Without knowing which species were collected or even to which families they belong, it remains unclear how the functional traits of species determine the responses of taxa to habitat disturbance and habitat fragmentation. In the case of saproxylic Hemiptera, we suspect that logging activities will provide additional deadwood resources for highly mobile species in the short term but will have adverse long-term consequences for the diversity of saproxylic species resulting from the removal of large-diameter trees with their associated deadwood microhabitats and fragmentation and disturbance of forest floor habitats caused by logging activities, which is likely to impact some of the dispersal-limited species associated with fine woody debris. Moreover felled but not immediately removed commercially less valuable logs might act as ecological traps when they are removed after they have been colonized by saproxylic species but before the new generation emerged. Forest fuel piles, for example, have been shown to act as such ecological traps in European forests (Hedin et al. 2008; Adamski et al. 2016). Further studies are needed to investigate the effect of forest disturbance and habitat fragmentation on tropical saproxylic species.

Several strategies have been proposed for managed forests to overcome the increased threat to many saproxylic species including Hemiptera. In Europe such integrative strategies include the retention and restoration of old growth structural attributes in forests (Bauhus et al. 2009) in combination with abandonment of small forest islands in combination with segregative elements such as nature reserves and even temporal and spatially dynamic conservation measures (Bollmann and Braunisch 2013). These efforts are aimed at ensuring the sustainable availability and connectivity of resources needed for the protection of saproxylic species in the long run. First evaluations of such integrative strategies show that attempts to retain deadwood during harvests, as implemented in a forestry department of Southern Germany, can increase deadwood amount and biodiversity (Doerfler et al. 2017, Doerfler et al. in prep.). However, long-term studies on the success of such strategies and possible adaptations are needed to guarantee the positive effect on saproxylic species, including threatened Hemiptera. Remnants of pristine tropical forests in places like Malaysia and Indonesia are increasingly fragmented by and embedded in large-scale palm oil plantations. Therefore, we also suggest examining the suitability of integrative elements such as artificial man-made deadwood habitats (i.e., piles of treetops, samplings, and other less valuable timber) in tropical forests. These elements might serve as valuable stepping stones which promote dispersal and genetic exchange among fragments and thus help to sustain viable populations, at least for mobile species.

In forest ecosystems faced with naturally occurring fires, in particular in boreal forest of Fennoscandia, Alaska, and Canada, an increasing awareness of the role of fire as an important ecological factor has led to the introduction of prescribed burning as restoration tool to imitate natural fires (Wikars 1992; Johnson and Miyanishi 1995; Haggstrom and Kelleyhouse 1996; Weber and Stocks 1998; New 2014). There are several studies that show that prescribed burning is an effective strategy to promote biodiversity (Hyvarinen et al. 2009), including saproxylic Hemiptera (Hägglund et al. 2015; Heikkala et al. 2017). *Aradus laeviusculus* Reuter, 1875, for example, that was considered extinct in Finland was rediscovered on burned restoration sites (Viiri and Eerikäinen 2012).

These examples show that a sustainable protection of saproxylic Hemiptera might be possible with careful forest management. However, to effectively protect these species, we first need to increase our basic knowledge of the habitat requirements and nutritional ecology of saproxylic Hemiptera, in particular their requirements for specific substrates and fungi, as well as on their dispersal propensities. The dispersal abilities of many Hemiptera species may be high (e.g., many *Aradus* Fabricius, 1803 species), as an adaptation stemming from a dependence on ephemeral resources, and thus it is likely that effective conservation measures can help to increase the distributions and population densities of these species (Ranius et al. 2011). Others, such as several litter-dwelling apterous, micropterous, or brachypterous taxa, have restricted dispersal propensities which make their protection more difficult. They occur predominantly in subtropical and tropical forests and will be most endangered by increasing devastation of primary rainforests (Heiss 2010c). In particular in the tropics and subtropics (Gorczyca 2006a) but also in many other ecosystems (Ulyshen et al. 2012), almost nothing is known about the requirements of saproxylic Hemiptera. These ecosystems are, however, facing high economic pressure.

9.6 Conclusion

Saproxylic Hemiptera comprise numerous ecologically unique species that are highly endangered and therefore of high conservation concern. All saproxylic Hemiptera are, however, insufficiently studied (Gorczyca 2006a; Heiss and Péricart 2007; Cassis and Schuh 2012; Asche 2015), meaning that a large number of species are still waiting to be discovered and described and the biology and ecology of most species are not known. More research on the ecology and habitat requirements is needed to protect these species. Therefore, a high priority should be given on gaining such basic autecological knowledge.

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Chapter 10
Diversity of Saproxylic Lepidoptera

Tomasz Jaworski

Abstract Larvae of surprisingly many Lepidoptera species depend on dead wood and wood-decay fungi and are thus considered saproxylic insects. This interesting group has been scientifically neglected for many years, and few studies have been conducted concerning its biology, taxonomy, distribution, and ecology. Merely several dozen species of saproxylic Lepidoptera are known from North European countries; however, the highest species diversity is observed in tropical forests, where only some studies on this group have been so far conducted. This chapter provides an overview of knowledge about the diversity of saproxylic Lepidoptera, based on the world subject literature published over the last century. The greatest species richness of saproxylic Lepidoptera has been identified within two families: Tineidae and Oecophoridae, but a number of other lineages of Lepidoptera also include saproxylic taxa. All Lepidoptera families known to contain saproxylic species are described here in systematic order. Examples of saproxylic species and genera are presented, and some aspects of their biology and ecology are discussed. Major threats to these insects, related to forest management, are briefly outlined. The needs and directions for further research on saproxylic Lepidoptera are highlighted.

10.1 Introduction

The occurrence of saproxylic species among Lepidoptera is quite surprising, given the fact that these organisms are primarily associated with the living plant parts, mostly foliage, on which Lepidoptera larvae usually feed. However, several out of more than 130 distinguished families of Lepidoptera (van Nieukerken et al. 2011) exhibit relationships with dead and moribund trees (or their parts) and, hence, are considered "saproxylic insects" within the meaning of the definition given by Speight (1989) and, more recently, by Alexander (2008). In general, the relationship

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relates to larval feeding on/in dead wood and wood-decay fungi. This unusual habit appeared, most likely independently, in various lineages of Lepidoptera as a result of several possible scenarios. Rawlins (1984) discussed hypotheses explaining Lepidoptera adaptation to fungivory and consumption of decaying wood. One possibility is that this feeding habit appeared as a consequence of a gradual transition from herbivory to obligate fungivory. The adaptation could have been evolutionarily promoted by periodic shortages of food, as in the case of autumn leaf fall, when caterpillars (particularly of leaf miners and leaf rollers) were forced to feed on the forest floor—on withered and dead leaves increasingly colonized by fungi. On the other hand, Lepidoptera species whose larvae forage externally often remain on the stems and branches when not feeding, and thus, in the absence of leaves, they might have been forced to tolerate other food sources, such as algae, lichens, and fungi growing on tree bark. Another interesting hypothesis relates to the oviposition habit of many Lepidoptera, who, instead of laying eggs directly onto the leaves, select more secure sites, including the forest floor or the bark of trees, to prevent attack of egg parasites and predators. In consequence, the diet of young caterpillars upon emergence might be constrained to such unusual food sources as leaf litter, tree fungi, etc. Bearing in mind the two hypotheses outlined, it is easy to understand larval adaptation to feeding also on dead wood permeated with fungal mycelia, which is indeed known for many saproxylic Lepidoptera.

10.2 Biology and Ecology

A more detailed description of the biology of some saproxylic Lepidoptera species is discussed in the section below, yet a few general aspects are worth presenting here. The most current knowledge is based on the biology of species occurring in the Palearctic region, where the majority of studies have been devoted to this issue. Knowledge with respect to tropical saproxylic Lepidoptera species has been largely missing.

In most discussed species, eggs are probably deposited directly on a feeding substrate or in its immediate vicinity, i.e., on the sporophores (fruiting bodies) of bracket fungi and in bark crevices. Apparently, this is common in Tineidae, whose larvae tunnel into the sporocarps of a host fungi (e.g., Komonen et al. 2001; Jaworski et al. 2016; Fig. 10.1) as well as in Oecophoridae—with larvae living under the tree bark (e.g., Peterson et al. 2007; Tokár and Jaworski 2015; Fig. 10.2). One of the consequences of such a hidden way of life is the exposure of larvae to harmful microorganism infections, particularly by entomopathogenic fungi—by and largely known to benefit from elevated humidity (e.g., Roy et al. 2006) that prevails in the fruiting bodies and dead wood. Furthermore, larval mobility is limited and they have less ability to avoid the attacks of predators and parasitoids by escaping, as many external-living caterpillars do (Gross 1993; Greeney et al. 2012). Because of this, larvae of many species cover the walls of their feeding galleries with silk, which partly isolates them from inhospitable environment. Of importance are also the

Fig. 10.1 Cross section of tinder fungus (*Fomes fomentarius*) sporocarp with visible corridors of larvae of *Scardia boletella* (Tineidae) moth (T. Jaworski)

Fig. 10.2 Larva of *Oecophora superior* Rebel (Oecophoridae) in rotting oak wood (T. Jaworski)

adaptive features of the larvae, identified in some families, such as hydrophobic properties of the cuticle, modifications of spiracles, and the presence of hairs, which protect the larval body from contact with decaying remains of food, excrement, etc. (Rawlins 1984). Frass is usually removed from the feeding substrate (Fig. 10.3), which limits the development of pathogenic fungi and secures the entrance to larval corridors from predators and parasitoids (Illidge 1895). This is particularly known in Xyloryctidae, Tineidae, and in some Gelechioidea. Larvae of some saproxylic Lepidoptera species live externally in portable cases (some Tineoidea) or hide in silken runaways covered with various remains, such as wood and fungal fragments (many Oecophoridae and Tineidae). Then they tunnel into the feeding substrate from the shelters (Fig. 10.4).

Larvae of species living in temperate and boreal zones overwinter and finish their development the following year (Jaworski et al. 2014, 2016). Pupation usually takes place in a fungal host (Tineidae) otherwise host tree wood or bark (many Oecophoridae), from which pupae partly extrude before adult emergence and empty exuviae can be later observed protruding from the feeding substrate (Fig. 10.5).

Fig. 10.3 *Fomitopsis rosea* sporocarp with abundant frass granules removed by larvae of *Agnathosia mendicella* (Tineidae) moth (note just emerged adult sitting on the sporocarp) (T. Jaworski)

Fig. 10.4 Larva of *Dryadaula irinae* (Tineidae) leaving its shelter to feed on stromata of the fungus *Hypoxylon fuscum* (T. Jaworski)

Although most species of saproxylic Lepidoptera are generalists with regard to the fungal host, some are known to prefer particular species of fungi for larval development (Komonen and Mutanen 1999; Komonen et al. 2012; Jaworski et al. 2016). Certain species are restricted to particular habitats, tree species, and show preferences toward various environmental factors (Jonsell et al. 1999; Jonsell and Nordlander 2004; Jaworski et al. 2016), and several species have been recognized as indicators of less disturbed, old-growth forests (Wergeland Krog 1998; Jonsell and Nordlander 2002; Fritz 2004).

Fig. 10.5 Pupal skin (*exuvium*) of *Montescardia tessulatellus* Zeller (Tineidae) protruding from birch polypore (*Piptoporus betulinus*) sporocarp and adult moth resting after emergence from pupa (T. Jaworski)

Diversity of saproxylic insects has been diminished in many areas of the world, particularly in European and North American countries, mainly due to long-term forest management focused on the production of timber and as a consequence—reduction of dead wood in forests. A number of studies have thus far been carried out to answer whether and how these processes affect various saproxylic insect faunas. Nonetheless, scarce studies have been devoted to this problem with respect to saproxylic Lepidoptera (e.g., Jonsell et al. 1998; Thorn et al. 2015).

10.3 Diversity of Saproxylic Lepidoptera

10.3.1 Methodological Remarks

Many groups of Lepidoptera show a variety of connections with trees, and often it is difficult to distinguish saproxylic from "non-saproxylic" species. For example, some Noctuidae, Gracillariidae, and Depressariidae overwinter under the bark and inside hollows of either living or dead trees, and some Tortricidae pupate in rotting wood. Many Tineidae and some Lycaenidae feed on lichens that grow mainly or exclusively on dead or moribund trees. These organisms are, therefore, partly dependent on dead wood, which largely corresponds with the classic definition of saproxylic species formulated by Speight (1989). However, the use of the aforesaid criterion, i.e., dependency on dead wood in a broad sense, inevitably leads to unrestrained increase in the number of species to be considered as saproxylic, not to mention practically an infinite number of intermediate forms of this life habit. Therefore, for the purpose of this review, a more synthetic definition, presented by Alexander (2008), is followed: *Saproxylic organisms are species which are involved in or dependent on the process of fungal decay of wood, or on the products of that decay, and which are associated with living as well as dead trees.* Hence, the taxa encompassing species whose caterpillars bore into woody tissue of shoots or mine the bark of living trees are excluded from this review (e.g., some Argyresthiidae, Tortricidae, Nepticulidae, Gracillariidae). The superfamily Cossoidea, with plenty of wood-boring species within Sesiidae and Cossidae, is also omitted here, mainly due to the fact that their larvae feed exclusively on living wood cells, from which they digest mainly sugars (Stokland 2012), so they are not dependent on fungal decay (although some authors consider them to be saproxylic; see Stokland and Siitonen 2012). Exceptions were made for some Hepialidae and Xyloryctidae, whose larvae are known to develop, at least partially, both in living and in dead trees. On the other hand, some Elachistidae that inhabit living, yet senescent trees, are discussed here.

In this review, the systematic order for Lepidoptera follows the one proposed by van Nieukerken et al. (2011), with some minor modifications. In general, available data on the biology of more than 130 families was surveyed, and all the families containing saproxylic species (*sensu* Alexander 2008) are included. For most families the overall number of taxa (genera, species) is given to indicate the share of saproxylic species. Basic knowledge about distribution of particular taxa is presented. Also, examples of saproxylic species with some remarks on their biology are discussed.

10.3.2 Review of Saproxylic Taxa

10.3.2.1 Hepialidae

The family Hepialidae Stephens, 1829 (ghost moths) comprises more than 600 species in over 60 genera (Nielsen et al. 2000; van Nieukerken et al. 2011), usually distributed in the southern hemisphere. Root feeding is often reported as the most common feeding behavior of hepialid larvae, yet they show a wide array of adaptation in this respect, including detritivory, leaf eating, stem boring, and even fungivory (Grehan 1989; Nielsen et al. 2000). Saproxylic species are known in relatively few genera. An interesting example are larvae of *Aenetus* Herrich-Schäffer (seven species known from Oriental and Australian regions), whose early stages feed on polypore fungi and in decaying wood (the litter phase), while later instars bore into wood of living shrubs and trees (the tree phase), where they complete development by feeding on callus (Grehan 1979; Martin 2010). Similar observations were also documented for some *Endoclita* Felder, with about 60 known species from Eastern and Southern Asia (Kalshoven 1965; Grehan 2017), and thus should be expected in other hepialids.

Hepialidae are sometimes synonymized with Anomosetidae Tillyard, 1919 (along with Paleosetidae Turner, 1922) (Regier et al. 2015). This family is represented by only one species, *Anomoses hylecoetes* Turner, hitherto known from Eastern Australia (Kristensen 1978). As reported by some authors, adult specimens were reared from larvae feeding in rotting logs (Grehan 2017); however, the detailed biology of this species has been until now unknown, and therefore the saproxylic status of this species requires confirmation.

10.3.2.2 Tineoidea

The superfamily Tineoidea is replete with saproxylic species and is presently divided into three families (but see Regier et al. 2014). In Eriocottidae Spuler, 1898, the small family comprising 6 genera and about 80 species, the biology of early stages is virtually unknown, and it is difficult to speculate about a possible number of saproxylic taxa. As a sister group of Psychidae and Tineidae, where the saproxylic habit occurs frequently, Eriocottidae may, however, contain saproxylic species, as it was suggested for example in the genus *Compsoctena* Zeller (Robinson 1986).

Saproxylic representatives of Psychidae Boisduval, 1829 (bagworm moths) are known in the subfamily Arrhenophaninae. Davis (2003) listed 5 genera and 26 species of Arrhenophaninae (according to the author: the family Arrhenophanidae), mostly from tropical forests of Southeast Asia, Australia, and the Neotropical region. This subfamily has been poorly studied and the biology of only a few species has been documented. Larvae of South and Central American *Arrhenophanes perspicilla* Stoll live in tough cases made of silk, from which they burrow into sporocarps of bracket fungi of the family Polyporaceae. The similar life history was reported for *Dysoptus prolatus* Davis from Costa Rica, whose larvae were found to feed on *Phellinus gilvus* (Schwein.) Pat. (Hymenochaetaceae) growing on a dead tree, as well as *D. argus* Davis, whose larvae are believed to be associated with fungi of the genus *Fomes* (Polyporaceae) (Davis 2003). Practically nothing is known about the biology of remaining representatives of Arrhenophaninae; nevertheless, their association with dead wood and wood-decay fungi is likely.

Tineidae Latreille, 1810 (fungus moths) (ca. 2400 species globally) comprise the majority of saproxylic taxa among Lepidoptera, most of which are obligate fungivores. The family is currently divided into 16 subfamilies, and the majority of them contain saproxylic species. Furthermore, a few subfamilies include taxa whose diet consists, at least partly, of decaying woody material, fungal mycelia, etc. (Robinson 2009; Gaedike 2015).

In Dryadaulinae, with two distinguished genera, nothing is known about the life history of *Brachydoxa* Meyrick (two species known from the Oriental region), and the biology of only some species of *Dryadaula* Meyrick (more than 40 species worldwide) has been recognized. Adults of *D. heindeli* Gaedike and Scholz and *D. caucasica* Zagulajev were reared from larvae found in rotting wood of broad-leaved trees infected by the smoky bracket (*Bjerkandera adusta* (Willd.) P. Karst.) from the family Meruliaceae (Gaedike and Scholz 1998; Jaworski et al. 2012, 2014).

The similar biology pattern was reported for *D. zinica* Zagulajev (Zagulajev 1979) and recently for *D. irinae* Savenkov (Jaworski et al. 2014). Larvae of *D. pactolia* Meyrick adapted to live indoors and are sometimes noted as pests in old cellars, where they damage cork stoppers in wine bottles (see, e.g., Gaedike 2015 and references cited therein).

The subfamily Erechthiinae comprises more than 170 species placed in 9 genera (Robinson 2009). The most species-diverse (and taxonomically problematic) is *Erechthias* Meyrick, with various trophic adaptations of larvae, including those of saproxylic species. This feeding habit has been so far reported for *E. minuscula* Walsingham and *E. diaphora* Meyrick from Australia and *E. simulans* Butler, known from many Pacific Islands, Australia, and East Africa, whose larvae develop in rotting wood and under the bark of various trees (Clarke 1986; Robinson 2009; Davis and Mendel 2013). Virtually nothing is known about the biology of other Erechthiinae species.

Euplocaminae contain 1 genus and 11 species, all restricted to the Palearctic region (Robinson 2009). The biology of only one European species, *Euplocamus anthracinalis* Scopoli, is known, whose larvae develop in decaying wood of broad-leaved trees (*Fagus*, *Quercus*, *Carpinus*, *Alnus*, *Crataegus*), and sometimes also bore into bracket fungi (Hannemann 1977; Gaedike 2015).

Although numerous in taxa (20 genera, more than 120 species), the subfamily Hapsiferinae has only a few species with documented biology. In *Dasyses* Stainton (12 species, known from the Old World), the life history of *D. rugosella* Stainton has been exhaustively described due to the importance of this species as the pest of yam (*Dioscorea* spp.) in Africa (Ashamo 2006) as well as of cultivated mushrooms in Thailand (Robinson 2009). This species develops also in rotting stems and the bark of several trees (*Cycas*, *Ficus*, *Mangifera*). Saproxylic species of Hapisferinae occur also in the genus *Tiquadra* Walker (35 species with worldwide distribution, except the Palearctic). In this genus the adults of *T. gypsatma* Meyrick, from Seychelles, were reared from old logs of *Pisonia* and coconut tree (*Cocos*). Furthermore, larvae of *T. maculata* Meyrick were reported to feed under the bark of dead trees of *Breonia*, *Endospermum*, and *Myristica* in the islands of Tonga and Fiji (Robinson 2009). In South America, *T. nivosa* Felder and *T. inscitella* Walker were reported from papaya (*Carica papaya* L.); the latter species was also observed on the coral tree *Erythrina* (Robinson 2009). Similar biology is probably characteristic for *Trachycentra* Meyrick (ca. 11 species known from the Oriental and Australasian regions) (Swezey 1942), *Parochmastis* Meyrick (4 Australasian species) (Robinson 2009), and perhaps for other genera of Hapsiferinae, but there are no details available on their biology.

Harmacloninae constitute one of the smallest subfamilies within Tineidae. Two genera are currently recognized, *Harmaclona* Busck and *Micrerethista* Meyrick, each with 11 species distributed pantropically (Davis 1998; Robinson 2009). Hitherto the biology of only one species has been described. Fletcher (1933) reported the rearing of *H. tephrantha* Meyrick (widely distributed in Southeast Asia) from *Buchanania latifolia* Roxb. log. It is justified to assume that similar biology is characteristic for other species in this subfamily.

With 11 genera and nearly 300 described species, Hieroxestinae is perhaps the most species-rich tineid subfamily with respect to saproxylic taxa. In *Opogona* Zeller (180 species worldwide), where various saprophytic forms of larval feeding occur (Robinson and Tuck 1997), the association with dead wood was frequently reported for *O. omoscopa* Meyrick (e.g., Davis 1978; Robinson 2009). Currently, the species has a global distribution due to its introduction with traded goods. Another cosmopolitan species should be mentioned here, i.e., *O. sacchari* Bojer (the banana moth), whose larvae are polyphagous and were found feeding on decaying wood of various trees (Davis and Peña 1990). Fletcher (1933) reported rearing of some other species of *Opogona* (*O. choleropis* Meyrick, *O. iolychna* Meyrick, *O. lamprocrossa* Meyrick) from decaying timber of various trees (e.g., *Terminalia bialata* Steud., *Shorea robusta* Gaertn., *Butea frondosa* Koen. ex Roxb.) growing in India and the Andaman Islands. Information about saproxyly of Australian *O. comptella* Walker and *O. papayae* Turner was provided by Common (1990) and Robinson (2009), respectively. Little is known about larval biology of the remaining Hieroxestinae, but saproxylic species should be expected in other genera, perhaps *Amphixystis* Meyrick (Fletcher 1933), *Phaeoses* Forbes (Robinson 2009), and *Oinophila* Stephens (Davis 1978).

In Meessiinae, another diverse group of Tineidae (35 genera, ca. 250 species worldwide), saproxylic species are known in a relatively few genera, and this is most probably, again, due to the lack of knowledge about the biology of most taxa. Lawrence and Powell (1969) reported rearing North American *Homosetia maculatella* Dietz (later synonymized with *H. marginimaculella* Chambers) from various fungi growing both on deciduous and coniferous trees, and thus similar specialization should be expected in larvae of other species in this genus (Robinson 2009). Meyrick (1937) described similar biology for *Oxylychna fungivora* Meyrick from Java. Adults of another representative of *Oxylychna* (altogether seven species distributed in the Oriental region), *O. euryzona* Meyrick, were reared by Fletcher (1933) from the wood of *Heritiera fomes* Buch.-Ham. in Bangladesh. The latter author also mentioned the rearing of another Indian Meessiinae species, *Trissochyta acraspis* Meyrick, from the wood and bark of "pomelo" (*Citrus maxima* (Burm.) Merrill), *Shorea robusta*, and *Dipterocarpus turbinatus* Gaertn. In *Agnathosia* Rebel, whose systematic position in Meessiinae is sometimes questioned, five Palaearctic and one Afrotropical species are known (Robinson 2009; Xiao and Li 2011). The biology of only two species has been described, namely, *A. mendicella* Hübner and *A. sandoeensis* Jonasson, the larvae of which develop in sporocarps of some wood-decay fungi (Jonasson 1977; Komonen and Mutanen 1999; Jaworski et al. 2012, 2014; Gaedike 2015). In *Stenoptinea* Dietz (three species known in the Holarctic), larvae were usually reported to feed on lichens covering the bark of trees (e.g., Petersen 1957; Bengtsson et al. 2008), but some observations indicate their trophic association with dead wood and wood-decay fungi (Lawrence and Powell 1969; Zagulajev 1979; Jaworski, unpublished observations). In monobasic European *Karsholtia* Gaedike, the biology of *K. marianii* Rebel has been recently described. Its larvae create silk tents, under which they feed on decaying wood of hornbeam (*Carpinus betulus* L.) and hazel (*Corylus avellana* L.) (Huemer 1998;

Vilhelmsen 2002). Knowledge about the biology of the remaining genera of Meessiinae is poor.

The life history of the majority of Myrmecozelinae (62 genera and over 320 described species) is unknown, and most species with documented biology are associated with nests of social insects (ants, termites, bees) or birds' nests, where their larvae feed on detritus (Robinson 2009). Nevertheless, saproxylic species occur in *Gerontha* Walker, with more than 25 described species, mostly from the Oriental, Palearctic, and Australian regions (Li and Xiao 2009; Robinson 2009). Fletcher (1933) gave a fairly exhaustive description of the biology of *G. captiosella* Walker, the species known from Sri Lanka and the Andaman Islands (Robinson 2009), whose larvae are borers of tree trunks and branches of *Shorea robusta*. Saproxylic behavior was mentioned by the same author for two species of *Drimylastis* Meyrick, i.e., *D. telamonia* Meyrick and *D. claussa* Meyrick, whose larvae were reported to feed in wood of various tree species, including *Buchanania latifolia* and, again, *Shorea robusta*. In *Moerarchis* Durrant (10 species), two Australian species are recognized as saproxylic, namely, *M. australasiella* Donovan, whose adults were reared from old logs of grass tree (*Xanthorrhoea*), and *M. inconcisella* Walker, reared from larvae living under the bark of *Salix* and *Eucalyptus* as well as in the stems of *Hibiscus* and *Acacia* (Robinson 2009). Other saproxylic Myrmecozelinae are found within the Holarctic genus *Haplotinea* Diakonoff and Hinton. Larvae of two known species, namely, *H. insectella* Fabricius and *H. ditella* Pierce, Diakonoff and Metcalfe, have been reported to develop on many types of food, including stored vegetable products, plant detritus, tree fungi, and decaying wood (Hinton 1956; Robinson 2009). Adults of *H. insectella* were recently reared from a hollowed log of apple tree (*Malus domestica* Borkh.) covered with fungi. However, it is unknown whether the larvae were feeding on wood, fungi, or other remains accumulated in the hollow space (Jaworski, unpublished observations), and thus the saproxylic status of this species is uncertain. A saproxylic way of life within the subfamily Myrmecozelinae is suspected for *Aphimallota* Zagulajev, with two species known from North America and Asia, and in *Tomara* Walker (monotypic, Oriental), but further studies are needed with regard to this issue.

There are 10 genera and almost 100 species reported for Nemapogoninae, and practically all species with known biology are saproxylic. This is particularly characteristic for the genus *Nemapogon* Schrank, comprising close to 70 species, mostly internal fungivores, distributed in the Holarctic and Oriental regions (in some cases introduced into other parts of the globe). In *N. granella* L.—one of the most common and widespread tineid species—larvae develop on a variety of wood-decay fungi, growing both on coniferous and broad-leaved trees (see, e.g., Gaedike 2015 for the list of host fungi). *Nemapogon granella* occurs in natural environments; however, it was also reported from anthropogenic conditions (e.g., houses, barns) as a common pest of stored food, including grain, nuts, dried fruits, mushrooms, etc., and cork (Hinton 1956; Zagulajev 1964; Robinson 2009; Trematerra and Lucchi 2014; Gaedike 2015). Another example of such adaptation is *N. cloacella* Haworth, known from the Palearctic and Nearctic regions, where it was introduced. Gaedike (2015) recently summarized knowledge on all the remaining European species of

Nemapogoninae and indicated fungivory for more than half out of 38 *Nemapogon* species known from the continent. Further records of saproxylic species in this genus are presented by various authors within the scattered literature (e.g., Hinton 1956; Zagulajev 1964; Lawrence and Powell 1969; Robinson 2009). In the genus systematically close to the previous one, *Archinemapogon* Zagulajev, nine species are currently known that are distributed practically throughout all world's regions. The biology of these species is similar to that of *Nemapogon*, and their larvae tunnel in sporocarps of various tree fungi, mostly Polyporaceae. In another genus, *Triaxomera* Zagulajev, the biology of two species is well known: *T. fulvimitrella* Sodoffsky and *T. parasitella* Hübner adults were reared from rotting wood of broad-leaved trees and from wood-decay fungi growing on this substrate (Jaworski et al. 2014; Dobrzański and Jaworski 2016). Gaedike (2015) suggested analogous behavior for two other European species, *T. baldensis* Petersen and *T. marsica* Petersen, and Miyamoto et al. (2002)—for Japanese *T. puncticulata* Miyamoto, Hirowatari and Yamamoto. There are currently known five to seven species in *Neurothaumasia* Marchand, all from the Palearctic region (Petersen and Gaedike 1996; Gaedike 2015). The biology of only one, *N. ankerella* Mann, has been relatively well documented. Spuler (1910) first noted that larvae of this species lived in the galleries of the great capricorn beetle (*Cerambyx cerdo* L.) in old oaks (*Quercus*), and this information was later repeated by other authors (e.g., Petersen 1957; Zagulajev 1964). The adults of this moth have been reared recently from logs of oak (*Quercus robur* L.), heavily attacked by larvae of a buprestid beetle *Coraebus undatus* F. (Jaworski et al. 2011). Another interesting finding with regard to this species is related to specimens reared in Azerbaijan from the stems of *Astragalus* (Fabaceae), infested by larvae of *Xylotrechus ilamensis* Holzschuh (Coleoptera, Cerambycidae) (J. Ługowoj, unpublished data). These observations verify an affinity of *N. ankerella* larvae for galleries of other saproxylic insects and suggest a preference for warmer habitats. In the genus *Hyladaula* Meyrick, two species are hitherto known, both saproxylic. Adults of *H. perniciosa* Meyrick were reared in Bangladesh from a mangrove tree species *Heritiera fomes*, and specimens of type series of *H. claviformis* Meyrick were obtained from the Andaman padauk (*Pterocarpus dalbergioides* Roxb. ex DC.) in the Andaman Islands (Fletcher 1933). In the Palearctic genus *Triaxomasia* Zagulajev, there are also known two species, i.e., *T. orientanus* Ponomarenko and Park and *T. caprimulgella* Stainton. The biology of the first is unknown, and the adults of the latter were recorded sitting on the bark of old trees, or else—reared from wood mold of a poplar (*Populus* sp.) (T. Jaworski, unpublished) and from some wood-decay fungi (Gaedike 2015). Information about feeding of *T. caprimulgella* larvae on insect remains left behind in spiders' webs published by Pelham-Clinton (1985) needs confirmation as this would be an unusual diet for Nemapogoninae. The saproxylic species within this subfamily are also found within the two monobasic genera, i.e., *Nemaxera* Zagulajev (Euro-Siberian) and *Vanna* Robinson and Nielsen (Australasian), whose adults, again, were reared from sporocarps of wood-decay fungi.

Scardiinae comprise 30 genera and about 120 described species and, as in the above described group, all the known genera contain saproxylic species. The larvae are mostly fungivores, boring into the sporocarps of wood-decay fungi and adjoining rotting wood. The biology of the genus *Tinissa* Walker (more than 30 species found in the Oriental, Afrotropical, and Australian regions) is virtually unknown; nevertheless, there is a strong evidence for fungivory of larvae (Robinson 1976; Yang and Li 2012). Similar biology has been documented for *Morophaga* Herrich-Schäffer, with over a dozen species known from all the world's regions, excluding the New World. The biology was described for some species by Robinson (1986). Gaedike (2015) listed fungal species from which two European species were reared, namely, *M. choragella* Denis and Schiffermüller and *M. morella* Duponchel. Another species, *M. formosana* Robinson, was recognized as a pest of a polypore fungus *Ganoderma lucidum* (Curtis) P. Karst, cultivated for medicinal purposes in Korea (Park and Wang 1990). In *Daviscardia* Robinson, nine species are known, with Neotropical and Nearctic distribution; however, the biology of only *D. coloradella* Dietz has been fairly known. Larvae of this species were observed feeding in the fruiting bodies of *Polyporus* and *Ganoderma* (Lawrence and Powell 1969). In another closely related genus, *Morophagoides* Petersen, nine species were reported (Robinson 2009); however, a few additional have been recently described (Osada et al. 2015). The genus is distributed in the Palearctic and New World and, once again, in all the species with known biology larvae are fungivorous (Lawrence and Powell 1969; Robinson 1986, 2009). Just like in the whole subfamily, this feeding habit is also observed in other genera of Scardiinae, including Holarctic *Scardia* Treitschke and *Montescardia* Amsel, with nearly ten and three species known, respectively. The biology of the red-listed species *Scardia boletella* F. has been especially well documented (e.g., Bury et al. 2014), and ecological studies on this species have been also carried out (Jonsell et al. 1998; Jonsell and Nordlander 2002; Fritz 2004). The Scardiinae comprise another saproxylic species—*Vespitinea gurkharum* Robinson and Carter, from Brunei, where a remarkable example of wasp mimicry was recorded (Robinson and Carter 1989). Knowledge on the biology of the remaining genera is fragmentary; therefore further studies are needed, particularly in the tropical regions.

The saproxylic habit has been also speculated for some Siloscinae and even Tineinae (Robinson 2009); however, this requires confirmation as larval diet of known representatives of these lineages consists mostly of animal remains (skin, wool, feathers, dead insects). There are probably many saproxylic species within taxa that are still unassigned to any subfamily of Tineidae. They were, however, excluded from this review due to their uncertain taxonomical status.

10.3.2.3 Gelechioidea

This superfamily consists of several Lepidoptera families, in which the saproxylic habit occurs sporadically. On the other hand, however, it is typical for Xyloryctidae Meyrick, 1890, with 60 genera and more than 500 described species (van Nieukerken et al. 2011)—found mainly in the Australasian region. Larvae of many species in the subfamily Xyloryctinae (e.g., *Eschatura* Meyrick, *Catoryctis*

Meyrick, *Cryptophasa* Lewin) have unusual sheltering strategy of boring tunnels into the stems and branches of living trees, e.g., *Acacia*, *Banksia*, and *Eucalyptus* (hence their common name: “timber moths”). Afterward, larvae move out, usually at night, to adjoining sites, where they feed on bark, leaves, or lichens (Illidge 1895; McMillan 2017). The entrances to the tunnels are often covered and masked with silk to protect larvae from predators. Some Xyloryctidae species are considered pests of cultivated plants, and one good example is the cacao webworm, *Pansepta teleturga* Meyrick, in Papua New Guinea (Bailey 1978).

Oecophoridae Bruand, 1851 comprise more than 300 genera with over 3300 currently known species (van Nieukerken et al. 2011) and are among the most species-diverse families of Lepidoptera. Oecophoridae larvae show diverse sheltering strategies, hence family vernacular name—concealer moths. Larvae feed either outside (usually protected by a silk web) or hidden under the bark/in the wood (Kim et al. 2016). In Oecophoridae, and especially within Oecophorinae, there are many saproxylic taxa that are often unassigned to subfamily. One example is the genus *Promalactis* Meyrick, with more than 170 species distributed mainly in the Oriental and Palearctic regions. Since Meyrick’s (1922) general information on larval feeding in dead wood and the bark (mainly of coniferous trees), the biology of only a few species has been recognized. Park (1981) reported the finding of *P. suzukiella* Matsumura pupae under the bark of *Prunus persica* (L.) Batsch growing in Korea and Japan, particularly in tree parts damaged by clearwing moth (Sesiidae) larvae. In the same region, pupae of another species, *P. odaiensis* Park, were found under the bark of pine trees (Park 1981). Saproxylic species are comprised of two genera which are endemic to New Zealand. These are *Hierodoris* Meyrick and *Izatha* Walker, with 18 and 40 species, respectively, whose larvae tunnel in dead wood and sometimes in sporocarps of bracket fungi (Hoare 2005, 2010). This habit is also typical of the Palearctic genera: *Oecophora* Latreille, *Harpella* Schrank, *Schiffermuelleria* Hübner, *Denisia* Hübner, *Batia* Stephens, and *Crassa* Bruand, whose adults were often reared from decaying wood attacked by fungi and xylophagous insects (Grabe 1942; Midtgaard 1985; Hannemann 1997; Tokár et al. 2005; Jaworski et al. 2011).

Another complex and perhaps the least-studied family of Lepidoptera is Elachistidae Bruand, 1850, with more than 160 genera and 3200 known species (van Nieukerken et al. 2011). The taxonomical status of several lineages within Elachistidae is unclear, and these include Parametriotinae with a few saproxylic taxa known. *Dystebenna* Spuler, a monotypic genus known from Europe and the Caucasus, is worth mentioning, in which larvae of *D. stephensi* Stainton develop under the bark of living, yet senescent oaks (Koster and Sinev 2003). The similar biology was observed in *Chrysoclista* Stainton, with about a dozen species known from the Holarctic, Oriental, and Australian regions. *Chrysoclista linneella* Clerck larvae live in the bark on tree trunks of old linden (*Tilia*) and may be detected by observation of extruded frass noticeable in the bark crevices (Koster 2002; Majka 2005). Larvae of European *C. lathamella* Fletcher and *C. splendida* Karsholt as well as those of North American *C. cambiella* Busck have similar life history strategies on willows (*Salix*) (Busck 1915; Koster and Sinev 2003).

The family Cosmopterigidae Heinemann and Wocke, 1876 comprises over 130 genera and nearly 1800 species, with many taxa being unrecognized with respect to their biology. Zimmermann (1978) listed several species within the highly diverse genus *Hyposmocoma* Butler (more than 300 species endemic to Hawaii), whose larvae bore into dead wood and the bark of various trees. Fungivory of Australian *Limnaecia scoliosema* Meyrick was reported by Common (1990).

10.3.2.4 Pyraloidea

There are surprisingly few species of saproxylic Pyralidae Latreille, 1809, given the diversity of this family (more than 1000 genera and nearly 6000 species). One of the few examples is *Apomyelois bistriatella* Hulst, the larvae of which feed on the sporophores of *Hypoxylon* Bull. and *Daldinia* Ces. and De Not. (Xylariaceae) growing on dead parts of trees (Robinson et al. 2010).

10.3.2.5 Noctuoidea

Erebidae Leach, 1815, with 18 recognized subfamilies, over 1700 genera, and nearly 25,000 species, is the most species-rich family of Lepidoptera (van Nieukerken et al. 2011; Zahiri et al. 2012). Larvae of most species feed on green plant parts, and saproxylic species occur infrequently—mainly in the subfamily Boletobiinae. The larvae of the Holarctic *Parascotia fuliginaria* L. feed externally on the sporocarps of birch polypore *Piptoporus betulinus* (Bull. ex Fr.) P. Karst. (Fomitopsidaceae) and *Trametes versicolor* (L.) Lloyd (Polyporaceae) and consume also some other fungal species (Franclemont 1985). The similar biology has been recently reported for several species of the New World genus *Metalectra* Hübner (Lafontaine and Schmidt 2010). In Japan, larvae of two other Boletobiinae species, *Anatatha lignea* Butler and *Diomea cremata* Butler, damage cultivated shiitake mushrooms, *Lentinula edodes* (Berk.) Pegler (Yoshimatsu and Nakata 2003, 2006). Hence, it should be expected that these species are saproxylic under natural conditions, as it is known for a closely related species, *Diomea rotundata* Walker (Kononenko and Pinratana 2013). Caterpillars of North American *Scolecocampa liburna* Geyer (Scolecocampinae) were reported as associated with dead wood (Moraes et al. 2016). Also, fungivory of larva of North American *Spilosoma congrua* Walker (Arctiinae) feeding on the fruiting bodies of *Trichaptum biforme* (Fr.) Ryvarden (Polyporaceae) was observed; however, it is unclear whether larvae consumed the fungus or algae covering the sporocarp, as algivory is known in some other Arctiinae (Moskowitz and Haramaty 2012).

Another large family, Noctuidae Latreille, 1809, consists of more than 1000 genera and above 11,000 described species (van Nieukerken et al. 2011). Little is known about saproxylic species within this family; nevertheless, larvae of *Paragona multisignata* Christoph (subfamily Calpinae) were reported as pests of shiitake mushrooms in Japan (Yoshimatsu and Kawashima 2016). Therefore, they may be also associated with other wood-decay fungi in forest environments. Caterpillars of *Sandava scitisignata* Walker (same subfamily) from Australia have been found under loose bark on trunks of dead trees, where they probably fed on fungi (Common 1990).

10.4 Conclusions

Although larvae of most Lepidoptera species feed on green plant parts, there also exists a diverse group of saproxylic species that are dependent on dead wood and wood-decay fungi. The habit of larval feeding on such substrates appeared independently in several lineages of Lepidoptera as a result of transition from herbivory to fungivory, most probably under the conditions of periodic deficiency of leaves and possibly also due to oviposition in the sites with fungi as easily available food sources for hatched larvae. The families of Lepidoptera containing the highest number of saproxylic species include Tineidae and Oecophoridae; nevertheless, this feeding habit is also known within several other taxa.

Information on saproxylic Lepidoptera is scattered across various publications, often published many years ago, in which the term “saproxylic” is practically absent. The biology of a relatively small number of saproxylic Lepidoptera has been so far recognized, primarily from the Palearctic and—to a lesser degree—also from the Australian region. At the same time, the greatest diversity of Lepidoptera saproxylic taxa is concentrated in the tropics, where the number of species with the known biology is extremely small, and some taxa require verification of their saproxylic status. Therefore, there is a need to intensify research on the biology and distribution of this group of insects.

Saproxylic Lepidoptera, along with other groups (mainly Coleoptera, Hymenoptera, and Diptera), play an important role in forest ecosystems as secondary wood decomposers. In addition, they provide food of predators and parasites, both closely related to dead wood (e.g., other saproxylic insects) and occasional visitors to this environment (birds, mammals). However, there is a lack of detailed knowledge about ecological links of the discussed group with other organisms, and scientific works on this subject are scarce.

Various interesting adaptations have been developed by saproxylic Lepidoptera to endure in dangerous environment of the interior of dead wood; however, in most species the mechanisms behind these adaptations have not yet been researched. Physiological adaptations of saproxylic Lepidoptera larvae that allow them to digest fungal mycelium and decaying wood are poorly understood. For example, it is not known whether and to what extent different species of fungi and wood of different tree species affect the growth and survival of larvae, and, perhaps, their abilities of defense against natural enemies.

Dead wood in forest ecosystems is a key element for the occurrence of saproxylic organisms, including many Lepidoptera. The modern, timber-oriented forest management has led to a decline in the quantity and quality of this crucial component, particularly in the European region. This has caused a number of negative effects on biodiversity, including deterioration of many saproxylic species. In recent years, many works have been devoted to this problem, particularly with respect to conservation of saproxylic beetles, but knowledge is lacking with respect to Lepidoptera. Consequently, there is a need for research on this generally unexplored group of organisms.

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Chapter 11
Wood-Feeding Termites

David E. Bignell

Abstract Termites originated from wood-feeding cockroaches and are dominant members of the saproxylic insect community in many tropical and subtropical biomes. Their ecological role comprises comminution (shredding) of dead organic material, bioturbation (mixing of organic and mineral material in soil horizons) and lignocellulose digestion (contributing to the decomposition arm of the global carbon cycle). The key adaptations of termites are their symbioses, mainly internal, with protists, archaea, bacteria and (in a special case) fungi. Thus the evolution of modern termites from the detritus-feeding common ancestor of termites and wood-feeding cockroaches can be reconstructed as a stepwise process to secure the transfer of increasingly specialised intestinal symbionts from parent to offspring. This selection resulted in the extant eusociality of all termites, characterised by generational overlap, proctodaeal feeding, altricial development, paedomorphosis and co-evolution with microorganisms. An account is given of their typical abundance, biomass, trophic diversification and impacts on soil health and the terrestrial carbon cycle. Termite behaviour associated with finding and consuming woody resources is also considered. An overview of the symbioses between termites and microbes is presented, focused on recent work revealing the relative contributions of host and microbiota to the digestion of lignocellulose. A separate account of the fungus-growing subfamily Macrotermitinae is added, as their impact on organic decomposition in Africa and Asia is substantial.

11.1 Introduction

With approximately 281 genera and 3000 species worldwide (Kambhampati and Eggleton 2000; Engel et al. 2009), termites (also known as isopterans) are relatively few in diversity compared to many other insect groups. There are over four times

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more ant species (12,516, according to Engel et al. 2009), and termite diversity is even exceeded by that of the non-eusocial members of their own order, Blattodea, with 4487 known cockroach species (Beccaloni 2012). Termites are nevertheless one of the most ecologically and economically important groups of invertebrates in the tropics and subtropics, where they play key roles in decomposition and soil processes and some species annually cause billions of dollars in damage to wooden structures, forest products and crops (Verma et al. 2009; Rouland-Lefèvre 2011). Termites originated as wood feeders, being most closely related to wood roaches of the genus *Cryptocercus*, but have since expanded their diet to include a wide range of foods including leaf litter, humus, grass, soil, dung and lichen. Jones and Eggleton (2011) provide a catalogue of genera, allocating each to a feeding group and biogeographical region, from which Bignell (2016) estimated that wood feeding (sensu stricto feeding groups I and II in Donovan et al. 2001) was the functional group of 26% of genera and 56% of all species. Wood feeding is represented in most higher termite taxa, including those not closely related phylogenetically, suggesting that some origins of wood feeding may be secondarily derived (Donovan et al. 2000; Inward et al. 2007a; Cameron et al. 2012; Bourguignon et al. 2015). Unlike ants, termites are largely restricted to the tropics and subtropics where they often dominate saproxylic insect assemblages in both abundance and impact on wood decomposition. Their absence at higher latitudes (excepting some representation in warm temperate biomes) appears due to a thermal restriction; however urban heat islands are not exempt from invasion by pest species.

The dominance of termites is made possible by their eusociality, which allows for the formation of huge colonies consisting in some cases of thousands or millions of individuals, combined with their symbioses with a variety of wood-digesting protists, archaea, bacteria and fungi. Nalepa et al. (2001) proposed that eusociality in termites evolved to ensure the fidelity of vertical transmission of internal (intestinal) symbionts from parents to offspring. Acquisition of the symbionts is assumed to be primary, allowing access to otherwise recalcitrant substrates, while selection for sociality is secondary, to improve their retention and drive co-evolution with the host. This thesis parallels the classical view that sociality in the Hymenoptera is also a derived trait, though by contrast arising from the basal genetic condition of haplodiploidy. Where other parallels between the two major groupings of social insects are becoming weaker, the area of symbiont fidelity remains a common thread. The hypothesis of co-evolution between termites and their symbionts is attractive in that it allows for progressive selections of communal behaviours and generational overlaps from solitary ancestors, through subsocial stages to a final eusociality in family-based colonies, all within a diplo-diploid genetic system in the host. In contrast, the alternative theory of inclusive fitness incorporates the precondition of high relatedness between siblings, perhaps reflecting the model of haplodiploidy, before generalised altruism can be selected. The termite-symbiont system is now portrayed as a captured and optimised external rumen, providing a continuous transition between the low-efficiency but widespread detritivory of many soil arthropods and the highly specialised feeding niches of modern isopterans (Bignell 2016).

Until recently termites were classified in the insect order Isoptera; however the sequencing of both nuclear and mitochondrial genes has shown that they are not sufficiently different from cockroaches to justify separation at the ordinal level (Inward et al. 2007a) and were consequently relegated to an epifamily, Termitoidae (Eggleton et al. 2007), within the order Blattodea (cockroaches and termites), though not without challenge (Lo et al. 2007). This taxonomic device carries the advantage that existing termite family names can be retained, although the number recognised even in the recent literature varies between 5 and 11 (summarised by Donovan et al. 2000; Legendre et al. 2008; Cameron et al. 2012). The basal families comprise the "lower termites" which are populated with flagellates, amongst other gut symbionts and are overwhelmingly wood feeders. The "higher termites" belong to the largest family, Termitidae, which contains 84% of all termite genera and 70% of species (Table 6.1 in Bignell 2016), and is agreed to be a monophyletic group of relatively recent (Miocene) origin (Engel et al. 2009). The definitive distinction between higher and lower termites is the lack of any flagellate intestinal symbionts in the former but also reflects a number of other advanced (i.e. derived) traits such as true workers, distinctive caste differentiation, the use of soil for construction, complex nest architecture, multiple-piece nesting (sensu Abe 1987) and a nutritional diversification which includes soil feeding. The Miocene explosion of the Termitidae continues to the present day, leading to them assuming a dominating ecological role in decomposition processes and soil conditioning throughout much of the humid tropics and beyond, comparable with that of earthworms in moist temperate biomes (Engel et al. 2009; Jouquet et al. 2011). It is tempting to link diversification with the absence of flagellates, especially as higher termite gut structure is broadly (and with the exception of the subfamily Macrotermitinae) more complex than that of lower termites (Donovan et al. 2000; Köhler et al. 2012); however it has not proven possible to identify the basal feeding habit of the Termitidae unequivocally (Inward et al. 2007b) and hence the obvious inference that the accidental or deliberate ingestion of soil particles destroyed the delicate flagellates remains just a hypothesis. Equally plausible, in view of the fact that the Macrotermitinae branch basally in every phylogenetic topology of the Termitidae (ibidem), is the proposition that the digestive burden initially passed from the gut biota to the external fungus garden, and thus the primary role of the flagellates in lignocellulose degradation became redundant (Inward et al. 2007b). Engel et al. (2009) speculate that Mesozoic termites may have had only minor ecological roles and that organic decomposition was in consequence a slower process; however it is also the case that termites are much less abundant in modern day tropical montane forests, yet there is no prima facie evidence that decomposition rates are diminished, if one allows for the overall temperature dependence of the process.

Termites have been classified on the basis of both nesting and feeding habits. The original nesting scheme was devised by Abe (1987) who recognised one-piece nesters that live and feed entirely within a single item of substrate (usually wood), intermediate nesters that live similarly but also forage to resources nearby, and separate-piece nesters which obtain food in a different place from the colony centre, also usually requiring material from outside the colony area to construct their nests

(Eggleton 2011). Subsequently, the intermediate category has been dropped, leaving the two recognised nest types as single-piece and multiple-piece (Korb 2008) or simply "wood dwellers" and "foragers" (Korb 2007; Korb et al. 2012). Diet-based classification systems were traditionally based upon careful observation of individual species in their natural habitats, dissection of the intestine (the hindgut) and from abdominal colour in the worker caste (wood feeders are typically brown or yellow; soil feeders are grey or black). The five modes generally agreed to exist are shown in Table 11.1, but the evolutionary sequence in which they appeared is not completely certain. Wood feeding on the single-piece model is agreed to be the basal habit, but wood feeding from multiple pieces is found in many lower and higher termites and may have re-evolved in the latter group (Donovan et al. 2000). Litter feeding (including grass cutting) may have the advantage that the material harvested is marginally richer in nitrogen; however increased emphasis on foraging also brings higher costs from the construction of galleries, runways and sheeting to protect against predation and exposure. Most notable is that more than half of termite genera (59%) are soil feeders, meaning that the gut contains large amounts of mineral material together with the organic matrix in which this is embedded, as well as with variable amounts of recognisable fragmented plant tissue, generally highly decayed (Sleaford et al. 1996; Donovan et al. 2001).

Donovan et al. (2001) devised a four-category feeding classification based on gut and mandible structure, combined with a systematic microscopical analysis of the intestinal contents in the principal hindgut chamber. The full scheme and a summary of the statistical methodology supporting it are given in Table 11.2. In an ordination of gut content data in 46 species representative of all heuristic feeding groups and the major taxa, it was found that silica and plant tissue fragments were best correlated with the principal axis, which therefore represents a humification gradient, and from this a minimum number of four objective groups could be identified, in increasing order of humification of the resource used. The gut and mandible morphological characters listed in the table can be used unambiguously to allocate live or preserved specimens to feeding group without the need to carry out the analysis of hindgut contents. There is no suggestion that the feeding groups represent clades as such; they merely comprise endpoint conditions for numerous parallel or convergent evolutions. Donovan's classification is partly challenged by Bourguignon et al. (2011) on the grounds that the stable isotope signatures of termite tissues ($\delta^{15}N$) do not permit a separation of groups I and II or III and IV. However, the classification is based on what the gut actually contains, not any presumption about the mechanism of digestion. The latter has only been investigated in the *Cubitermes* clade of group IV (Brune and Ohkuma 2011).

Eggleton and Tayasu (2001) devised a system of seven "lifeways" which combine feeding and nesting groupings. This proves useful for documenting and understanding the biogeography of termites (Davies et al. 2003), but the advantage of the Donovan scheme is that it employs the minimum number of categories necessary to understand community feeding structure and therefore in large measure niche differentiation. It can be conceded that fungus growers require a feeding group of their own, as the gut contents vary more with age and caste than in other termites (see

Table 11.1 Heuristic feeding modes after Bignell (2016), cross-referenced to Donovan's scheme derived from gut structure and content analysis (Donovan et al. 2001)

Mode	Descriptions	Approximate % of all termite genera[a]	Approximate % of all termite species[b]	Corresponding feeding groups in Donovan's scheme
Woody items consumed by different species in all stages of decay, including living trees, bushes	Termites feeding on wood and excavating galleries in large items of woody litter, which in some cases become colony centres. This group may also include species with arboreal (carton) nests, epigeal (soil or carton) nests or subterranean nests; also includes some Macrotermitinae cultivating fungus gardens	26	52	I, II
Litter, including dry standing grass, dung and organic detritus at the soil surface	Termites that forage for leaf litter and small woody litter; includes some mound building and subterranean Macrotermitinae, also epigeal mound builders and arboreal nesters of the Nasutitermitinae (nasute soldiers), which forage on the surface of the litter layer	13	20	II
Soil/wood, including humus	Termites feeding only or predominantly within soil under or plastered within logs or feeding within highly decayed wood that has become friable and soil-like; workers dark-bodied	37	16	III
Soil, including mound walls	Termites distributed in the soil profile, surface litter (leaves and twigs) and/or epigeal mounds, feeding on mineral soil; workers dark-bodied	22	10	IV
Lichen and algae, including tree bark	Termites that forage for lichen, mosses and algae on the bark of trees	<1	2	II

[a] Allocations to feeding modes based on 204 genera listed by Jones and Eggleton (2011)

[b] Allocations to feeding modes from Jones and Eggleton (2011) and totals per mode based on 2365 species listed in Appendix 1 of Kambhampati and Eggleton (2000)

Table 11.2 Feeding group classification of Donovan et al. (2001), modified after Dahlsjö et al. (2014)

	Diagnostic gut morphological characters			Typical gut contents		
Group	Malpighian tubules	Rt. mandible molar plate ridges	Enteric valve	Silica	Plant tissue fragments	Examples
I	8 or more			Low	High	Lower termites
II	4 or less, attached at mesenteron/P1 junction only	Prominent	No armature between ridges	Low or moderate	High, but with variable degrees of humification	Representatives of *Amitermes* clade *Cornitermes* clade *Nasutitermes* clade
IIF	4, as above	As above	As above	Low, excepting older workers	High	Macrotermitinae
III	4 or less, attached as above or otherwise	Vestigial	Unsclerotised ridges	Moderate or high	Moderate	Representatives of: *Anoplotermes* clade *Termes* clade *Cornitermes* clade *Nasutitermes* clade
		Absent	Some sclerotisation	Moderate or high	Moderate	
IV	4 or less, attached as above or otherwise	Absent	At least half the ridges 50% sclerotised	High	Low	*Apicotermes* clade *Cubitermes* clade Representatives of: *Anoplotermes* clade *Amitermes* clade *Termes* clade *Cornitermes* clade *Nasutitermes* clade

This allows unknown specimens to be allocated to an objectively defined feeding group without resort to gut content analysis and without subjective assessment of natural history and abdominal colour. Clades follow Kambhampati and Eggleton (2000) below). This is recently recognised by Dahlsjö et al. (2014), who add a fifth category, FGIIF, to accommodate the Macrotermitinae.

Perceptions of termites as pests often dominate thinking about these insects although relatively few taxa deserve this label (Evans 2011; Rouland-Lefèvre 2011; Rust and Su 2012), commonly those with strong invasive potential (Evans et al. 2013). The ecological benefits of wood-feeding termites, e.g. their roles in decomposition and soil processes, are widely recognised but generally receive less attention (Schuurman 2005; Ulyshen 2016). Insights gained from research on the digestion of lignocellulose by termites and their symbionts may also have important industrial applications. The current consensus is that cellulases are synthesised by both the host termite and several of its intestinal symbionts, including flagellates where present, and all are active during the digestive process. Interest in what both host and symbiont genomes may encode is therefore keen, and in this context, it is intriguing to consider that in addition to enzymes such as cellulase, hemicellulase, laccase, lignase and phenoloxidase, with presumptive lignocellulolytic capabilities when mixed in vitro (e.g. Ke et al. 2011; Raychoudhary et al. 2013; Sethi et al. 2013; Karl and Scharf 2015), glucanases with antifungal properties are also included in the digestome of wood-feeding species (Rosengaus et al. 2013; see also Chouvenc et al. 2009, 2013).

This chapter follows a similar structure to Bignell (2016), the most recent attempt to review the whole of termite biology in the context of evolution, microbiology and ecology, excepting Šobotnik and Dahlsjö (2017) in which the emphasis is more morphological, developmental and behavioural. In preparation, almost 200 additional articles have been reviewed, including 50 of direct relevance published after 2014 (as of July 2017), but the text has been reduced in length to meet page limits and to reflect the focus on the wood-feeding functional group. My objectives in this chapter are to review the (1) global impacts of termites, (2) evolution of termites from wood-feeding cockroach ancestors, (3) diversity and roles of symbionts, (4) process of finding and consuming wood, (5) fungus-growing termites as a special case and (6) the question of whether lignin is degraded by termites.

11.2 Global Impacts of Termites

Environmentally, the main impact of termites is their role as soil ecosystem engineers in the tropics and subtropics, a function matched on the global scale only by earthworms and ants (Bignell 2006; Jouquet et al. 2011; Brussaard et al. 2012). This role arises principally from detritivorous habits and a high abundance and biomass, combined with tunnelling and the various constructions made with mineral and organic materials, the net effect of which is to condition soil (i.e. to facilitate drainage and intimately mix its organic and inorganic constituents) and drive the decomposition arm of the carbon cycle (Lavelle and Spain 2001). It should be noted that decomposition is not simply mineralisation of dead tissue as CO_2 (and to some extent as CH_4); it also includes nitrification and the creation of long-term carbon pools in soils, both of which promote and sustain fertility. There is also a shredding role, overlooked in many assessments of termite ecological importance (Berge et al. 2008; Ulyshen and Wagner 2013). Evidence that termite populations promote crop yields and can help to rehabilitate degraded soils and biologically impoverished landscapes is given by Mando and Miedema (1997), Bonachela et al. (2015), Evans et al. (2011) and Erpenbach and Wittig (2016).

Following early work by Yamada et al. (2005), a series of papers by Jouquet and co-workers (e.g. Jouquet et al. 2004, 2005, 2012, 2015) pointed to the important role of termite mound and runway building in pedogenesis and nutrient recycling. Constructions involve particle selection, generally favouring clays (e.g. Oberst et al. 2016), and may also concentrate organic matter and some nutrients (Rückamp et al. 2011; Dambros et al. 2016). The larger mounds may consequently support a separate community of plants and function as point-scale biodiversity refugia (Jouquet et al. 2011; Joseph et al. 2013; Davies et al. 2016; Seymour et al. 2016); however this is not inevitably the case, and parent soil type is still reflected in constructions (Jouquet et al. 2015). Field exclusion experiments (not using insecticides) have recently resumed following a period of abeyance when they were considered impractical for soil organisms and show that the presence of termites, with some other insects, accelerates woody decomposition (Stoklosa et al. 2016). Litterbags accessible to termites show that there is a preference for larger sized woody items, at least in warm temperate forests, a conclusion also reached by Nobre et al. (2008) using a line intersection sampling approach.

Termite population ecology is reviewed by Bignell and Eggleton (2000) and Lepage and Darlington (2000), from which estimated live biomass across all termite habitats ranges up to 11 g m^{-2} and numerical density up to 10,000 individuals m^{-2}, with 510–1150 g of live weight in the largest nests, but there are great differences between habitats, and the data in these two reviews now need to be updated. In general, termite species richness and abundance decline with decreasing rainfall and increasing altitude, but even with these restrictions, landscape-level calculations suggest that termites are the dominant soil invertebrates across much of the tropics and subtropics. Changes result both from the removal (or addition) of microhabitats specific for each group and from changes in physical conditions that accompany canopy reduction (Gillison et al. 2003). Disturbance of natural or seminatural habitats is therefore usually damaging to termite populations, but wood feeders tend to be better adapted to moisture conservation (Davies et al. 1999; Lavelle and Spain 2001) and may therefore become dominant in secondary assemblages (e.g. Jones et al. 2003). But even the most resilient forest termites cannot recover from complete tree clearances; consequently, the conversion of natural woodlands to other uses often begins a degenerative sequence in which biodiversity, soil fertility, soil ecosystem resilience and soil physical stability all decline (Bignell et al. 2005; Fig. 11.1). The effects of fires, both natural and human-induced, are reviewed by Davies et al. (2010). From the few studies in the literature, there is a reduction of biomass and activity, and also of functional group composition, but effects on species richness are unclear (Dosso et al. 2012; Davies et al. 2012). Modern studies on altitudinal gradients are reported by Donovan et al. (2002), Inoue et al. (2006),

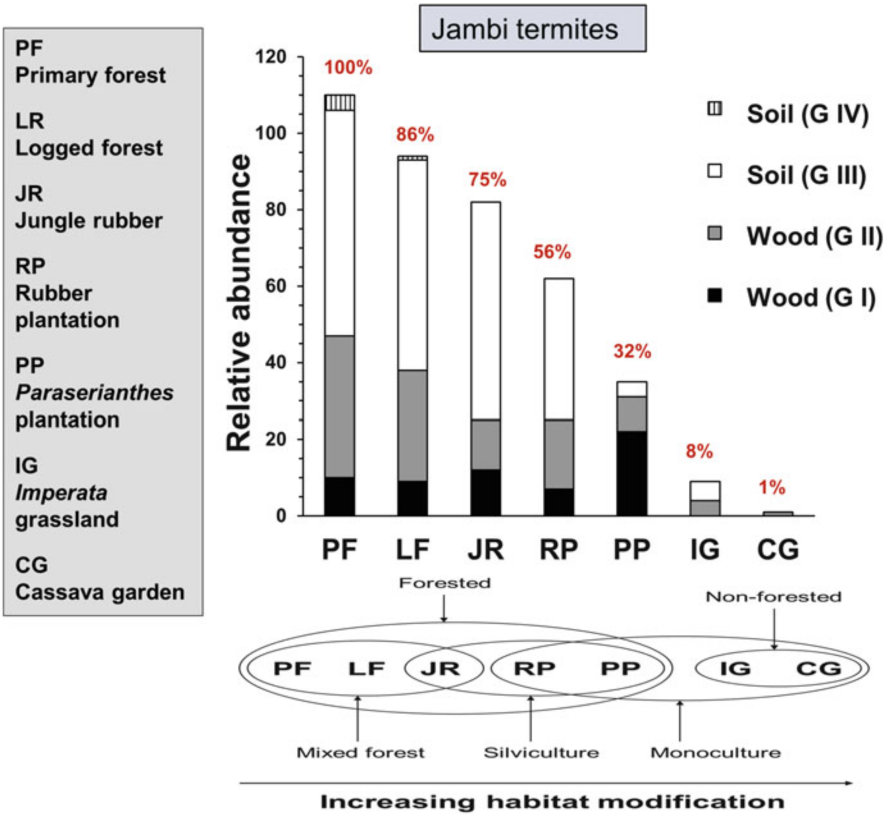

Fig. 11.1 The relative abundance (as captures per 100 m transect) of termite species in four functional (feeding) groups as defined by Donovan et al. (2001) across a land-use intensification gradient in Jambi Province, Sumatra. The land-use linkages shown in the lower part of the figure rationalise the principal disturbances and their intensities. Percentages in red above the histogram bars show species richness in each land use relative to primary forest. Broadly, the gradient shows the resilience of wood-feeding forms to moderate disturbance. Based on Jones et al. (2003)

Palin et al. (2011) and Nunes et al. (2017). Diversity and indirect absolute abundance (relative frequency in samples) declined with increasing elevation and though there is as yet no evidence of montane specialists, termite contributions to wood and litter decomposition are small above about 1000 m.

In natural savannas, there are different dynamics, as most termite species are strongly adapted to moisture conservation and land use changes tend to manifest themselves in the reduction of woody resources on which termites feed (Bignell and Eggleton 2000; Bignell 2006). Evidence of intercontinental variations in typical termite abundances and biomasses is presented by Davies et al. (2003), updated by Dahlsjö et al. (2014). Improvements in approaches to sampling in savannas (e.g. Davies et al. 2013) have made estimates of termite abundance, biomass and seasonality (reflecting rainfall) more reliable and show that termites have an optimal range for activity, being inactive when conditions are excessively wet or dry or else too cold (Davies et al. 2015).

Greenhouse gas emissions by termites attract attention from time to time. Measurements averaged across a wider range of species and feeding groups have suggested that termites mediate about 2% of the CO_2 flux to the atmosphere from all terrestrial sources, but this apparently low figure conceals the physical processing (comminution) role of termites of up to 30% of net primary production in some habitats (Bignell 2006; Bignell et al. 1997). The few detailed studies at landscape level also suggest significant contributions, for example, Konaté et al. (2003) estimated that in the Guinea savanna of West Africa, CO_2 emissions by termites represented 4.9% of above-ground net primary production and 11.3% of the carbon not mineralised by annual fires. An earlier study in a similar savanna by Wood and Sands (1978) had concluded that termites were responsible for about 20% of total carbon mineralisation (roughly the same as mammalian herbivores and bush fires, respectively), while Yamada et al. (2005) estimated that 11.2% of above-ground wood and leaf litter was mineralised by termites in the dry evergreen forest of Thailand.

Methane is a specifically microbial end product, and the archaeal organisms producing it appear to be part of the gut community in every termite; however emissions from the termites themselves vary greatly between species reflecting the extent to which other, acetogenic, microbes are present and active. Global emissions to the atmosphere from termites are now estimated to be no more than 4–5% of all sources and may in fact be much less because methane has been shown to be oxidised in mound materials and the soil adjacent to nests (reviews by Bignell 2010; Velu et al. 2011; Ho et al. 2013). Termites are mentioned as significant sources of atmospheric methane in Chap. 6 of the most recent report of the Intergovernmental Panel on Climate Change (Ciais et al. 2013), with the estimate of global emission (11 Tg yr^{-1}) unchanged since the previous report in 2007, despite the new evidence. No upward or downward trajectory is predicted, and the data utilised by the Panel do not consider the evidence of local methane oxidation in or around termite nests. The methodologies employed in scaling-up from laboratory and field measurements to global fluxes are reviewed by Sugimoto et al. (2000).

11.3 Termites Are Eusocial Cockroaches

The idea that termites are descended from cockroaches can be traced back to Cleveland et al. (1934) who described intestinal morphology and the hindgut flagellates in the subsocial wood-feeding cockroach *Cryptocercus punctulatus*, which is found in eastern North America, and demonstrated experimentally that the degradation of cellulose depended on the presence of the protists. *C. punctulatus* and eight other described species in the genus found elsewhere in North America and in parts of Asia stand apart from other cockroaches in their partial, though not complete, resemblance to termites such that the more the biology of the two groups is investigated, the more inevitable becomes the conclusion that these wood-feeding cockroaches and termites share common ancestry (Lo et al. 2003; Legendre et al. 2008). However the ancestor itself, which is likely to have been Mesozoic, has not been discovered; neither is there any living termite which in its traits of social organisation, developmental morphologies or symbioses with microbes is quite as simplified as those of the cockroach. Overwhelming evidence is now available from morphological characters and genomic analysis of both hosts and symbionts that termites and *Cryptocercus* together behave as a single clade more convincingly than the combination of all termites and any other taxon of cockroaches.

The similarities between *Cryptocercus* and modern, single-piece lower termites are (a) they make nests in large, slowly decaying logs which serve as both protected living space and food; (b) the hindgut accommodates obligate parabasalid and oxymonadid flagellate symbionts with similar or identical taxonomic affiliations and which have limited distributions in other hosts; (c) the symbionts are vertically transmitted from older to younger cockroaches by anal trophallaxis (proctodaeal feeding) which also serves as a source of food for the younger nymphs; (d) the nests contain biparental family groups which are at least semi-social, that is, the nurture of neonates (feeding and protection) is initially carried out by both parents but then passes to older nymphs which are themselves nutritionally mature and can feed on wood, i.e. alloparental care; (e) hatchlings and early nymphs are exceptionally small, unsclerotised and unable to consume or digest lignocellulose, i.e. altricial: and (f) the rate of growth of progeny is slow and their reproductive maturation retarded or inhibited entirely by the social setting (Nalepa and Bandi 2000). The ability to degrade cellulose is not a unique common feature as the secretion of endogenous cellulase is widespread amongst cockroaches and in terms of genetic potential also many other invertebrates (Bignell 1977; Maekawa et al. 2003; Lo et al. 2003), nor is *Cryptocercus* the only semi-social cockroach (Pellens et al. 2007). Other parallels exist, for example, at a higher level of resolution there are similar symbioses between intestinal flagellates and ectosymbiotic bacteria (Noda et al. 2006), and the fat body endosymbiont *Blattabacterium*, almost universal in cockroaches, is also found in *Mastotermes darwiniensis*, the most basal of living termites. However, the six key similarities listed above have been sufficient for Nalepa (2010, 2011) to argue that altricial development and paedomorphosis (the retention of juvenile traits by the majority of colony members) are key empirical antecedents of eusociality in termites, overlying the attendant selection and internalisation of microbial symbionts which in many other detritivorous invertebrates contribute to the external rumen.

Nalepa et al. (2001) argue that when the termite ancestor achieved subsociality and filial coprophagy, possibly in the swamp forests of the Upper Carboniferous (Scott and Taylor 1983), the pace of the evolution of the mutualism with microorganisms accelerated to a symbiosis with co-evolution of host and microbe, thereby driving selection for further and more extreme altricial development, proctodaeal trophallaxis and, eventually, paedomorphosis, resulting in the typical eusocial character states of termites. A further consequence of this internalisation process would have been a slowing of intestinal transit times, which is manifestly achieved by elongation, convolution and compartmentalisation of the alimentary canal (Bignell 1994, 2011). The termite therefore internalises the consortium comprising the external rumen, the ultimate advantage of which is that freshly dead plant materials may be consumed before these materials are colonised by bacteria and fungi and without prior need of microbial conditioning (Wood 1976). However the question of where the flagellates came from remains open. Contemporary leaf litters and soil contain free-living flagellates as well as other kinds of protists, but the *Cryptocercus*/termite community is of an apparently basal though probably heuristic eukaryote grouping, the Archezoa, which lack conventional mitochondria and live anaerobically in animal intestines without free-living relatives (van der Giezen 2009). In lower termites with flagellates, the protists are shed from the hindgut during moulting; however they are re-established directly by anal trophallaxis without the need to pass through the encystment stage, which in other associations between archezoans and arthropods is stimulated by the endocrine changes preceding the moult. In *Cryptocercus*, at least some of the flagellate population is retained in the hindgut during moulting and reinoculation via trophallaxis or by ingesting faeces is unnecessary (Nalepa 2017). Significant and at least partly autochthonous bacterial microbiotas have been described in *Cryptocercus*, representatives lower termites and in the Termitidae, including the Macrotermitinae (Dietrich et al. 2014; Brune and Dietrich 2015). These bacterial biotas are to some extent homologous and have major metabolic roles including facultative nitrogen fixation, and some are endosymbionts in their own right within the flagellates.

11.4 Catalogue and Roles of Symbionts

Tables 6.8 and 6.9 in Bignell (2016; also available in modified form in Bignell and Jones (2014) give alphabetical listings, respectively, of the protists and prokaryotes more commonly reported as intestinal associates of termites, together with brief statements of their status and/or biology and citations of recent reviews in which further details of each symbiont can be found (current to December 2014). The lists are not complete, and in many cases the stated roles are presumptions; however it should be clear that the biodiversity of the intestinal ecosystem is very high, perhaps two to three times greater than any other comparable (and investigated) microcosm (Ohkuma 2008; Kudo 2009; Brune 2011). Across all lower termites, up to 80 genera and roughly 500 species of flagellates have been described, but the species number in any one termite host species is not greater than about 30 (Radek 1999). There is a large range of size, from about 300 μm to about 10 μm in the greatest dimension, thought to reflect a division of functional roles. A few can be cultured (anaerobically), and much of what is known about the overall metabolism of flagellates derives from such in vitro investigations (Brune and Stingl 2005; Ohkuma 2008; Kudo 2009). Up to 20 prokaryotic phyla are represented across termites as a whole, some of them novel to science, and the majority of species, perhaps 90%, are uncultivable by current methodologies (ibidem). Structure provides only a partial picture of the diversity: while perhaps 20–30 morphotypes can be distinguished in the transmission electron microscope in a typical termite species, molecular sequencing commonly allows several hundreds of phylotypes to be identified (Brune 2011).

In numerical terms, prokaryotic gene sequences (normally 16S rRNA) are frequently dominated by *Spirochaetes*, *Bacteroidales*, *Firmicutes* and *Clostridiales*, together comprising an estimated 80% of the gut bacteria (Ohkuma 2008). Other types represented include *Actinobacteria*, *Planctomycetes*, *Proteobacteria*, *Mycoplasmatales* and the *Elusimicrobia* (proposed phylum, formerly Termite Group 1) (Ohkuma 2008; Kudo 2009). Archaea contribute about 10% of the gene signals. In lower termites these affiliate to the Methanobacteriaceae, while in higher termites the Methanomicrobiales and Methanosarcinales are better represented. It is difficult to correlate the actual emissions of methane from termites (i.e. the in vivo efflux) against their taxonomy, except that the highest measured weight-related rates seem to be associated with soil feeding (Nunes et al. 1997). All termites probably have the potential to evolve the gas, but the internal balance between methanogens and other microorganisms capable of reductive acetogenesis (from CO_2 and H_2) determines how much escapes the insect's integument (Brune 2006). Local oxidation by methanotrophs in soil and nest materials may further reduce net fluxes to the atmosphere (Sugimoto et al. 2000). The intracellular symbiont *Blattabacterium*, universal in the fat body tissues of cockroaches where it occupies membrane-bounded vesicles within special cells known as mycetocytes, is found only in the basal termite *Mastotermes darwiniensis*. The symbiont has a more versatile nitrogen metabolism that the insect host, with the capacity to synthesise amino acids and vitamins, and recycle excretory urea and NH_3 into glutamate, which is a usable product (Sabree et al. 2009). While this observation confirms the common ancestry of termites and cockroaches, it is not clear why *Blattabacterium* has been deleted in all other termites unless the role of nitrogen recycling has been taken over by an organism from the gut community. Metabolism of urates in the hindguts of lower termites was demonstrated by Potrikus and Breznak (1981), while assistance with the synthesis of organic nitrogenous compounds is a suggested role for the Endomicrobia (also proposed as name for the former Termite Group I), which are abundant internal symbionts of many flagellates (Ohkuma 2008; Brune 2012). However, Endomicrobia also occur in *Cryptocercus* and other cockroaches, neither is the need for strict nitrogen conservation evident in the broader feeding habits of the Blattaria (see above). Termite guts may also contain specialists, for example, the high-pH compartments of the anterior hindguts of many higher termites are dominated by alkaliphile *Clostridiales* (Thongaram et al. 2003) and *Planctomycetes* (Köhler et al. 2008).

Even within established microbial ordinal and family level taxa, termite symbionts will tend to form unique monophyletic lineages (Ohkuma 2008), distinct from those of other habitats where representatives of the same orders and families are found. This applies to flagellates (assessed from 18S rRNA) as well as to eubacteria, leading to the conclusion that diversity in gut communities is autochthonous, vertically transmitted and does not reflect microbial diversity in the surrounding environment. With Archaea, it is less clear: Donovan et al. (2004) showed that euryarchaeal communities in the gut of a (physically) large soil-feeding termite, *Cubitermes fungifaber*, varied from site to site within the same region, as did communities in the parent soil used as food. However at each site, there was little overlap between the gut community and the soil community. Further, termites and their microbial symbionts demonstrate co-cladogenesis, that is, the phylogenies of the flagellates, and their termite hosts are often (though not invariably) congruent, and similarly those of the flagellates and their own prokaryotic associates such as the Endomicrobia. This implies co-speciation in all three partners to the overall symbiosis, from which it can be argued that the acquisition of symbionts by ancestral termites was an ancient, possibly singular event. Numerous lineages of intestinal prokaryotes are common (i.e. monophyletic) between termites and blattid cockroaches, which allows acquisition to be dated to about 130 mya (Brune 2012). However, the same type of symbiont can form distinct lineages in differing major termite taxa (e.g. Tai et al. 2015), which is sometimes argued to indicate multiple independent acquisitions. In a minority of cases, co-divergence is not evident, even from high resolution sequencing studies, in which event a case can be made for host switching or symbiont replacement (Ohkuma 2008).

While phylogenetic analyses thus strongly support the argument that termite gut symbionts are ancient, diverse, permanent, unique and autochthonous, there have been few studies of the corollary requirement, which is that allochthonous visitors are actively suppressed (but see Chouvenc et al. 2009, 2013; also Rosengaus et al. 2014 for evidence of antifungal activity). That the termite host might regulate the microbial community structure and composition via selective trophallaxis, gut motility, active secretion, selective absorption or any combination of these has entirely escaped consideration, although it might explain the evolution of the mixed segment in many higher termites. Conceptual imbalances in research on termite gut biotas and the (then) small amount of evidence that intestinal community composition varies with age, caste and diet were reviewed by Bignell (2011), but new evidence has emerged that the structure of the intestinal microbial community changes in response to age and caste (Otani et al. 2014; Li et al. 2016), diet (Miyata et al. 2007; Raychoudhary et al. 2013; Karl and Scharf 2015; Mikaelyan et al. 2015; Duarte et al. 2016) and termite functional group (He et al. 2013; Rossmassler et al. 2015; Mikaelyan et al. 2017). Morphological evidence of differential microbial configurations in separate parts of the hindgut has been available for many years (e.g. see Bignell et al. 1983) but is now confirmed by genomic approaches (e.g. Köhler et al. 2012; Tai and Keeling 2013; Rossmassler et al. 2015; Mikaelyan et al. 2017). The obvious corollary that termites can actively regulate their intestinal microbiotas through a neuroendocrine mechanism has never been explored despite the extensive current knowledge of insect physiology, which would permit the design of an experimental approach (Bignell 2011). In higher termites excepting the Macrotermitinae, such a mechanism would likely operate through the mixed segment (Bignell 1994).

In higher termites, flagellates are absent, but the hindgut becomes relatively elongated and compartmentalised, although to a greatly varying extent in different lineages (Bignell 1994), and broadly less so in wood feeders than soil feeders. It is assumed that a large part of any hindgut microbiota is lost when moulting takes place and is replaced by proctodaeal trophallaxis from nestmates; however the dynamics of this process are documented only for flagellates in lower termites (Brugerolle and Radek 2006; Nalepa 2017), from which it emerges that all are voided during the moulting period (Nalepa 2017).

Prokaryote communities change progressively in composition through the several compartments of the higher termite gut (reviewed by Ohkuma and Brune 2011; Brune and Ohkuma 2011). In both lower and higher termites, there are steep and to some extent reciprocal radial gradients of hydrogen and oxygen from the periphery to the centre of the gut lumen (Brune and Ohkuma 2011). Oxygen enters the intestine continuously by diffusion and is actively consumed by components of the microbiota, making the periphery of the larger compartments (or the single paunch) micro-oxic and the centre anaerobic. At the same time, hydrogen is generated by core fermentations and exerts a high partial pressure at the centre, declining to the periphery as it is consumed by complementary metabolisms such as reductive acetogenesis, methanogenesis and (facultatively) nitrogen fixation (Brune et al. 2000). Much of the microbiota, including all of the flagellates in lower termites and the majority of prokaryotes in all termites, are susceptible to oxygen poisoning and their distributions, both radial and axial, are affected accordingly. Up to 20% of the prokaryotes are associated with the micro-oxic zone adjacent to the gut wall, including any methanogens which are present, so it appears that the majority of the symbionts are anaerobes or capable of anaerobic metabolisms. However, it is possible to isolate and culture facultative and even obligate aerobes from the contents of termite guts (e.g. Bignell et al. 1991; Watanabe et al. 2003; Lefèvre et al. 2009; Matsui et al. 2012). The significance of such organisms in vivo, especially those showing capability to modify or partially degrade lignin or analogues of lignin (cf. Harazano et al. 2007; Ngugi et al. 2007), remains uncertain.

As evidenced by the numerous studies of termite cellulases and other enzymes degrading plant structural polysaccharides and polyaromatic compounds in termites or in their microbial associates, significant advances have been made in the understanding of termite digestion in the last decade, prompted in part by the application to new genomic and metagenomic technologies (König et al. 2006; Watanabe and Tokuda 2010; Brune and Ohkuma 2011; Bignell 2011). It now seems clear that genes encoding functional cellulase and in many cases also xylanase (hemicellulase) are carried by all termites and can be expressed in many to produce active enzymes which are secreted in large amounts mostly from the salivary glands (in lower termites) and from the midgut epithelium (in higher termites). The cellulase is of the endoglucanase variety, which fragments the microfibrils irregularly and lacks the ability of many other naturally occurring cellulases to bind physically to its substrate. Despite these inefficiencies, the combination of this secretion and the fine mastication of ingested woody material achieved by the dual actions of chewing by the termite's mouthparts and grinding by the muscular proventriculus (gizzard) produces a crude digest, which passes into the hindgut. In lower termites fine wood particles are internalised by the larger flagellates (via endocytosis) and degraded within membrane-bounded vesicles in the protist cytoplasm. Cellulases purified from flagellate cells are of the glycosyl hydrolase and cellobiohydrolase (exoglucanase) varieties, as well as endoglucanases, and seem sufficient to degrade the remaining polymers efficiently to disaccharides and monosaccharides. Earlier suggestions that endosymbionts within the flagellates may be involved in the polysaccharide degradation can now be dismissed by genomic evidence. It is assumed that individual flagellate species specialise on different particle sizes or on cellulose fractions of differing degrees of depolymerisation or in the degradation of hemicelluloses, which bind and to some extent protect the cellulose microfibrils. The smallest flagellates do not take up wood particles. In wood-feeding higher termites, metagenomic data suggest the hindgut prokaryote community encodes and expresses a comprehensive set of enzymes capable of degrading structural plant polysaccharides, distinctive from but complementary to those of the host insect (Warnecke et al. 2007). Overall digestive efficiencies for the structural polysaccharides are high in both lower termites and wood-feeding higher termites, approaching 90%. However, the crude lignin fraction is not much reduced in bulk and increases as a component of faeces (Hopkins et al. 1998; Griffiths et al. 2013). Detailed information on intestinal enzymes (of whatever provenance) can be found in Scharf et al. (2011), Ke et al. (2011), Sethi et al. (2012, 2013) and Rosengaus et al. (2014).

There is no direct evidence that the end products of these polysaccharide degradations are glucose and xylose; however this may be presumed as the subsequent metabolism includes a primary fermentation yielding acetate, protons, carbon dioxide and hydrogen in the molar ratios 1:1 and 1:2 (Tholen and Brune 2000). Acetate is known to support the aerobic respiration of termite tissues and is probably absorbed directly across the hindgut wall, though no definitive proof of this exists nor is there evidence of an active transport mechanism although this would be consistent with epithelial ultrastructure (Bignell 2000). There are a large number of ancillary reactions, of which acetogenesis, methanogenesis, hydrogen evolution, urate dissimilation, ammonia assimilation (to glutamate) and lactate fermentation are known examples, but the very high diversity of the microbiota and the fact that so many are as yet uncultivated suggests many other symbiotic interactions exist, perhaps including detoxification of allelochemicals in the food and antibiosis focussed on allochthons in the gut (Hongoh 2011; see also Peterson and Scharf 2016) and in the nest (Matthew et al. 2012; Chouvenc et al. 2013; Rosengaus et al. 2014). Nitrogen fixation, exclusively a prokaryotic process, can take place on a facultative basis, though the need for this is offset in many termite species by the selection of plant detritus which is well conditioned by environmental microorganisms, especially fungi, and which consequently has a greater organic nitrogen content than living or freshly dead wood (Rouland-Lefèvre 2000: see also Riggins et al. 2014; Clay et al. 2017). Amino acid and cofactor (vitamin) synthesis by prokaryotes also ultimately benefits the host and the entire symbiont community. This complex of processes maintains redox balance and minimises end product inhibition of the primary reactions (Brune and Ohkuma 2011). There seems to be a fundamental difference in the physical processing of wood particles between lower and higher termites: in the former fibres fractured by the mouthparts and gizzard apparatus, and perhaps part dissolved by termite cellulases, are incorporated into vesicles within the flagellates where they are degraded, whereas in higher termites (excepting the Macrotermitinae), fibres are colonised by bacteria, notably specialists of the *Fibrobacteres* (T3 phylum) and certain lineages of *Spirochaetes* (Mikaelyan et al. 2014).

Dietrich et al. (2014) examined the phylogenetic clustering of gut bacteria in cockroaches (assumed to be generalist feeders) and four functional groups of termites (wood feeders, soil/humus feeders, grass harvesters and fungus growers). In the resulting ordination, broad taxonomic affiliations as cockroaches, lower termites, higher termites (Termitinae and Nasutitermitinae) and higher termites (Macrotermitinae) could still be readily distinguished, suggesting that evolutionary history as well as feeding habit is a determinant of the intestinal microbial assemblage. Subsequent work seems divided between support for history (e.g. Rahman et al. 2015, addressing both lower and higher termites; Tai et al. 2015, for the flagellates of lower termites) and dietary preference (e.g. Mikaelyan et al. 2015, a study confined to higher termites but embracing all the main trophic functional groups).

The relative impacts of history and diet (the latter equated with intestinal environment) are reviewed by Tai and Keeling (2013) in the context of sequencing strategies best able to reveal true diversity and the usefulness of the termite hindgut as a model for the evolution of complex microbial communities. An earlier (and essentially pre-genomic) pair of models is presented in Bignell (2000), offering the alternative hypotheses that (a) all termites contain the same microbial functional groups but have designed the intestine differently to promote particular symbionts best suited in each case to the preferred dietary substrates and (b) that symbiont sets have been progressively acquired to permit the degradation of more and more humified substrates (such as humus and soil organic matter) which are more abundant in nature than freshly dead or relatively undecomposed wood. The technical success and very high resolution of genetic sequencing, as well the large number of papers reporting novel microbes in termites, have favoured the second hypothesis, but some recent work with germ-free or gnotobiotic cockroaches re-emphasises the role of the physical and chemical intestinal environment in structuring the gut microbiota (Mikaelyan et al. 2016; Tegtmeier et al. 2016). It is notable in the study of Mikaelyan et al. (2015) that principal component analysis of intestinal microbial communities in higher termites characterised by the 16S rRNA genes clusters them clearly by host trophic functional group across phylogenetic boundaries.

11.5 Finding and Consuming Wood

Evans et al. (2005), Nobre et al. (2007a), Rust and Su (2012) and Cypret and Judd (2015) summarise recent arguments that food consumption by wood-feeding termites does not take place at random. For both wood dwellers and foragers (sensu Korb 2007; Korb et al. 2012), resource size and quality can be assessed before mass recruitment of workers takes place, not only to maintain niche fidelity but also to regulate the production of neotenic reproductives (as an alternative to alates) in relation to overall food availability for the colony in question. Experimental evidences for vibroacoustic mechanisms of both size determination and detection of the presence of competing species (and possibly predators) in drywood termites were given by Evans et al. (2005, 2007, 2009). It is also now clear that excavation within large items of wood is not random either, as demonstrated by Himmi et al. (2014, 2016a, b) who employed X-ray tomography to map tunnels and galleries made by the drywood species *Incisitermes minor* in commercial softwood timbers without dissecting the wood or disrupting the colony. The images suggested that softer layers, for example, sapwood and springwood, were preferred for hollowing out. It was also possible to determine the distribution of castes within the gallery systems and to show that the internal arrangement of tunnels was subject to frequent change. It is often observed that larger items of woody detritus may be attacked by termites from different colonies of the same species or even by two or more different species (Evans et al. 2007; Nobre et al. 2007b). Aggression between the competitors in the same resource item is not automatic, especially in seasons when lower temperatures or dry conditions reduce colony growth and territorial expansion (Nobre et al. 2007b). If intersections of tunnelling systems occur, there may be a period of aggression, followed by walling up to create a de facto boundary (Jost et al. 2012).

Many wood feeders forage away from the colony centre and may simultaneously contact and use a number of food sources, with workers allocated accordingly to retrieve nutrients (Traniello and Leuthold 2000). Galleries, lined tunnels, aerial runways and epigeal sheetings are manifestations of these behaviours, but are difficult to analyse systematically in the field, especially for subterranean termites. Also, anecdotally, field observation suggests that occupancy in resource items connected to the colony centre is very variable (for the few examples where data are available, see Collins 1983; Berge et al. 2008; Nobre et al. 2008). Knowledge of the foraging process is therefore largely based on two-dimensional laboratory arena studies. Broadly, there is no evidence of directional tendencies towards candidate food items (Reinhard et al. 1997; Grace and Campora 2005; Nobre et al. 2007a; Lee and Su 2010; Jeon et al. 2010; Lima and Costa-Leonardo 2012), which seems to exclude the possibility of detection of woody items via volatile chemicals; however inherent systematic patterns are present in the early stages of exploration, modified only by the discovery of food or by encounters with habitat discontinuities (barriers to tunnelling or runway construction, also changes in soil bulk density; Grace and Campora 2005; Nobre et al. 2007a; Lima and Costa-Leonardo 2012). It is however established that once contact with suitable food is made, recruitment for additional foragers is by a trail pheromone (Hanus et al. 2012; review by Costa-Leonardo and Haifig 2010).

For subterranean termites, foraging essentially consists of two activities: digging and bifurcation. Fractal mathematics has been employed to analyse early foraging patterns and in some cases shows that these come close to being the most efficient explorations of space before suitable food items are encountered. Current thinking about termite constructions is still dominated by the theory of stigmergy

(Korb 2011), first proposed by Grassé (1959), which (broadly interpreted) holds that organisms such as termites with simple repertoires of individual behaviour can nevertheless generate complex structures without a central colony intelligence (or informatic directive) simply by responding consistently to simple cues in their immediate environment. Thus, a termite worker carrying wet soil is more likely to deposit this on a similar recent deposit by a nestmate if this emits a suitable chemical cue and less likely if the cue indicates that space for additional deposits is not available. Tunnels, walls, galleries, pillars, arches, runways and sheetings can therefore be self-assembled on this basis with consistent architecture but not necessarily in a precisely and previously determined position. This accounts for the identical centimetre-scale design of nests, galleries and runways but also the individually unique and apparently random fine-scale topologies of almost every termite construction on the planet, within and between species, at the single colony level. Bifurcation may be explained on the same principle: a digger not receiving the signal to continue in a straight line may then branch for at least a time and emit a trail pheromone that causes others to follow the branch until the cue fails to be reinforced by the discovery of new resource. Further discussion of directional selection by termites at a branching node is given by Sim et al. (2012).

11.6 Fungus-Growing Termites: A Special Case?

In the higher termite subfamily Macrotermitinae, a monophyletic basally branching clade, the primary symbiosis is with basidiomycete fungi of the genus *Termitomyces*, and the interactions with the host involve levels of behavioural complexity and sophistication not seen in other termites. Further, these termites have a prominent ecological role in Old World savannas, amounting to dominance of decomposition processes in arid areas (Wood and Thomas 1989; Dangerfield et al. 1998; Bignell and Eggleton 2000; Korb and Aanen 2003; Jouquet et al. 2011). Two species-rich genera (*Macrotermes* and *Odontotermes*) also have high apparency in savanna landscapes, leading to a growing literature on the role of their mound nests as keystone structures (e.g. Moe et al. 2009; Darlington 2012; Sileshi and Arshad 2012: O'Connor 2013). The diet seems to combine woody and herbaceous detritus with a large measure of flexibility, which can confer pest status in some circumstances (Lepage et al. 1993; Rouland-Lefèvre 2011). Although the basic biology of the interactions between termites and their symbiotic fungi is well described (Sands 1969; Martin 1987; Darlington 1994; Traniello and Leuthold 2000; Rouland-Lefèvre and Bignell 2001; Nobre et al. 2011), its interpretation remains controversial (review by Nobre and Aanen 2012). The uncertainties concern (1) the fidelity of host and symbiont co-evolution and (2) the precise benefits that each partner gains from the other. Underlying these fundamental issues is the question of whether the relationship is a genuine symbiosis or subjugation of the termite by the fungus. In fungus-growing termites, there are secondary relationships with bacteria; however the overwhelming attention given to the fungi has allowed these additional putative symbioses to be overlooked until quite recently (see Hongoh et al. 2006; Mackenzie et al. 2007; Mueller et al. 2008; Pinto-Thomas et al. 2009). In workers of fungus-growing termites, there is a prokaryotic gut microbiota comparable in size and distribution to that of other non-soil-feeding higher termites, and short-chain fatty acids are accumulated in the hindgut (Anklin-Mühlemann et al. 1995). However, bacterial diversity seems to be reduced in comparison with other higher termites (Poulsen et al. 2014). Culture-independent sequencing analyses have shown that the community is dominated by termite-specific clades of *Firmicutes*, *Bacteroidetes*, *Proteobacteria* and *Actinobacteria*; however potentially cellulolytic taxa are also present, while *Spirochaetes* are poorly represented. The gut bacterial community does not resemble those detectable in fungus comb, mound materials or parent soil, so it is reasonable to assume that the microbiota is specific to the host, as in other termites (Bignell 2011; Nobre and Aanen 2012).

The Macrotermitinae are active foragers, principally retrieving (in different taxa) woody detritus, leaf litter and standing dead grass, though with some flexibility. They will also consume standing dead wood and can achieve pest status in arable fields, tree and shrub plantations, and against wood in service, especially where natural mulch and crop residues are removed by clearance or burning (Rouland-Lefèvre 2011). Pest status is frequently allocated to termites of the genus *Microtermes*, which is inconspicuous on the surface of the ground but often both diverse and abundant in the soil column and may have an impact on carbon turnovers and soil conditioning out of proportion to its apparency (Wood and Sands 1978; Bignell and Eggleton 2000). In all Macrotermitinae forage is returned to the nest, usually a complex mound partly or almost completely subterranean or else a network of underground galleries and chambers, where it is consumed by workers. After a rapid transit of the gut, the pellets (assumed to be largely undegraded, but see Li et al. 2017) are used to construct a characteristic fungus comb on which the symbiont fungus grows rapidly and exclusively in a composting process which degrades all the major plant structural components (lignin, cellulose, hemicellulose and pectin), although to varying extents in different genera, and increases the nitrogen content relative to carbon (Hyodo et al. 2000, 2003). The fungus combs are housed in specially constructed, usually subterranean, chambers where they are attended by workers, soldiers and nymphs. Termites consume (at different times in their life cycle) fungal conidia (i.e. asexual spores) and ageing fungal mycelium, producing semi-fluid final faeces, which are separated from live galleries (Rouland-Lefèvre and Bignell 2001). Subterranean fungus combs contribute significantly to CO_2 effluxes from savanna soils (Konaté et al. 2003), while Wood (1976) pointed out that consumption (i.e. retrieval) of forage by Macrotermitinae per unit of termite biomass was at least five times as great as that of any other isopterans. Both observations can be attributed to the strongly aerobic metabolism of the fungus combs, and the ecological importance of the subfamily is thereby underlined.

Controversy attaches to the role of the fungus. It can be agreed that the consumption of conidia from an established fungus comb and the rapid incorporation of these spores into new comb via termite faeces is an efficient mechanism for within-colony propagation of the symbiont strain and may help to exclude allochthonous fungi, although other antibiotic systems are likely to be in place. However, the conidia are rich in proteins, which have been identified in several species of *Macrotermes* as cellulases and xylanases including (as might be expected in a basidiomycete) an exocellulase and exoxylanase. These observations supported an elegant thesis, the acquired enzyme hypothesis, which held that fungal and endogenous termite enzymes combined to degrade polysaccharides efficiently in the insect's gut (summarised by Martin 1987 and based on evidence obtained from *Macrotermes natalensis* in southern Africa). However, investigations of a wider range of species and genera within the Macrotermitinae failed to confirm the universality of the enzyme synergism, and although in vitro hydrolytic activities against plant polymers by fungal tissues other than the conidia appear to be low, it remains unclear whether conidial polysaccharidases are directly important in termite digestion (summarised, with other hypotheses on the termite-fungus relationship, in Rouland-Lefèvre and Bignell 2001; Bignell 2011). Amongst termites, the Macrotermitinae are the most effective degraders of plant residues as there are losses in lignin and polyphenolic fractions in the composted forage which are not evident when woody materials are processed in other subfamilies and families. It is also indisputable that senescent fungus comb is a nutritious food, rich in nitrogen, and that the organisation of the alimentary canal in fungus growers, in contrast to soil feeders, is not radically different from that of other wood-feeding higher termites, excepting the absence of a mixed segment, or for that matter from the guts of lower termites. Emphasising the point that interactions between fungus and termite host probably differ between taxa within the Macrotermitinae, Nobre and Aanen (2012) suggest that the relationship has evolved primarily to support strong growth of the fungus, the passage of fresh forage and conidia through the termite gut serving to mix the substrate with fungal, termite and possibly bacterial enzymes which facilitate efficient degradation of plant material in the comb. This is still a mutualism as both partners benefit and further constitutes the re-establishment of an external rumen. The crucial requirement of the thesis, that lignocellulose-degrading enzymes are not secreted in large amounts in the mature mycelium, is seemingly borne out by the data currently available. An additional advantage to the fidelity of the symbiosis is that only fungi concentrating their enzyme secretion in their conidia can be propagated in the fungus comb, i.e. cheaters producing no enzymes or no conidia would be easily outcompeted by any strain of *Termitomyces* present. At the same time, the possibility of individual strains of the symbiont fungus changing its host termite species opportunistically is allowed, which also accords with the most recent reconstructions of phylogeny.

In a multi-laboratory collaborative study, Poulsen et al. (2014) carried out a complete metagenomic analysis of *Macrotermes natalensis*, its *Termitomyces* symbiont and intestinal bacteria, focused on the degradation of complex carbohydrates. They found comprehensive genetic potential in the fungus to digest plant polysaccharides and cleave lignin, but more restricted capacity in the termite and its intestinal bacteria except for oligosaccharide degradation, notionally the final stage of the overall process, which appears to be efficient. The hypothesised relationship is therefore a partitioning between fungus and bacteria in which the former attacks polysaccharides and the latter oligosaccharides, with the further proposal that the intestinal microbiota is more cockroach-like in composition and less diverse than in termites not cultivating fungi. Whether such a unifying thesis for the Macrotermitinae will accommodate all the observed diversities of feeding and digestion within the subfamily and reports of low enzyme activities in living mycelium remains to be seen. Significant additional information about differences in the bacterial gut microbiotas with age (and therefore differing contributions to the overall digestive process) and the novelty of such communities are given by Mathew et al. (2012), Zhu et al. (2012), Makonde et al. (2013, 2015) and Li et al. (2016). These variations need to be explained before the overarching hypothesis of Poulsen et al. (2014) can be accepted for all fungus growers.

11.7 Relative Processing of Polysaccharides and Lignin

Despite a lack of definitive evidence, it is widely accepted that insect gut systems do not have the ability to degrade lignin (Ohkuma 2003), and in the landmark metagenomic study by Warnecke et al. (2007), no genes of known lignin-degrading enzymes were found in the wood-feeding higher termite *Nasutitermes corniger*. In wood feeders, the efficiency of polysaccharide digestion, as determined by proximate analysis, ^{14}C tracers and NMR spectroscopy, approaches 90% (Esenther and Kirk 1974; Breznak 1982; Li et al. 2006; Hopkins et al. 1998; Ohkuma 2003; Katsumata et al. 2007), but the extent of lignin degradation is unclear by these methods of assessment (Geib et al. 2008). Early work with ^{14}C-lignin fractions fed to termites showed that more label was mineralised as $^{14}CO_2$ than could be accounted for by labelled impurities in the substrate (e.g. Cookson 1987); however Breznak and Brune (1994) explain why this is still not conclusive evidence that the core polymer is degraded since peripheral hydrolysable moieties more easily acquire the label. Katsumata et al. (2007) used ^{1}H and ^{13}C NMR to show that *Cryptotermes brevis* (a lower termite) could effect minor changes to lignin, notably increased formation of C–C linkages in guaiacyl nuclei and a decrease in aliphatic hydroxyl groups. Although the analysis was conducted on the Björkman fraction, which is extracted in organic solvents after wood is fine milled, the lignin was still able to re-complex with polysaccharide, evidence that major digestion had not occurred. This contrasts with some lignin analogue and precursor studies, for example, Butler and Buckerfield (1979) showed that 64% of ^{14}C in labelled ferulic acid and 16–32% of ^{14}C in various enzymatically polymerised coniferyl alcohols were mineralised as $^{14}CO_2$ after feeding to *Nasutitermes exitiosus*, a wood-feeding higher termite (lacking protists). Moreover, oxygen is a co-substrate for aromatic ring cleavage (Katsumata et al. 2007), but much of the termite gut is micro-oxic, including the hindgut where most of the microbial biomass is located (Brune et al. 1995).

Many studies have confirmed that faeces of wood feeders are enriched in lignin (Hopkins et al. 1998; Katsumata et al. 2007; Griffiths et al. 2013), but reports that microorganisms isolated from termite guts can degrade lignin preparations or lignin analogues in vitro have reignited interest in the context of bioprospecting (König et al. 2006; Harazano et al. 2007; Ngugi et al. 2007; Bignell 2011). However, the reactions involved are peripheral, for example, oxidations of aromatic aldehydes and alcohols to the corresponding acids. Harazano et al. (2007) were able to make use of 16S DNA sequencing to identify the bacteria involved as novel strains of *Burkholderia* and *Citrobacter*, and suggested that such reactions were basically for detoxification purposes within the intestinal ecosystem, and not major digestive pathways. However it is also thought possible that fungal or actinobacterial enzymes ingested with the wood or even secreted within the gut may have a synergistic role in lignin modification. In another development, Taprab et al. (2006) showed that laccase was detectable in the fungus combs of *Macrotermes gilvus*, *Odontotermes* sp. and *Microtermes* sp. from Thailand and coded by a gene whose sequences indicated a similarity with enzymes from white-rot fungi known to have strong lignin-degrading abilities, but the synergistic peroxidase characteristic of free-living lignin-degrading fungi could not be detected.

Geib et al. (2008) produced mass spectra of lignin in undegraded softwood and faecal frass of *Zootermopsis angusticollis*, following tetramethylammonium hydroxide (TMAH) thermochemolysis, a method they state accounts for all components of native lignin, and showed that gut passage caused side chain oxidation, ring demethylation and ring hydroxylation. These changes were interpreted as sufficient to expose the polysaccharide components of wood for digestion. Further support for the modification of lignin during gut passage is provided by Ke et al. (2011), whose analyses by pyrolysis mass spectrometry and infrared spectroscopy were interpreted to show partial depolymerisation and ring cleavage in the lower termite pest species *Coptotermes formosanus*, while Cov et al. (2010) identified phenol-oxidising laccase transcripts in the salivary glands of *Reticulitermes flavipes*. In the same termite, a number of other candidate enzyme gene sequences with apparently synergistic actions on host and symbiont cellulases and hemicellulases in vitro were obtained from whole gut extracts (Sethi et al. 2012). Adding depolymerised lignin to a high-purity cellulose diet also resulted in the expression of a cocktail of transcripts resembling those of enzymes of the lignase/laccase/phenoloxidase family and in addition increased the yield of glucose. Further evidence of synergism was obtained from enzymatic constructs incorporating elements of termite, flagellate and fungal cellulases, which were tested against model substrates (Sethi et al. 2013). In the same termite, feeding on wood was found to lead to a pattern of gene expression different from that when paper was consumed and suggestive of a broadly detoxifying element in enzyme secretion in addition to cellulase production (Raychoudhary et al. 2013). Allocation of the respective productions of specific saccharolytic enzymes to particular symbionts remains uncertain, but an experimental approach using selective antibiotics in the diet indicates that host insect, flagellates and intestinal bacteria all contribute to the overall capacity of the system, i.e. the holobiont (Peterson et al. 2015).

In a pioneering study, Tokuda et al. (2014) made a metabolomic analysis of digestion and assimilation after the dampwood termite *Hodotermes sjostedti* was fed with a purified ^{13}C cellulose. This produced evidence of some digestion in the foregut: a combination of grinding by the mandibles and gizzard and the action of an endogenous endocellulase secreted by the salivary glands. The hydrolysate was further metabolised by β-glucosidases in the midgut, with the products entering glycolysis and the TCA cycle, accompanied by some transfer of label into amino acids. Further cellulolysis, more significant in quantitative terms, was demonstrated in the hindgut which is populated by (mainly) parabasalian flagellates and was synchronised with volatile fatty acid (mainly acetate) production in which succinate is an intermediate, possibly indicating a role for anaerobic and aerotolerant bacteria, which are also present and commonly in close associations with the protists. The production of amino acids in the midgut may make use of organic nitrogenous compounds synthesised by hindgut bacteria but passing into the anterior intestine of nestmates via trophallaxis.

A recent study of the fungus-growing *Odontotermes formosanus* by Li et al. (2017) employed microscopy, NMR and thermochemolysis to compare the properties of a candidate food (poplar wood) before and after the short processing through the guts of young workers, and the status of all the principal polymers in forage as the fungus comb matures. Aliphatic (side-chain) depletion was significant and lignin microfibril length reduced by the young workers; in addition guaiacyl units in the lignin matrix were reduced relative to syringyl. This is interpreted as “pretreatment”, facilitating the subsequent degradation of lignin by the fungus. Just as surprising, in addition to lignin the fungus preferentially degrades and utilises xylans (hemicelluloses), thus leaving the more easily digested glycan oligosaccharides, for older workers to digest via their gut bacteria, as suggested by the earlier study by Poulsen et al. in *Macrotermes* (2014; see Sect. 6 above), together with free glucose which the termites can presumably assimilate themselves or make available to the intestinal microbiota. The available evidence thus points to very sophisticated mutualisms in the Macrotermitinae.

The evolutionary perspective is that termite and symbiont gene expression systems complement one another to achieve efficient lignocellulose digestion (Scharf and Tartar 2008). Sufficient lignin polymer is disrupted to maximise the access of other enzymes to cellulose and hemicellulose, which remain the principal targets of digestion. Prosaically, “depolymerisation of lignin” is a term with several current interpretations.

11.8 Conclusion

Wood feeding is clearly basal in termites and is represented in all subfamilies within the Termitoidae. However, a broad trend of trophic diversification towards humus and soil feeding can be seen in many phylogenies, as well as radically revised relationships with the microbial consortia which synergise with the insect host to make lignocellulose digestion efficient. A number of wood-feeding species are local or invasive pests, classified heuristically as drywood, dampwood, subterranean and fungus-growing termites; however the main environmental impacts of the remainder are comminution (shredding), organic decomposition and soil conditioning in the tropics and subtropics. The microbial community associated with termites is unique in nature and with one notable exception has co-evolved with the host in a strict mutualism, though there are some conserved elements of the microbiota in all taxa, which give a large competitive advantage over other invertebrates using dead wood as a resource. However wood feeding carries some disadvantages, such as a shortage of nitrogen and potential exposure to both predators and desiccation; these lock both termites and microbes into mutual dependence and termites into eusociality.

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Part II
Ecology

Chapter 12
Insect-Fungus Interactions in Dead Wood Systems

Tone Birkemoe, Rannveig M. Jacobsen, Anne Sverdrup-Thygeson, and Peter H. W. Biedermann

Abstract Fungi can provide insects with nutrients and essential elements, detoxify plant defenses in recently dead wood, and protect or, in contrast, attack and digest insects. Insects can affect fungi through feeding or propagule dispersal. Fungal grazing may induce changes in fungal chemistry, morphology, and growth. Insect-fungus interactions in dead wood span a wide gradient of specificity from indirect interactions through shared habitats to obligate mutualisms. When based on insects reared from polypores, insect-fungi interaction networks may exhibit a degree of specialization similar to that of pollinators and plants, whereas when based on wood-decay fungi isolated from insects sampled at dead wood, the degree of specialization appears closer to animal-mediated seed dispersal. Exchange of dispersal and nutrition is the basis for most obligate insect-fungus mutualisms. Adaptations to these mutualisms seem to have evolved rapidly, and for some insects there has been a feedback between the evolution of fungus farming and sociality. Several recent studies indicate that insect-vectored dispersal might be an important complement to wind dispersal also for non-mutualistic saproxylic fungi, potentially providing targeted dispersal to suitable substrates. We propose a theoretical framework for the effectiveness of insect-vectored spore dispersal. Insect-fungus interactions are an essential component of forest ecosystems, influencing species richness, wood decay, and nutrient cycling. Several aspects of insect-fungus interactions are unknown and require further study, but availability and development of molecular methods may rapidly advance this field of research.

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12.1 Introduction

Insects and fungi are the most abundant eukaryotic organisms in dead wood. The high species diversity and the old evolutionary history, dating back to Early Ordovician for insects (Misof et al. 2014) and at least Late Silurian for fungi (Sherwood-Pike and Gray 1985; Misof et al. 2014), are indicative of a long history of cohabitation, which likely resulted in reciprocal adaptations and intricate interactions. Based on our current knowledge, the main interactions between fungi and insects can be grouped into four functional relationships:

1. Nutrition. This includes insects feeding on fungi and fungi feeding on insects. The fungi provide insects with some essential nutrients and wood-degrading enzymes. In insect-fungus mutualisms, fungi may be provisioned with new substrate or "fertilized" in different ways by the insects. The insects may also be fed upon by pathogenic fungi and fungal parasites or can be immobilized or killed by ectomycorrhizal fungi (Klironomos and Hart 2001).
2. Dispersal. Insects disperse fungi in passive ways or in highly specialized transmission organs.
3. Detoxification. Fungi degrade tree defenses that would be toxic to insects.
4. Protection. Insects protect fungi by farming as known from leaf-cutter ants, termites, and several ambrosia beetles. Fungi may also protect insects by reinforcement of nest-wall structures (Schlick-Steiner et al. 2008) or fighting microbial pathogens (Florez et al. 2015), although this is less studied.

All four functional interactions can be based on loose relationships, or the interaction can be tight such as facultative or obligate mutualism. In the dead wood system, indirect interactions also occur as both fungi and insects modify the dead wood, changing the habitat for the other group.

Many reviews have covered insect-fungus interactions, including several of the functions mentioned above (Wheeler and Blackwell 1984; Wilding et al. 1989; Vega and Blacwell 2005; Shaw 1992; Boddy and Jones 2008). Surprisingly, despite insects and fungi being among the most species-rich taxa in dead wood ecosystems, no review has focused on their interactions in the dead wood environment. The comprehensive book *Biodiversity in Dead Wood* (Stokland et al. 2012) only includes the most common interactions in addition to an overall description of fungivores. Thus, the aim of this book chapter is to address this knowledge gap and summarize the available knowledge on insect-fungus interactions in the dead wood system (Fig. 12.1).

We start by summarizing knowledge of fungi and fungivores in dead wood and discuss the adaptions to, and effects of, insect fungivory. Then we critically review the indications that insects might disperse non-mutualistic saprotrophic fungi to dead wood, an interaction with potential effects for species composition and ecosystem services, before giving an overview on the ecology and evolution of insect-fungus mutualisms. We end with summarizing some important indirect interactions between

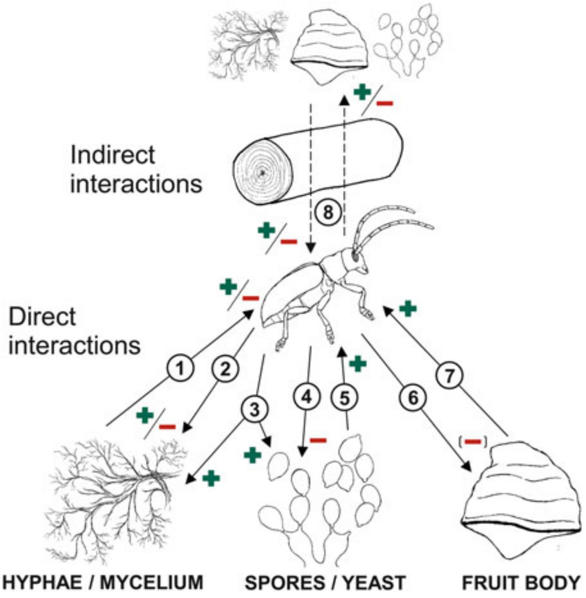

Fig. 12.1 An overview of insect-fungus interactions and their effects discussed in this review. (1) Fungal mycelium provides an important food resource for insects but can also benefit insects by detoxifying tree defenses, enzymatically degrading the wood, or even by producing antibiotics that protect the insects against pathogens. Fungi may also protect ants by stabilizing nest structure. Other fungi, however, can feed on insects, immobilizing and killing them with mycelium and toxins. (2) Many insects feed on fungal mycelium and hyphae, and the effect on the fungus is usually negative, but the effect of this grazing can be stimulatory in some cases. Furthermore, other insects such as fungus-farming ambrosia beetles provide protection for fungal growth. (3) Insects can disperse fungal propagules such as spores, hyphae, or yeast cells, with positive effects for the dispersed fungus. This is well known from mutualistic insect-fungus associations, but there is mounting evidence that such interactions might also be important for non-mutualistic species. (4) Spores and yeast cells fed on by insects can be destroyed during digestion. (5) Spores or yeast cells can benefit insects as a main food source for fungivores or as additional nutrients for opportunists or generalists. (6) Insects feeding on fruiting bodies can have a negative effect on the fungus. However, often the fruiting bodies are already dead, and the feeding therefore has little effect on the fungus. (7) Insects feeding on fruiting bodies benefit nutritionally, and fruiting bodies can also provide shelter and protection for insects. (8) Both insects and fungi can affect each other indirectly through their effects on their shared habitat. These indirect effects can be positive or negative. Drawing by R. M. Jacobsen

insect and fungi in dead wood and discuss the consequences and implications of all insect-fungus interactions in a broader perspective. Due to the close proximity of dead wood to the soil ecosystem, well-known examples of interactions from this system are included.

12.2 Fungi in Dead Wood

Here we will provide a short introduction to the ecology of saproxylic fungi in dead wood (Fig. 12.2). For more detailed information on these fungi, we refer to the many excellent reviews and books on this topic, e.g., Rayner and Boddy (1988), Boddy (2001), Boddy and Jones (2008), or Stokland et al. (2012).

Most of the saproxylic fungi known to cause significant mass loss during wood decay belong to the white-rot and brown-rot fungus groups in the phylum *Basidiomycota*, which predominately degrade cellulose and lignin or only cellulose, respectively (Boddy 2001; Kubartová et al. 2015). The soft-rot ascomycete fungi are also common in dead wood and predominantly contribute to cellulose degradation but to a much lesser extent than the basidiomycetes (Boddy 2001; van der Wal et al. 2015). High-throughput DNA-sequencing analyses have recently shown that there are relatively larger numbers of ascomycete fungus species in dead wood but that the basidiomycetes seem to occupy larger volumes of wood (Kubartová et al. 2015; Ottosson et al. 2015; Strid et al. 2014; van der Wal et al. 2015). Basidiomycetes have a much more complex enzymatic machinery (Floudas et al. 2012) and thus dominate ascomycetes, especially during intermediate and late stages of wood decay (Ottosson 2013; Rajala et al. 2015).

Prior to the development of molecular methods such as high-throughput sequencing, fungal communities in dead wood were recorded by fruiting body surveys. Therefore, studies of saproxylic fungi have usually focused on species with macroscopic fruiting bodies, mainly of the polyphyletic group called polypores or bracket fungi [*Basidiomycota*, e.g., Gilbertson and Ryvarden (1986)]. Molecular methods have shown that although fruiting body surveys do not capture the entire fungal community in dead wood, they reflect the most abundant species that dominate the substrate (Ovaskainen et al. 2013). The discrepancy between the methods explains why species richness of fungi seems to peak at intermediate stages of decay in fruiting body surveys (Jönsson et al. 2008; Lindblad 1998), while species richness continues to increase with wood decay according to molecular analyses (Kubartova et al. 2012; Ovaskainen et al. 2013; Rajala et al. 2015). In advanced decay stages, dominant basidiomycete species such as polypores are replaced by a large number of species with inconspicuous fruiting bodies (Kubartova et al. 2012) and soil fungi (e.g., mycorrhiza) that colonize the dead wood (Makipaa et al. 2017; Rajala et al. 2012).

The succession of fungus species during wood decay is linked to their abilities to overcome tree defenses, enzymatically degrade wood, and compete with other fungi (Rayner and Boddy 1988). Put simply, several plant-pathogenic (e.g., blue-stain fungi) and soft-rot ascomycete fungi (e.g., *Chaetomium* spp., *Ceratocystis* spp.) typically dominate in dying trees and early stages of decay, as they are well adapted to overcome tree defenses by metabolizing specialized toxic plant compounds such as terpenes and phenolics (Krokene 2015). These fungi grow relatively quickly through the tracheids and plant vessels but have relatively poor cellulolytic and no ligninolytic capabilities. They consume the cell contents, leaving the structural

Fig. 12.2 Examples of saproxylic basidiomycetes (**a**–**e**) and ascomycetes (**f**). (**a**) The tinder fungus *Fomes fomentarius*. Photo by George Chernilevsky—Own work, Public Domain. (**b**) The red belt conk *Fomitopsis pinicola*, here with a gathering of beetles on its spore-producing hymenium. Photo by R. M. Jacobsen. (**c**) The artist's conk *Ganoderma applanatum*, with its copius production of spores clearly visible as brown powder beneath the fruiting body. Photo by George Chernilevsky—Own work, Public Domain. (**d**) The turkey tail *Trametes versicolor*. Photo by Hans-Martin Scheibner—Own work, CC BY-SA 3.0. (**e**) The resupinate fruiting body of *Phlebia centrifuga P. Karst.*, a polypore mainly found in old-growth forest. Photo by A. Sverdrup-Thygeson. (**f**) The green elf cup *Chlorociboria aeruginascens (Nyl.) Kanouse ex C. S. Ramamurthi, Korf and L. R. Batra*, an ascomycete whose hyphae can dye the wood green. Photo by H. Krisp—Own work, CC BY 3.0

components of the cell walls more or less intact (Nilsson 1976; Rösch and Liese 1971). Also, they are poor competitors and are thus replaced by the “true” wood-decaying fungi, i.e., white- or brown-rot basidiomycetes. These species grow through the wood relatively slowly by substantial degradation of the recalcitrant lignocellulosic plant cell-wall structure (Rayner and Boddy 1988). Molecular methods have also revealed that fungi with a variety of other ecological roles are present in dead wood (Ottosson et al. 2015). While fungi known to be wood-decaying are the most abundant, endophytic, plant-pathogenic and entomopathogenic, mycoparasitic, mycorrhizal, and lichenized species have also been isolated from dead wood (Ottosson et al. 2015). Some wood-decay fungi can switch between different modes, colonizing living trees as plant pathogens and switching to a saprotrophic mode as the tree dies (Boddy 2001). Furthermore, many species of saprotrophic fungi have been found to be latently present as endophytes in the wood of the living tree, presumably waiting for the breakdown of the tree defensive system due to weakness or death of the tree (Chapela and Boddy 1988; Parfitt et al. 2010).

12.3 Fungi as Providers of Nutrition, Detoxification, and Protection for Insects

Fungal mycelium contains many times more nitrogen and phosphate relative to carbon in comparison with undecayed wood (Swift and Boddy 1984). Decayed wood, being a mixture of both substances, has ratios of intermediate values (Boddy and Jones 2008). Insect tissue also contains much higher concentrations of nitrogen and phosphorous than the wood itself; undecayed pine wood had 1500–2000 and 500–900 times less concentrated N and P than the cerambycid and buprestid beetles feeding on it (Filipiak and Weiner 2014; Filipiak 2018; see Chap. 13). Thus, based on these nutrient contents alone, adding fungi to the diet should be highly favorable for saproxylic insects.

Essential elements such as K, Na, Mg, Zn, and Cu are also scarce in dead wood and can limit larval growth (Filipiak and Weiner 2017). Similar to N and P, the concentrations of these elements have been found to increase with wood decay and are likely to be transferred from the surroundings by fungi (Filipiak et al. 2016; Filipiak and Weiner 2014). Recent research has shown that the fungal communities in dead wood and soil do indeed interact closely, moving nutrients between the substrates (Makipaa et al. 2017). Most insects lack key enzymes for sterol biosynthesis (Clark and Block 1959). Plant sterols are rarer in xylem than in phloem, and other sterols, like the fungal ergosterol, might therefore help with biosynthesis of juvenile hormone and thus insect development. Thus, from the insect point of view, adding fungi to the diet reduces the quantity of food needed and provides essential elements for growth.

Fungi not only serve as biomass with potential nutritional value but are also active catalytic agents with diverse metabolic capabilities. Many wood-feeding insects carry one or a few species of yeasts in their digestive tracts (Vega and Dowd 2005; Suh et al. 2005). Although there are few studies of the functions of these yeasts, they seem to help the insects with degradation of the lignocellulosic plant biomass (Tanahashi et al. 2010; Vega and Dowd 2005; Urbina et al. 2013) and probably aid in the detoxification of toxic plant chemistry (Dowd 1992). Filamentous fungi growing within the wood may also benefit insects through their liberation of wood-degrading and detoxifying enzymes, especially if these enzymes remain active in the insect gut and thereby augment or extend the insects' digestive capabilities (Martin 1983). This facilitation of enzymatic degradation and detoxification is of primary importance in the wood wasp and bark beetle mutualisms with fungi (see Sect. 12.6) but very likely also plays a role in many non-mutualistic insect-fungus interactions like some lower termite brown-rot interactions (Becker 1965). However, recent studies of beetle genomes (Cerambycidae, *Anoplophora glabripennis* Motschulsky; Buprestidae, *Agrilus planipennis* Fairmaire; Scolytinae, *Dendroctonus ponderosae* Hopkins) have revealed that some wood-boring insects are not dependent on associating with fungi, bacteria, or protozoa to degrade wood, as they have acquired many plant-degrading and detoxifying enzyme families such as P450 or GST horizontally from microbes (Keeling et al. 2013; McKenna et al. 2016).

A final and almost unstudied role is the protective function that fungi may have for insects in wood, such as by outcompeting antagonistic organisms (e.g., fungal entomopathogens) (Castrillo et al. 2016), including the production of antibiotics (Florez et al. 2015). The use of fungi in ant nest construction as known for Old World *Lasius* ants (Formicinae) of the subgenera *Dendrolasius* and *Chthonolasius* (Schlick-Steiner et al. 2008; Seifert 2006) can also be seen as an example of fungi physically protecting insects.

12.4 Fungivory and Its Effects

12.4.1 Dead Wood Fungivores

Species of most insect orders living in dead wood are known to feed on fungi, although species of Diptera and Coleoptera dominate. Primarily fungivorous Diptera include the highly numerous fungus gnats (Sciaroidea: Bolitophilidae, Diadocidiidae, Ditomyiidae, Keroplatidae, and Mycetophilidae), gall midges (Cecidomyiidae), and species of flat-footed flies, *Agathomyia* spp. (Platypezoidea: Platypezidae) (Halme et al. 2013; Økland 1996, 1995; Hanski 1989; Jakovlev 2011; Ulyshen 2018). Among the beetles, species of the families Ciidae, Cryptophagidae, Endomychidae, Erotylidae, Leiodidae, Melandryidae, Ptiliidae, Mycetophagidae, Staphylinidae, and Tenebrionidae include a large number of primarily fungivorous species living in dead wood (Gimmel and Ferro 2018; see Chap. 2). Several so-called fungus-farming insects, like ambrosia beetles (Platypodinae and Scolytinae) and ship-timber beetles (Lymexylidae), also feed more or less exclusively on mutualistic fungi cultivated within their tunnel systems in wood (see Sect. 12.6). Fungi are also farmed by fungus-farming termites (Macrotermitinae), a subfamily which originated about 60 million years ago from wood-feeding “lower termites” (Brune 2014). Today fungus-farming termites live apart from wood within huge mounds, but they collect plant material (especially grass but also wood pieces) as substrate for their fungi (Nobre et al. 2011). Although these fungivorous termites comprise relatively few species, they are highly abundant and important decomposers within their distribution range in Africa and Asia (Brune 2014; Jouquet et al. 2011). In Lepidoptera, the only groups with primarily fungivorous species seem to be Oecophoridae and Tineoidea (Rawlins 1984; Lawrence and Powell 1969) living in and feeding on fruiting bodies of polypores (Jaworski 2018; see Chap. 10). Fungivores also occur in smaller insect orders such as Thysanoptera (thrips) but here mainly in the suborder Tubulifera (Mound 1974). Thrips can be abundant in early stages of wood decay in tropical forests. In addition to the abovementioned insects, other invertebrates usually defined as soil fauna such as mites, Collembola, isopods, and nematodes can be numerous in dead wood (Zuo et al. 2014). Fungi represent an important food source to these species (Pollierer et al. 2009). For an overview of arthropods feeding on fungi in general, see Table II, Appendix, in Wilding et al. (1989).

The choice of diet might interact with one of the most fundamental insect traits: body size. In Germany, approximately 52% of the saproxylic beetle species are assumed to feed on wood and/or phloem (xylophages), 18% on fungi, and an additional 10% on a mixture of fungi and wood (xylomycetophages) (Koehler 2000). In this dataset, the species feeding directly on dead wood are much larger than the fungivores (mean body length of 8.3 mm vs 2.4 mm), whereas species feeding on a mixture of wood and fungi have intermediate length (5.3 mm) (Fig. 12.3). The Jarman-Bell principle based on mammalian herbivores but extended

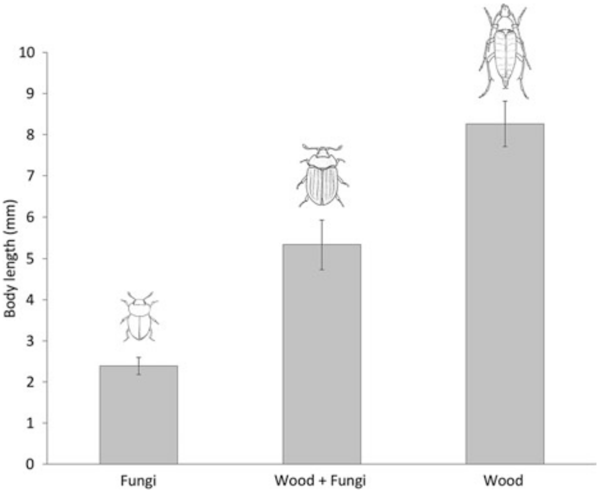

Fig. 12.3 Body size (mean ± 95% confidence intervals) vs diet in saproxylic beetles from Germany. Number of species is 185 (fungi), 109 (fungi and wood), and 542 (wood) (Koehler 2000). Drawings of representative species by R. M. Jacobsen

to primates, whales, and fruit bats (Müller et al. 2013) states that gut capacity remains a constant fraction of body size whereas the specific metabolic rate decreases with increasing body mass (Owen-Smith 1988). Thus, for many mammals, larger species can tolerate a lower quality diet than smaller species. It is interesting that the same pattern in body size and food quality is found among saproxylic beetles.

Our knowledge of insect feeding modes in the dead wood system is limited and based on much anecdotal evidence. The relative percentage of species being recorded as fungivores and the number of species including fungi as part of their diet are likely to be higher than present estimates. Filipiak and Weiner (2014) argue that the wood-feeding beetles (xylophages) in their study are in fact fungivores or mixed wood and fungi feeders (xylomycetophages), as their wood diets are supplemented with fungi that gradually infect the decaying wood and provide essential nutritional elements. They calculate that without fungi in their diets, these wood feeders would need between 40 and 85 years in order to gain the essential nutrients needed to develop into adults. Detailed studies of stag beetles also point toward fungi as an important part of their xylophagous diet (Tanahashi et al. 2009). Fungal, bacterial, and protozoan endosymbionts might further aid digestion in the gut (Ceja-Navarro et al. 2014; Suh et al. 2005; Brune 2014). Studies of the soil ecosystem using stable isotopes show that most litter arthropods are actually feeding on ectomycorrhiza or predating on invertebrates rather than feeding on the litter itself (Pollierer et al. 2009). Similar studies from the wood ecosystem spanning a large number of species would be highly valuable.

12.4.2 *Insect Specialization on Fungal Growth Forms*

Fungi can be divided into filamentous fungi and yeasts based on their growth form (Vega and Dowd 2005). Yeasts are predominantly unicellular and reproduce asexually by budding, although several species can also produce hyphal growth and some reproduce sexually by producing ascospores. Filamentous fungi in wood on the other hand grow vegetatively as hyphae and often reproduce sexually by fruiting bodies that produce fungal spores. The different forms of fungal growth represent highly different food resources for insects (Fig. 12.1).

Yeasts and yeast-like fungal growth are important for insects in dead wood as many wood-feeding species carry yeasts within their digestive tracts (Vega and Dowd 2005; Suh et al. 2005). Unfortunately, there is little research on the role of these gut yeasts, but they may provide the insects with enzymes for digestion and supply essential amino acids, vitamins, and sterols (see Sect. 12.3) (Tanahashi and Hawes 2016; Tanahashi et al. 2010; Suh et al. 2005). Some yeast-like fungi in the ascomycete genera *Ophiostoma* and *Alloascoidea* play essential nutritional roles in the facultative and obligate mutualisms with bark, ambrosia, and ship-timber beetles (see Sect. 12.6). Yeasts have also been isolated from the guts of fungivorous beetles, where they might be nutritionally important, help with digestion of fungal polysaccharides or detoxification, or simply stem from the beetle's actual food source (Suh and Blackwell 2005; Suh et al. 2005). Several yeasts have been isolated from dead wood (Kubartova et al. 2012; Strid et al. 2014; van der Wal et al. 2015) and might therefore present a food source or supplement for saproxylic insects, but this remains to be studied.

Hyphal growth of filamentous or yeast-like fungi in more or less dense mycelium is present within and outside wood structures and is likely to be included in the diet of many insects, even those normally identified as wood-feeding (Filipiak et al. 2016). Hyphae are a predictable resource that can be abundant in dead wood for many years. As many as 102 species of fungus gnats have been reared from dead wood or bark impregnated with fungi from Finland and Russian Karelia (Jakovlev 2011). Hyphal feeders can also be found among other Diptera, Coleoptera, Thysanoptera, Collembola, Isopoda, nematodes, and mites in dead wood. Hyphae may aggregate to form linear organs known as cords (Boddy et al. 2009). These might be less palatable than looser mycelium or hyphae; whereas millipedes and isopods are known to feed on cords, smaller invertebrates such as Collembola, mites, and nematodes do not (Crowther et al. 2011b).

Fruiting bodies are fed upon by Coleoptera, Lepidoptera, and Diptera (Lawrence 1973; Rawlins 1984; Gilbertson 1984; Lawrence and Powell 1969; Komonen et al. 2004; Økland 1995; Jakovlev 2011). They can be soft and short-lived such as in many ascomycetes and some polypores or hard and long-lived as in many perennial polypores. Both softness and longevity are likely to affect the insect's use of fungal fruiting bodies (Lawrence 1989; Hanski 1989). Thorn et al. (2015) found that most Ciidae, a beetle family specializing on saproxylic fruiting bodies, preferred annual fruiting bodies. Schigel et al. (2006) further differentiate annual polypores into three groups based on their longevity (ephemeral, sturdy, and hibernating), but differences in species preferences for these groups have never been formally tested. Generally, the hard and perennial polypore basidiocarps are mainly fed upon in their various stages of decay (Jonsell and Nordlander 2004).

Spores are only available during restricted time intervals. They are fed upon by a large number of opportunists (Hågvar 1999; Schigel 2011) and a few specialists. The specialists include larvae of minute beetles feeding on spores within the spore tubes of polypores (Ptiliidae, Limulodidae, and *Hylopsis* sp. in the Corylophidae) (Dybas 1976; Lawrence 1989). Species in the predominantly spore-feeding tribe Nanosellini (Ptiliidae: Ptiliinae) actually include the world's smallest beetles (*Scydosella musawasensis* Hall from Nicaragua and *Vitusella fijiensis* Hall from Fiji), which are only 0.3 mm long (Hall 1999) (Fig. 12.4, Europe's smallest beetle in the same tribe). Larger fungivores have specialized on spore feeding at the polypore surface (hymenium) (Leiodidae, *Zearagytodes maculifer* (Broun); Corylophidae, *Hylopsis* sp.) (Kadowaki et al. 2011b). Thysanoptera in the subfamily Idolothripinae are also specialized spore feeders found on dead wood in the wet tropics (Mound 1974).

Fig. 12.4 Europe's smallest beetle, *Baranowskiella ehnstromi* Sorensson, is only 0.5 mm long and lives on spores in the pore tubes of polypore *Phellinus conchatus* (Pers.) Quél. Reprinted with permission from Ole Martin©

12.4.3 Effect of Fungivores on Fungi

Whether fungivory affects fungal fitness is largely unexplored. Only a few cases of extensive damage to living fruiting bodies are known. First, the two specialist beetles *Octotemnus glabriculus* (Gyllenhal) and *Cis boleti* Scopoli (Ciidae) may reduce the spore-producing surface (hymenium) of *Trametes versicolor* (L.) Lloyd by 30–64% (Guevara et al. 2000). Second, the larvae of *Agathomyia wankowiczii* (Schnabl) (Diptera: Platypezoidea: Platypezidae) form galls in *Ganoderma applanatum* (Pers.) Pat that can cover most of the hymenium (Hanski 1989). Finally, the beetle *Cypherotylus californicus* Lacordaire (Erotylidae) is able to destroy soft polypores (Basidiomycetes: Polyporaceae) such as *T. versicolor* and *Bjerkandera adusta* (Willd.) P. Karst. before spore production occurs (Graves 1965).

Spore feeders might also potentially decrease fungal fitness, if a large proportion of spores are destroyed. The effect of gut passage might be species-specific (see Sect. 12.5.3). Digestion of spores from *Ganoderma cf. applanatum* by the specialist spore-feeding beetle *Zearagytodes maculifer* (Broun) has been shown to reduce germination rate relative to undigested spores, suggesting a potential decrease in fungal fitness (Kadowaki et al. 2011a).

In woodland soil ecosystems, mycelium-feeding invertebrates can affect fungal growth. For instance, lab manipulations have shown that high Collembola grazing intensity can cause mycelium extension of the wood-decay fungi *Hypholoma fasciculare* (Huds.) P. Kumm. and *Phanerochaete velutina* (DC.) Parmasto to decrease, while low grazing intensity can cause an increase (Crowther et al. 2012).

Compensatory fungal growth at low grazing intensities has also been indicated for three soil living ascomycetes when Collembola numbers were reduced by predatory mites (Hedlund and Öhrn 2000). In a more complex system with several animal groups and as many as seven wood-decay fungi, the micro- and mesofauna (nematodes and Collembola) were able to increase fungal growth through stimulatory grazing, whereas the macrofauna (isopods and millipedes) only reduced fungal growth (Crowther et al. 2011b).

If the effect of body size in dead wood parallels that in soil, small fungivorous beetles and dipterans (similar to soil mesofauna) might increase fungal growth at wood surfaces, while larger beetles (similar to soil macrofauna) might reduce fungal growth. As for fungi growing within the dead wood itself, the effect of grazing is unclear. Not surprisingly, Crowther et al. (2011a) noted that grazing isopods only reduced fungal growth outside the wood blocks. However, tunneling beetles feeding on a mixed wood and fungal diet may have the potential to reduce or stimulate fungal growth even within dead wood.

In insect-fungus mutualisms, ambrosia beetles have been shown to stimulate nutritional yeast-like "ambrosial growth" of their farmed *Ambrosiella* fungi (Ascomycota) (French and Roeper 1972; Biedermann 2012; Batra and Michie 1963). Outside of wood, fungus-farming termites stimulate the growth of nutritionally important nodules (unripe mushrooms) in the *Termitomyces* spp. (Basidiomycota) they cultivate, and leaf-cutter ants induce hyphal swellings (gongylidia) in their cultivars (Mueller et al. 2005). The exact mechanisms underlying these inductions remain unstudied so far.

Fungi are known to compete for resources, often with well-known hierarchies of inferior and dominant species (Holmer et al. 1997; Boddy 2000). Grazing by soil invertebrates has been found to influence or even reverse outcomes of competitive interactions in soil between wood-decomposing fungi. Crowther et al. (2011a) demonstrated that nematodes stimulated growth of an inferior competitor, whereas isopods restricted a dominant competitor (Crowther et al. 2011a). Grazing therefore altered the competitive hierarchy and ensured coexistence of two fungal species, which also affected wood-decay rates. Thus, grazing intensity and food preferences of fungivorous invertebrates might alter fungal-mediated nutrient cycling and decomposition. Invertebrates may also directly modify the enzymatic profiles in fungi, potentially inducing strong overall effects on wood decay (Dyer et al. 1992).

12.4.4 Fungal Defense Against Fungivores

If invertebrate feeding activity reduces fungal fitness, fungi might have evolved defense mechanisms. Although there are presently few examples of reduced fitness due to fungivory, several physical and chemical defense mechanisms have been suggested. Hackman and Meinander (1979) as cited in Hanski (1989) suggest that sporulation in soil, physical protection of fruiting bodies prior to sporulation, and production of milky sap and toxic or repellent chemicals might defend fruiting bodies against colonization of fungivores. Also, the perennial polypores are often hard and difficult to digest which prevents invertebrate feeding prior to decay. Fruiting bodies of agarics are generally short-lived and small, which might ensure escape from fungivores in time and space (Hanski 1989). Finally, compensatory growth by yeasts may be an adaptation to lower damage due to insect grazing (Vega and Dowd 2005) as may translocation of nitrogen to ungrazed mycelium within a fungal organism (Boddy and Jones 2008).

Fungi produce an almost endless diversity of organic compounds not required for growth or metabolism, and many of these are known to be highly toxic to animals (Rohlfs 2015). Some of these secondary metabolites are likely to function as defense against invertebrates. Rohlfs (2015) critically reviewed the evidence for such a function and concluded that invertebrate grazing (Collembola and fruit flies) on *Aspergillus* spp. might indeed increase production of fungal secondary metabolites. The production of these metabolites subsequently decreased grazing. Collembola grazing on *Aspergillus* has also been found to increase production of sexual fruiting bodies, which remain ungrazed even at high grazing pressures. This response likely evolved to escape grazers by reproduction and ensure fungal fitness. Interestingly, induced chemical defenses by the fungus can be overcome by Collembola when feeding in groups (Stötefeld et al. 2012), a mechamism also known from gregariously feeding insect leaf herbivores. The chemistry of the induced metabolites varies, but a recent finding shows that the terpenoid compounds that function as juvenile hormones in insects are synthesized in *Aspergillus* as response to *Drosophila* grazing (Nielsen et al. 2013). The presence of this compound significantly decreased the weight of adult flies. Similar terpenoid compounds are well known from plant defenses (Toong et al. 1988). Finally, some fungi secrete chitinolytic enzymes (Klironomos and Hart 2001), enabling them to digest insects. This makes fungal grazing a potential dangerous activity.

12.4.5 Insect Specialization on Fungi

The specificity of interactions between insects and fungi outside the well-known, highly specific, mutualistic interactions is generally assumed to be low or at least much lower than in plants and their associated herbivores (Hanski 1989; Hackman and Meinander 1979). Insects living inside polypores may represent a notable exception to this pattern (Paviour-Smith 1960; Orledge and Reynolds 2005; Jonsell and Nordlander 2004). Jonsell and Nordlander (2004) estimated that almost half of the beetles and moths hatching from ten polypore species they investigated in Scandinavia were monophagous (defined as less than 20% of hatched individuals found outside the main host). A strong tendency for closely related fungi to function as hosts for the same beetles has also been found when analyzing only ciid beetles (Paviour-Smith 1960; Orledge and Reynolds 2005; Thorn et al. 2015). Recent studies have also shown that phylogenetic relationship of fungi is indeed important to explain host use in fungus gnats (Poldmaa et al. 2016); several species can be associated with polypore species or genera (Sevcik 2001, 2003; Jakovlev 2011). Studies of fungus gnats associated with ascomycete fruiting bodies are still scarce, but preferences also appear to occur in these interactions (Jakovlev 2011). Thus, both beetles and fungus gnats are likely to have coevolved with and specialized on certain fungi. Defensive compounds produced by the fungi have potentially driven this process.

There are also indications that spore-feeding insects have preferences for certain species or genera of fungi. Hågvar (1999) investigated potential spore-feeding adult beetles visiting the two common polypores *Fomitopsis pinicola* (Sw.) P. Karst. and *Fomes fomentarius* (L.) Fr. in forests in Norway (Fig. 12.2). He found only a slight overlap in beetle species on the two fungi even though they sporulated within the same time period. In total, based on all literature known to us, as many as 134 species of beetles have been found to visit these two polypores, but only 27% (36) have been recorded from both (Kaila et al. 1994; Nikitsky and Schigel 2004; Schigel 2011; Hågvar and Økland 1997; Hågvar 1999; Krasutskii 2007b). Thus, even potential spore feeders (and their predators) appear to distinguish between the two polypores. Fäldt et al. (1999) found that *F. pinicola* and *F. fomentarius* emit different volatiles and that the scents are modified during sporulation. Most likely, insects can use these signals to locate their hosts (Fäldt et al. 1999; Jonsell and Nordlander 1995).

Fungi identified by molecular methods from adult saproxylic beetles sampled from dead wood also indicate species-specific interactions and possibly feeding preferences (Jacobsen et al. 2018a). The degree of specialization between 17 species of saproxylic beetles and 22 wood-decay agaricomycete fungi was similar to the specialization known from seed dispersing animals and plants (Blüthgen et al. 2007). Yamashita et al. (2015) conducted the same analysis of network specialization on beetles emerging from living and decomposing polypores, which resulted in a higher degree of specialization, approaching values known from pollinator networks. As discussed above, the host specificity of species with larval development within fruiting bodies is expected to be higher than for spore feeders, which fits well with the difference shown between these two studies. However, both studies indicate specialization on fungal hosts.

Insect preferences for hyphae of different fungi need to be determined by experimental work in the lab. At present, hardly any studies have been carried out in the dead wood system. *Xestobium rufovillosum* de Geer thrives in wood with eight different species of fungi (Fisher 1940, 1941) which might indicate polyphagy in this species. However, this effect might also be caused by indirect effects, such as an ability to use wood decomposed by a wide range of fungi (see Sect. 12.7). Many of the wood-feeding termites (i.e., Kalotermitidae, Rhinotermitidae, Termitidae) have a strong preference and develop better on wood infested by some brown-rot fungi (Basidiomycota) but are repelled by most white rots (Basidiomycota) and many soft rots (Ascomycota) in laboratory settings. The effect of fungi may also depend on the termite species, with some fungi having even opposing fitness effects on the insects (Becker and Kerner-Gang 1963; Becker 1964, 1965). For comparison, fungivorous soil invertebrates feeding on hyphae are regarded as generalist feeders although the mesofauna (mites and Collembola) appears more specialized than the macrofauna (earthworms, diplopods, slugs, and snails) (Maraun et al. 2003) and species-specific preferences do occur (Newell 1984; Tordoff et al. 2008; Crowther and A'Bear 2012; Jørgensen et al. 2003).

In the obligate mutualisms between insects and fungi, specificity for certain partners is usually high. In the best studied bark and ambrosia beetles, every beetle species is associated with one or two fungus species, which serve as their primary food source (Harrington 2005; Beaver 1989; Francke-Grosmann 1967; Mayers et al. 2015). Although host switches do occur over evolutionary time scales, there is coevolution between the beetles and the fungi (Farrell et al. 2001). It is not known what unique coadaptations occur in specific partnerships, but it has been shown that switches between highly related *Ambrosiella* fungal mutualists (Ascomycota) between two sister species of *Xylosandrus* ambrosia beetles (Scolytinae) resulted in significant fitness losses compared to the native partnerships (Kaneko and Takagi 1966). Also, *Dendroctonus* bark beetles failed to incorporate non-native strains of their *Entomocorticium* mutualist (Basidiomycota) into their mycetangia. These findings indicate beetle adaption to particular genotypes of mutualistic fungi (Bracewell and Six 2015). Thus, these Scolytinae-fungus partnerships are maintained by the selectivity of mycetangia and at least partly also by characteristic fungal volatiles that can be highly attractive to the beetles (Biedermann and Kaltenpoth 2014). However, there are exceptions in the mutualisms between some Xyleborini ambrosia beetles and their *Raffaelea* fungal mutualists, which seem to be less specific as beetles can develop equally well by feeding on several different *Raffaelea* species, which they also transmit within a semi-selective mycetangium (Saucedo et al. 2017). The additional secondary fungal flora of mostly ascomycete soft-rot, blue-stain fungi and yeasts that is found in bark and ambrosia beetle nests can be highly variable and depends mostly on the tree substrate, other organisms in the vicinity of the nest, and environmental conditions (Beaver 1989).

12.4.6 Fungi Might Interact with Few or Many Insect Species

As discussed above, several insects have been found to specialize on fungi. One question of particular interest to conservation is whether certain fungi are more preferred than others, thus hosting a higher species richness of associated insects.

In obligate mutualisms of ambrosia and ship-timber beetles, every fungus species is associated with one (or rarely several; see Sect. 12.4.5) beetle species and not found free-living (Harrington 2005; Beaver 1989). Some fungi involved in facultative mutualisms of bark beetles and a few ambrosia beetles can be found associated with different beetles species, but no single fungus dominates in these interactions (Kirisits 2004; Six 2012; Saucedo et al. 2017) (see Sect. 12.6.2). Such associates, in particular species of the genera *Ceratocystis*, *Ophiostoma*, *Entomocorticium*, and *Alloascoidea*, can be also found free-living as plant pathogens or endophytes.

Fungal fruiting bodies are discrete units from which insects can be collected or reared, and therefore insect communities associated with fungi are well known from these structures. The lack of beetles visiting or feeding on 82 out of 198 investigated polypore species in Finland indicates that some species are inferior as insect hosts (Schigel 2012). Whether this difference relates to toxicity, nutrient content or fungal structural characteristics are unknown. Many of the avoided polypores were common species.

Rather than looking at species, Thorn et al. (2015) focused on polypore traits and insect species richness in southern Germany. They hypothesized that ciid species richness would increase with increasing fruiting body size, niche diversity (fungal growth form), durability (annual < perennial), abundance, and decreasing phylogenetic isolation of the host fungus. These traits have previously been found to affect species richness in herbivore-plant and parasite-host systems. Their hypotheses were generally confirmed, with the exception that species with annual fruiting bodies had higher ciid species richness than the perennial species. *Trametes versicolor* (Fig. 12.2d) had the overall highest species richness of ciids (16).

Despite an obviously skewed sampling effort and no formal testing, the importance of fruiting body abundance for harboring a high diversity of insects has been noted by several authors. Yamashita et al. (2015) hatched 82 beetle species from polypores in tropical Malaysia: 53 (65%) hatched from *Ganoderma* which made up 61% of the total fungal biomass and 19 (23%) from *Phellinus* which made up 17% of the biomass. Many insect species have also been hatched from common polypores such as *Fomes fomentarius* in Norway (36 species) (Thunes et al. 2000), *Fomitopsis pinicola* in Fennoscandia (139 species) (Komonen et al. 2004), and *Polyporus squamosus* (Huds.: Fr.) Karst. in Germany (264 species) (Gilbertson 1984). The most common polypores also harbored the highest number of insects in the Czech and Slovak Republics (Sevcik 2003).

12.5 Insect-Vectored Dispersal of Non-mutualistic Fungi

Saproxylic fungi are a diverse group, and their dispersal ecology might be equally diverse, although for many species, it is poorly known (Watkinson et al. 2015). In general, saproxylic fungi are assumed to disperse primarily by airborne spores (Ingold and Hudson 1993; Junninen and Komonen 2011; Norros et al. 2012), although some species can also reach their substrate by hyphal cords in the soil (Boddy et al. 2009; Coates and Rayner 1985). A few species of fungi are known to be dispersed by bark beetles, ambrosia beetles, ship-timber beetles, or wood wasps (Batra 1963; Harrington 2005) (further discussed in Sect. 12.6.3). Transmission of fungi by termites is probably unimportant as termites show a preference for slow-growing fungi (Becker 1965) that need to be established in the wood ahead of termite arrival. However, the role of invertebrates in fungal dispersal might be underestimated, as has been suggested several times (Talbot 1952; Harrington 2005; Malloch and Blackwell 1992; Norros 2013; Watkinson et al. 2015).

In order to disperse fungi to dead wood, an insect would first have to get in contact with propagules of a saproxylic fungus and then transport the propagules internally or externally in a manner that leaves an adequate percentage viable. These propagules should be disposed at a suitable substrate and in a suitable microclimate for the fungus, which is likely when insect and fungus habitat preferences match. Many insects may fulfill some or all of these criteria, thus functioning as dispersal vectors with different effectiveness.

12.5.1 Insect-Vectored Dispersal of Polypores

The ideal insect vector for saproxylic fungi would be a species that visits sporulating fruiting bodies and subsequently seeks out dead wood of a type suitable to the fungus. Several saproxylic insects seem to be attracted to fungal odors (Jonsell and Nordlander 1995; Johansson et al. 2006). Fäldt et al. (1999) showed that odor emission from fruiting bodies increases during sporulation, which they suggested could be an adaptation to attract insect spore vectors. Sporulating fruiting bodies do attract a large number of insect visitors, most of which are saproxylic (Hågvar 1999; Schigel 2011; Nikitsky and Schigel 2004; Krasutskii 2006, 2007a, b, 2010; Park et al. 2014; Yamashita et al. 2015). Interestingly, many of these insect species develop in dead wood, not in fruiting bodies. For instance, the nitidulid beetles *Glischrochilus quadripunctatus* (L.) and *G. hortensis* (Geoffroy) both visit sporulating polypores (Hågvar 1999; Krasutskii 2007a, b; Nikitsky and Schigel 2004; Schigel 2011), but their main habitat seems to be weakened or recently dead trees (Dahlberg and Stokland 2004). Nitidulid beetles have been shown to carry fungal plant pathogens to wounds on living trees (Hayslett et al. 2008; Cease and Juzwik 2001). When sampled from fresh dead wood, *G. quadripunctatus* and *G. hortensis* were found to frequently carry DNA from several different fungi, including DNA from polypores such as *Trametes versicolor* and *Fomes fomentarius* (Jacobsen et al. 2017). Jonsell and Nordlander (1995) showed that *G. hortensis* is attracted by the odor of *F. fomentarius*, explaining its frequent presence on sporulating fruiting bodies of that polypore (Schigel 2011; Kaila et al. 1994; Hågvar 1999; Nikitsky and Schigel 2004). Fruiting bodies of *F. fomentarius* often accumulate thick layers of spores on their upper side, where many insect visitors can be found, especially during the night (Hågvar 1999). This accumulation of spores might increase the odor and attractiveness of the fruiting bodies to insect visitors, and as such it might be an adaptation to insect-vectored dispersal.

Several other saproxylic beetles sampled from fresh dead wood, such as *Endomychus coccineus* (L.) (Endomychidae) (Fig. 12.5a), *Xylita laevigata* (Hellenius) (Melandryidae), and *Rhizophagus* spp. (Monotomidae), have also been found to frequently carry fungal DNA from a diversity of fungal taxa, including several polypores and other wood-inhabiting species (Jacobsen et al. 2017). There are a few polypore taxa involved in dispersal mutualisms with wood wasps and ambrosia beetles (see Sect. 12.6), but bark and ambrosia beetles have also been found to carry propagules of fungi they are generally not thought to depend on such as *Fomitopsis pinicola*, *Trichaptum abietinum* (Dicks.: Fr.) Ryvarden,

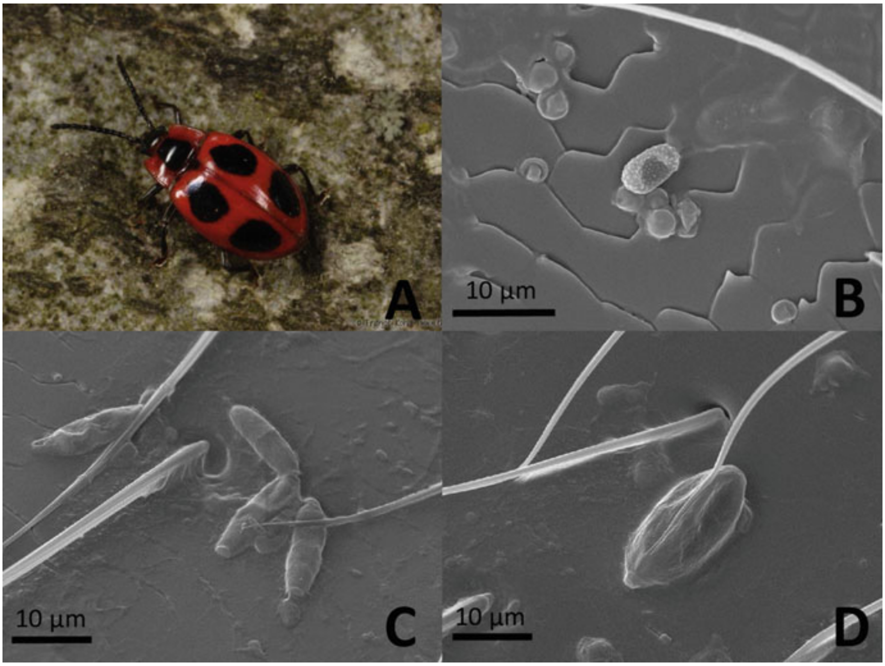

Fig. 12.5 Scanning electron microscope pictures (**b**, **c**, **d**) of what are most likely fungal spores on the exoskeleton of a fungivorous beetle, *Endomychus coccineus* (**a**). Photo by (**c**) Frithjof Kohl, reprinted with permission. The beetles were sampled from freshly dead aspen wood and stored at −80 °C prior to scanning (Jacobsen et al. 2017). (**b**) A few of the larger spores with coarse outer structure were found on the beetles, while the smaller spores were found in large numbers and might be yeast cells covered by biofilm. (**c**) The fusiform shape and the horizontal cross walls of these spores are typical of mold fungi in the genera *Cladosporium* and *Cladophialophora* (Marie Davey, pers. com.). (**d**) Several of these large spores were found on one beetle

Heterobasidion annosum (Fr.) Bref., *Stereum sanguinolentum* (Alb. and Schwein.) Fr., and *Cryptoporus volvatus* (Peck) Shear (Castello et al. 1976; Harrington et al. 1981; Pettey and Shaw 1986; Strid et al. 2014; Six 2012). Several of these species have also been isolated from beetle galleries without being present in the surrounding wood, suggesting that the bark beetle galleries provided their point of entry into the wood (Persson et al. 2011).

12.5.2 Insect-Vectored Dispersal of Wood-Inhabiting Microfungi

Although basidiomycete polypores may be the most important fungal taxa when it comes to mass loss during wood decay (Boddy 2001; Kubartová et al. 2015), molecular analyses have shown that there is a diversity of yeasts and ascomycete taxa present in dead wood (Ottosson et al. 2015; van der Wal et al. 2015; Strid et al. 2014). The role of these taxa in the dead wood is poorly known (Ottosson et al. 2015; van der Wal et al. 2015). They might contribute to wood decay directly or depend on prior decomposition by cellulolytic or lignolytic fungi (Rayner and Boddy 1988; Ottosson et al. 2015; Rajala et al. 2011) and have even been suggested to produce a synergistic effect on wood decay together with basidiomycetes (Blanchette and Shaw 1978). Several of the yeasts and filamentous ascomycete taxa isolated from wood have also been isolated from saproxylic insects (Greif and Currah 2007; Strid et al. 2014; Six 2003; Jacobsen et al. 2017), indicating that these fungi might be dispersed by insects. It has also been shown that phoretic mites on bark beetles function as vectors for certain microfungi (Blackwell et al. 1986; Hofstetter and Moser 2014). Dispersal by insects has been suggested previously for species like *Oidiodendron* spp. and *Myxotrichum* spp. that produce a peculiar spore-containing structure called reticuloperidium (Fig. 12.6) (Greif and Currah 2003). Spores in a reticuloperidium are contained within a network of rigid and thick-walled hyphae, often with hooked or barbed appendages. Greif and Currah (2003) showed that (1) these reticuloperidia easily attach to hairs on the exoskeleton of insects and (2) when the insects groom themselves, the reticuloperidia are torn apart and the spores are released. While the significance of this has not been tested in the field, these are intriguing observations.

12.5.3 Viability of Spores After Insect-Vectored Dispersal

Several studies show that some fungal spores can survive transport both on insect exoskeletons and within insect guts (Lilleskov and Bruns 2005; Tuno 1999; Lim 1977; Drenkhan et al. 2016). For instance, *Mycodrosophila* flies that visited sporulating fruiting bodies of *Ganoderma applanatum* excreted and dropped up to several hundred thousand viable spores (Tuno 1999). Basidiospores of *Ganoderma* species have double spore walls which might be an adaptation to dispersal by insect vectors, whereas their small proteospores are probably better suited for wind dispersal (Nuss 1982). Lim (1977) found that the basidiospores of *Ganoderma philippii* (Bres. and Henn.) Bres. would only germinate after passage through the gut of tipulid fly larvae. Digestion by the fly larvae seemed to reduce the spore wall thickness without damaging the spore content, which appeared to benefit germination. The emerging adult flies subsequently came into contact with the spores previously excreted by the larvae and thousands of spores attached to their exoskeletons. Thus, *G. philippii* seems to be adapted to dispersal by tipulid flies, and the flies might benefit from dispersing the fungus that their larvae feed on. However, studies of another *Ganoderma* species found that passage through the gut of a specialist spore-feeding beetle reduced germination rate (Kadowaki et al. 2011a). Digestion by this beetle species apparently reduces the originally thick spore walls to the extent that the

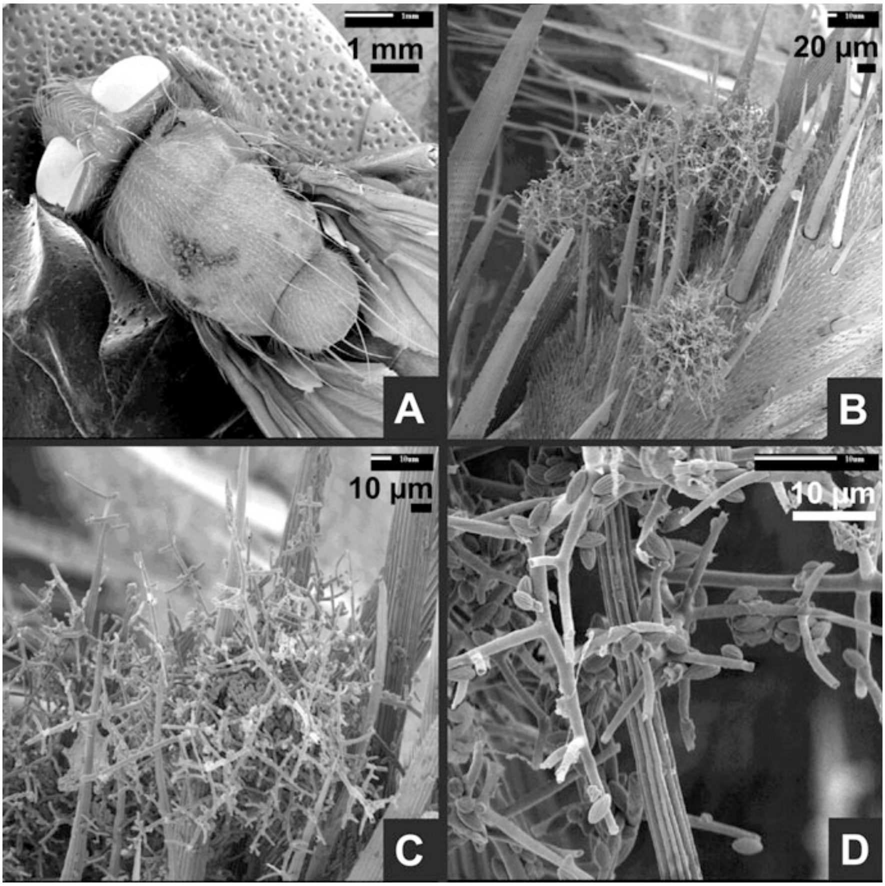

Fig. 12.6 Scanning electron microscope picture of the reticuloperidium of *Myxotrichum deflexum* attached to the hairs of the fly *Neobellieria bullata* (Parker). Reprinted with permission from Greif and Currah (2003)

spores burst open. Thus, whether passage through insect guts is beneficial or detrimental to spore germination seems to depend on traits of both the fungus and the insect.

12.5.4 Effects of Insect Vectors on the Fungal Community in Dead Wood

Although several studies show that insect-vectored dispersal of saproxylic fungi is a distinct possibility, it is difficult to estimate the significance of this dispersal mode for the fungal community. However, there are a few published field studies that provide indications of the importance of insect-vectored dispersal for wood-inhabiting fungi, including both long-term observational studies (Weslien et al. 2011; Jacobsen et al. 2015) and short-term experimental studies (Jacobsen et al. 2018b-Submitted; Müller et al. 2002; Strid et al. 2014).

In a field study by Weslien et al. (2011), fruiting bodies of the polypore *F. pinicola* were found to occur more often on dead wood that had previously been colonized by the bark beetle *Hylurgops palliatus* Gyll. The authors suggested that spore dispersal by *H. palliatus* might have caused this correlation, as its flight period coincided with the spring sporulation of *F. pinicola*. Jacobsen et al. (2015) showed that an abundance of the nitidulid beetle *G. quadripunctatus* or the leiodid beetle *Agathidium nigripenne* (Fabricius) during the first years after tree death increased the probability that fruiting bodies of the polypore *Ganoderma applanatum* were found on the dead trees several years later. They suggested spore dispersal as the most likely mechanism to cause these patterns, especially in light of previous knowledge of insect-vectored spore dispersal for *Ganoderma* species (Tuno 1999; Lim 1977).

To experimentally assess the effect of insects on community assembly of wood-inhabiting fungi, Müller et al. (2002), Strid et al. (2014), and Jacobsen et al. (2018b-submitted) used net cages with mesh sizes of 1 mm or less to exclude invertebrates from recently felled logs. Müller et al. (2002) put spruce logs in cages and opened half of the cages for 3 weeks in May during the flight periods of their study species, resulting in colonization of these logs mainly by the bark beetles *H. palliatus* and *Trypodendron lineatum* (Olivier). Logs colonized by *H. palliatus* tended to have a higher diversity of fungi, while logs colonized by *T. lineatum* had a higher frequency of the fungi *Trichoderma* sp., *Antrodia serialis* (Fr.) Donk, and *Phlebia gigantea* (Fr.) Donk. In theory, the ambrosia beetle *T. lineatum* would not be expected to vector wood-decaying polypores that might be detrimental for its nutritional fungal mutualists. However, it was not clear whether the effect of the beetles was due to dispersal of propagules or some other interaction. For instance, beetle entry holes and tunnels can increase access to the wood for the fungi even if the beetles do not bring fungal propagules to the wood (Leach et al. 1937).

To separate the effect of bark beetle tunneling and the effect of potential propagule dispersal, Strid et al. (2014) combined the exclusion experiment with drilled holes in spruce logs to mimic bark beetle tunnels. These artificial holes had a much weaker effect on the fungal community than exclusion of invertebrates. The exclusion treatment contrasted caged logs with uncaged logs, and there was also a positive control consisting of logs baited with bark beetle pheromones. Molecular analyses were used to analyze the fungal community in wood samples from the different treatments and in samples of bark beetles. The fungal community of the bark beetle samples was most similar to that of the pheromone-baited logs, whose fungal community in turn was more similar to that of uncaged logs than caged logs. Furthermore, several fungal taxa that were isolated from the bark beetles were significantly more frequent in uncaged logs, e.g., *Stereum sanguinolentum*, *Bjerkandera adusta*, and *Sistotrema brinkmannii* (Bres.) J. Erikss. (Strid et al. 2014). These results show that bark beetles have a significant effect on the fungal community in dead wood and that part of this effect probably stems from propagule dispersal of non-mutualistic fungi.

Jacobsen et al. (2018b-Submitted) excluded invertebrates from aspen logs, thereby studying the influence of saproxylic insects in a community where bark beetles were not numerically dominant. Jacobsen et al. (2018b-Submitted) included ethanol-baited logs as positive control and a control for microclimatic effects of the cage, which was lacking in the previous exclusion experiments. The experimental treatments were postulated to form a gradient from low invertebrate colonization in caged logs, intermediate/normal in cage control and control logs, to increased colonization of ethanol-baited logs. This gradient was reflected in the fungal community composition, especially in abundance of certain fungal taxa in the logs, such as the polypores *Trametes versicolor* and *T. ochracea* (Pers.) Gilb. and Ryvarden that had low abundance in caged logs and high abundance in ethanol-baited logs. As *T. versicolor* had been isolated from saproxylic insects such as *G. quadripunctatus*, sampled in the same time and place as the exclusion study (Jacobsen et al. 2017), it is likely that insect-vectored propagule dispersal contributed to the effect of invertebrate exclusion on the fungal community (Jacobsen et al. 2018b-Submitted).

12.5.5 Adaptations to Insect-Vectored Dispersal

If insect-vectored dispersal can increase the fitness of wood-inhabiting fungi, this might have resulted in adaptations to this dispersal mode. The spore-containing reticuloperidium of certain ascomycete taxa mentioned previously might be such an adaptation (Sect. 12.5.2). Spores with appendages like spikes or hooks have been found to attach easily to invertebrate exoskeletons (Lilleskov and Bruns 2005) and might be adaptive for external dispersal by invertebrate vectors (Halbwachs and Bâssler 2015). Likewise, the sticky spores produced by blue-stain fungi (i.e., the ascomycete genera *Ophiostoma*, *Leptographium*, *Ceratocystis*, *Grosmannia*, *Ceratocystiopsis*) easily adhere to their bark beetle vectors and facilitate external dispersal (Harrington 2005). The thick spore walls of *Ganoderma* species seem to be adaptive for internal dispersal by insect vectors (Lim 1977; Nuss 1982). Finally, fungi in mutualistic associations with insects (Sect. 12.6) typically grow in a yeast-like form (“ambrosial growth”) to get picked up in the spore-carrying organs (mycetangia/mycangia[1]) of the adult wood wasps and bark, ambrosia, or ship-timber beetles (Francke-Grosmann 1967; Six 2003). There might also be less obvious adaptations in the chemical composition of spores, such as lack of defensive compounds, but the chemical defense of most fungi is poorly known (see Sect.

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[1] A fungus spore-carrying organ was first discovered and termed *mycetangium* by Francke-Grosmann (1956). Batra (1963) coined the term *mycangium* for the same structure. Although *mycangium* is now commonly used in the literature, it is incorrect from an etymological point of view [see discussion about this in Francke-Grosmann (1967)]. Therefore, we use *mycetangium* in our research and suggest others to do so too.

12.4.4). Fruiting body morphology might also facilitate spore dispersal, for instance, by resulting in the accumulation of thick spore layers on top of the fruiting body that attract insect visitors (Hågvar 1999). This is especially characteristic for sporulating fruiting bodies of *F. fomentarius* and *G. applanatum*.

The insects on their side might not have adaptations specifically for dispersal of fungi if their interaction stems from opportunistic spore feeding. While spore feeders might benefit from increasing the prevalence of fruiting bodies in their habitat, such an indirect selection pressure might not result in adaptation. However, if the larval development benefits from the presence of fungi dispersed by the adult insects, the selection pressure will be stronger. This is the basis of the evolution of obligate insect-fungus mutualisms, which has led to the development of the selective fungus-bearing pockets in insect exoskeletons called mycetangia in several insect groups (see Sect. 12.6). Mycetangial structures have been found in a range of insects not known to engage in mutualisms with fungi, although their function as organs for dispersal of fungi is often inferred and not demonstrated (Grebennikov and Leschen 2010). Females of several species of saproxylic stag beetle (Lucanidae) have mycetangia that they use to vertically transmit *Scheffersomyces* yeast species (Ascomycota) to their offspring during oviposition (Tanahashi et al. 2010). These yeasts are also transferred to the wood, but their main function is probably xylose fermentation in the guts of developing larvae, and they therefore seem to be primarily endosymbionts (Tanahashi and Hawes 2016). Unfortunately, most of the presumably non-mutualistic insect species with mycetangium-like structures remain understudied.

12.5.6 Implications of Insect-Vectored Dispersal

To summarize, several studies support the hypothesis that insects can be important dispersal agents also for non-mutualistic saproxylic fungi, but the effect of insect-vectored dispersal is difficult to quantify. Animal-mediated seed dispersal, which has many similarities with insect-vectored spore dispersal, can be assessed with a framework that shows how different aspects of the animal vector contribute to seed dispersal effectiveness (SDE) (Schupp et al. 2010). In Fig. 12.7, we propose a similar framework for studies of spore dispersal effectiveness (SpDE), which might help structure and focus future research efforts.

In any case, insect-vectored dispersal does not have to replace wind dispersal to be of importance to saproxylic fungi. Insect-vectored dispersal could be a complementary form of dispersal that is especially important under certain circumstances. The most obvious difference from wind dispersal is that insect-vectored dispersal has the potential to be targeted toward the preferred substrate of the fungi, while wind dispersal is completely random. Studies comparing wind-dispersed and animal-dispersed plants have shown that animal-mediated seed dispersal can increase tolerance to habitat fragmentation (Montoya et al. 2008; Marini et al. 2012), as long as the animal vector is present in the fragments (Cramer et al.

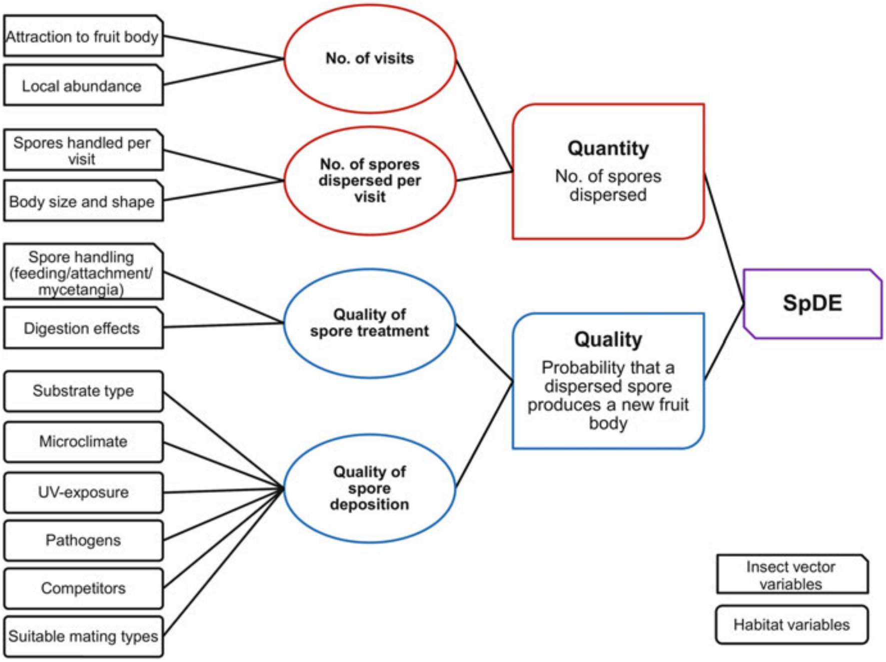


Fig. 12.7 A theoretical framework for studies of spore dispersal effectiveness (SpDE) of insect or animal vectors of fungal spores (or other propagules). The list of variables is not exhaustive. The figure is adapted from the seed dispersal effectiveness framework described in Schupp et al. (2010)

2007). Similarly, targeted dispersal by insects might help certain fungi persist in fragmented forests with low volumes of dead wood.

12.6 Symbioses Between Insects and Fungi in Dead Wood

All animals live in symbiotic associations—from antagonism to mutualism—with microorganism that plays an important role for pathogenicity and host nutrition (Whitman et al. 1998; Zilber-Rosenberg and Rosenberg 2008). Insects living in wood are no exception—mutualistic bacteria and fungi are of essential importance for many saproxylic insects as they help degrade plant-defensive compounds, digest recalcitrant plant polymers, or synthesize and assimilate essential nutrients (Dowd 1992; Klepzig et al. 2009; Riley et al. 2016). These microorganisms are usually carried within the intestinal tracts of the insects ("gut symbionts"), but there are also a few cases where symbionts are cultivated externally (henceforth termed "ectosymbionts"). Many wood feeders in the beetle families Cerambycidae, Passalidae, Scarabaeidae, Tenebrionidae, Lucanidae, and Elateridae seem to rely on gut symbionts, in particular yeasts, but the exact functions of these gut symbionts remain understudied, and the little that is known is reviewed elsewhere (Davis 2014; Vega and Dowd 2005; Tanahashi and Hawes 2016; Urbina and Blackwell 2012; Urbina et al. 2013). On the other hand, wood-feeding termites in the families Kalotermitidae, Rhinotermitidae, and Termitidae rely on gut bacteria, archaea, and protozoa for wood digestion (Brune 2014), although they profit from feeding on wood decayed by some Basidiomycetes. Here we focus on the insects that engage in facultative or obligate ectosymbioses with fungi, including all taxa that grow yeast-like or filamentous fungi in their tunnels within wood, i.e., the bark and ambrosia beetles in the Curculionidae, the ship-timber beetles (Lymexylidae), and the hymenopteran wood wasps (Siricidae) (Six 2013, 2012; Thompson et al. 2014) (Fig. 12.8). The obligate farming mutualism between termites (Macrotermitinae) and *Termitomyces* fungi is outside of wood (although the substrate for growing the fungus can include small pieces of wood) and has been reviewed repeatedly (e.g., Wood and Thomas 1989; Aanen et al. 2002; Mueller et al. 2005; Nobre et al. 2011), so we discuss it only briefly in relation to the other obligate mutualisms.

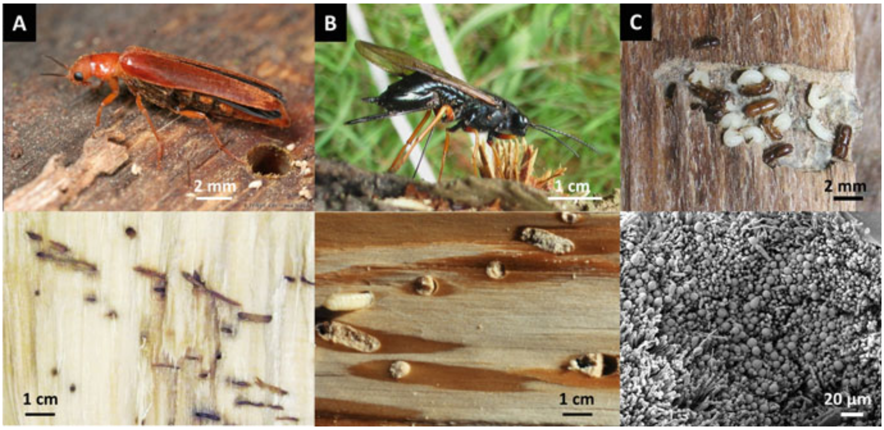


Fig. 12.8 Overview of the three known insect groups that engage in obligate ectosymbiotic mutualisms with fungi within wood. (**a**) Ship-timber beetles (Lymexylidae). An adult female of the Palearctic *Elateroides dermestoides* (L.) after emergence from its tunnel (©Frithjof Kohl) and tunnels of larvae in fir wood (*Abies alba* Mill.) below (©P. Biedermann). (**b**) Wood wasps (Siricidae). Adult female of the Holarctic sawfly *Sirex noctilio* F. on pine (*Pinus radiata* D. Don) bark (©Michaellbbecker, CC BY-SA 3.0) and a larva and tunnels below (©Vicky Klasmer, CC BY-NC 3.0 US) (**c**) Ambrosia beetles (Scolytinae). Brood chamber with multiple larvae and adult females of the globally distributed facultatively eusocial fruit-tree pinhole borer *Xyleborinus saxesenii* Ratzeburg in beech (*Fagus sylvatica* L.) (©P. Biedermann) and SEM picture of nutritional "ambrosial growth" of *Raffaelea sulphurea* (L.R. Batra) T.C. Harr., the ascomycete fungus mutualist of this species (SEM with 200× magnification made by the Elektronenmikroskopisches Zentrum Jena; ©P. Biedermann)

12.6.1 Characteristics of Wood Favoring Insect-Fungus Mutualisms

Mutualisms between species require environmental stability and often evolve between animals and microbes in poor/restricting habitats due to benefits of division of labor (Boucher et al. 1982; Bourke 2011). Both characteristics are fulfilled in living and dead wood for insects and fungi: First, insects and fungi occur in close vicinity within wood, often for several insect/fungus generations due to the relative stability of wood as a habitat. Second, both insects and fungi have many complementary characteristics and can therefore benefit each other in various ways (Six 2012; Beaver 1989; Mueller et al. 2005; Vega and Blacwell 2005). The primary benefit insects can provide to fungi is probably the targeted dispersal (relative to wind dispersal) of spores into new or inaccessible habitats such as the cambium or xylem of trees (see Sect. 12.5). Insects with advanced fungiculture that actively farm their fungal crops also provide nutrients and protection to the fungus (Table 12.1). The insects, on the other hand, may profit directly by feeding on the fungus (acquiring mostly amino acids and sterols) or indirectly through fungal detoxification of defensive plant compounds (phenolics, terpenoids) and degradation of plant polymers (lignin, cellulose, pectin) (see also Sect. 12.3). Insects may also make use of fungal volatiles to attract conspecifics or mating partners, or they can use antibiotics produced by fungi to protect themselves against pathogens or fungal competitors (Table 12.1).

12.6.2 Facultative Mutualisms Between Insects and Ectosymbiotic Fungi Within (Dead) Wood

Many wood-feeding insects, like lower termites, longhorn beetles, and bark beetles, engage in facultative associations with filamentous fungi. They develop perfectly well without fungi but profit when certain fungi (e.g., some brown rots in termites, some blue-stain fungi in bark beetles) are present in the surroundings of the nest or within the ingested wood substrate (Geib et al. 2008; Six 2012; Klepzig et al. 2009; Becker and Kerner-Gang 1963; Becker 1964; Becker 1965; Amburgey 1979; Cornelius et al. 2002; Ayres et al. 2000). Fungi co-occurring with insects in freshly dead wood are often plant pathogens or at least fungi capable of detoxifying defensive plant chemistry, which can help the insects to colonize the wood. In later stages of wood degradation, insects can profit from close contact with saprophytes and their externally secreted plant-polymer degrading enzymes (see Sect. 12.3). The original hypothesis that all insects fully rely on microorganisms for these purposes (Buchner 1965; Martin 1983) has been rejected, however, as recent studies reveal that many wood-boring beetles harbor plant-degrading and detoxifying enzyme within their genome (see Sect. 12.3). Therefore, even if some of these insects profit from a wood diet supplemented with fungi (see Sects. 12.3 and 12.4.1) and the fungi benefit from

Table 12.1 Overview of major obligate ectosymbioses between insects and fungi within dead wood

	Bark beetles (Scolytinae: Curculionidae)		Ambrosia beetles (Platypodinae and Scolytinae: Curculionidae)				Ship-timber beetles	Wood wasps	Moisture ants
Insect hosts	Ipini (e.g., *Ips*)	Tomicini (e.g., *Dendroctonus*, *Tomicus*)	Platypodinae (e.g., *Platypus*, *Austroplatypus*, *Crossotarsus*)	Corthylina (e.g., *Corthylus*, *Gnathotrichus*, *Monarthrum*)	Xyloterini (e.g., *Xyloterinus*, *Trypodendron*)	Xyleborini (e.g., *Xylosandrus*, *Xyleborus*, *Anisandrus*, *Xyleborinus*, *Ambrosiodomus*)	Lymexylidae (e.g., *Atractocerus*, *Elateroides*)	Xiphydriidae, Anaxyelidae, Siricidae	Formicinae (*Dendrolasius*, *Chthonolasius*)
Primary mutualistic fungi									
Ascomycetous taxa	*Ophiostoma*, *Grosmannia*, *Ceratocystiopsis*, *Ceratocystis*, *Endoconidiophora*[a]	*Ophiostoma*, *Grosmannia*, *Ceratocystiopsis*, *Ceratocystis*, *Ogataea*[a]	*Raffaelea*	*Meredithiella*, *Raffaelea*, *Ambrosiozima*	*Phialophoropsis*	*Ambrosiella*, *Raffaelea*, *Fusarium*	*Alloascoidea*	*Daldinia*, *Entonaema*	Undescribed Ascomycetes
Basidiomycetous taxa	*Entomocorticium*	*Entomocorticium*, *Phlebiopsis*	–	–	–	*Flavodon*	–	*Cerrena*, *Amylostereum*	
Age of symbiosis (Mya)[b]	?	?	90–110	40–58	32–51	17–25	?	?	25–44
Mode of feeding[c]									
Adults	Pm	Pm	M?	M?	M?	M	No food	No food	Omnivorous
Larvae	Pm	Pm	Xm	Xm	Xm	M, Xm[d]	Xm	Xm	Omnivorous
Type of fungiculture									
Mode of nesting	Phloem tunnels	Phloem tunnels	Xylem tunnels	Xylem tunnels	Xylem tunnels	Xylem (phloem) tunnels and chambers	Xylem (phloem) tunnels	Xylem tunnels	Carton nests
Mode of fungiculture[e]	Primitive	Primitive (Advanced)[f]	Advanced	Advanced	Advanced	Advanced	Primitive	Primitive	Primitive
Nutritional role of fungal mutualists[g]									
Nutrition (amino acids, sterols)	?	+	++	++	++	++	++	+	–
Fungus acquired enzymes[h]	?	?	?	?	?	+[d]	?	++	–
Detoxification of phenolics and terpenoids[g]									
Detoxification of tree defenses[i]	++	++	?	?	?	?	?	+	–

(continued)

Table 12.1 (continued)

	Bark beetles (Scolytinae: Curculionidae)		Ambrosia beetles (Platypodinae and Scolytinae: Curculionidae)				Ship-timber beetles	Wood wasps	Moisture ants
Protective role of fungal mutualists[g]									
Protection against other fungi[j]	?	?	?	?	?	+	?	?	?
Reinforcement of nest structure	–	–	–	–	–	–	–	–	++

Not displayed are six additional scolytine ambrosia beetle lineages that are hardly studied [Premnobiini, Hyorrhynchini, Bothrosternini, Scolytodes, Camptocerus, and Scolytoplatypodini; see Kirkendall et al. (2015)]

[a] It is unclear if all these taxa are obligate mutualists of the beetles

[b] Age of origin of fungiculture (Jordal and Cognato 2012; Jordal et al. 2011)

[c] Distinctions originating from the scolytine beetle literature [e.g., 20]: M (mycetophagy = eating fungal mycelium, fruiting bodies, or specific fungal structures), Pm (phloeomycethophagy = eating phloem and fungal biomass), Xm (xylomycetophagy = eating xylem and fungal biomass)

[d] Only in larvae of the genus *Xyleborinus* and probably *Xylosandrus* and *Ambrosiodomus* (De Fine Licht and Biedermann 2012; Biedermann 2012; Kasson et al. 2016)

[e] Primitive fungiculture is defined by only dispersal and seeding of fungi; advanced fungiculture additionally involves the active care of fungal crops (cf. Mueller et al. 2005)

[f] Possibly advanced fungiculture in some *Dendroctonus* spp.

[g] "++," very important role; "+," role present; "?" not investigated

[h] Digestion of recalcitrant plant polymers by fungus acquired enzymes that are active in the insect gut or fecal exudates (Kukor and Martin 1983; Martin 1979, 1992; De Fine Licht and Biedermann 2012; Thompson et al. 2014)

[i] Terpenoids, phenolics (Dowd 1992; Krokene 2015)

[j] Protection against antagonistic fungal competitors or pathogens, either by association with competitive fungal mutualists [e.g., *Flavodon ambrosius* with *Ambrosiodomus* spp. (Kasson et al. 2016)] or production of antibiotics by fungal mutualists (Florez et al. 2015; Nakashima et al. 1972)

dispersal (see Sect. 12.5), selection might not be strong enough to develop coadaptations for protecting and facilitating a mutualistic partnership (Martin 1992).

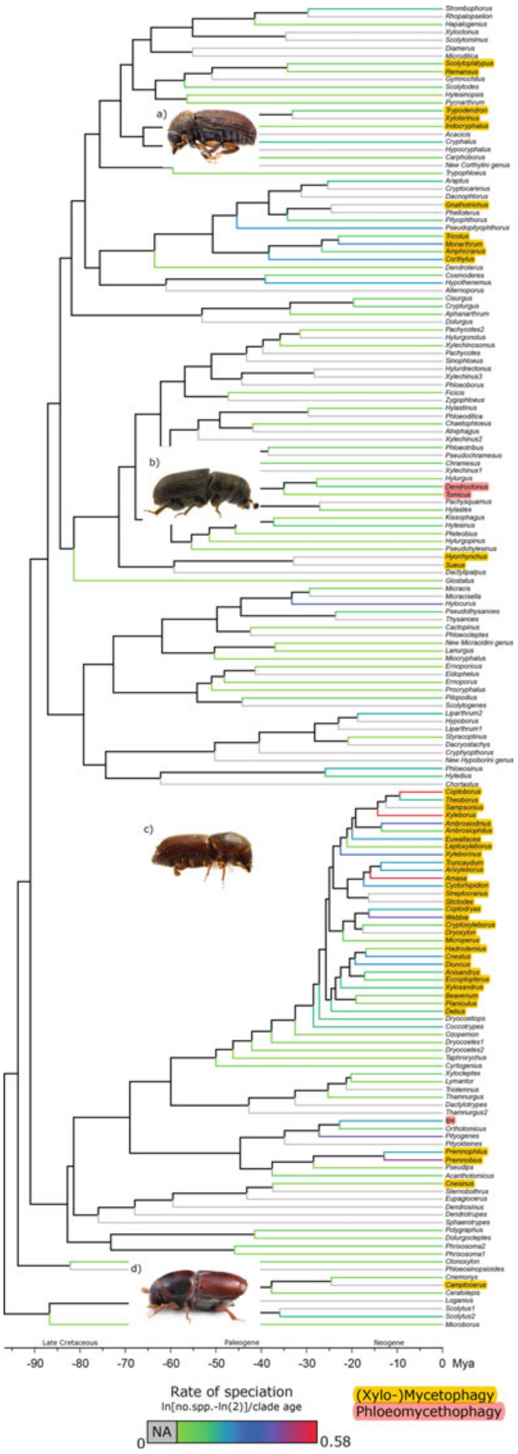
Partnering with another species involves costs of dependency. Therefore, the partnership can only be stable if fitness interests of partners are aligned and the association is protected against "cheaters" in either species that do not reciprocate benefits provided by the partner (Bourke 2011; Boucher et al. 1982; Doebeli and Knowlton 1998; Bronstein 2015). Maintaining close contact and reciprocation between species is often difficult in ephemeral habitats like dead wood, where species-specific interactions can easily be broken up by invasion of non-mutualistic fungi (conspecific "cheaters" or heterospecifics) (Biedermann and Rohlfs 2017). This is probably the reason why obligate insect-fungus mutualisms (see below) have only evolved in wood-boring insects that colonize living or recently dead wood. This habitat is free of other interfering fungi and so a partnership can be established reliably throughout the development period of the insects and be maintained over generations by vertical transmission of fungal spores between the insects.

12.6.3 Evolutionary Origin of the Obligate Mutualisms Between Insects and Ectosymbiotic Fungi

Four saproxylic insect groups have evolved obligate farming mutualisms with fungi: some bark and ambrosia beetles (Curculionidae; at least eleven independent origins, ~3500 species), ship-timber beetles (Lymexylidae; one independent origin, ~50 species), wood wasps (Xiphydriidae, Anaxyelidae, Siricidae; one independent origin, ~270 species), and termites (Macrotermitinae; one independent origin, ~330 species) (Table 12.1, Fig. 12.8). These mutualisms evolved between 17 and 110 million years ago during periods of global warming (Jordal and Cognato 2012; Farrell et al. 2001) and have resulted in adaptive radiations, especially in many lineages of the scolytine ambrosia beetles and in particular in the tropics (see Fig. 12.9) (Jordal et al. 2001; Hulcr and Stelinski 2017). Termites are the only one of the four lineages that originated in wood but adopted fungus farming after transitioning to other diets like dry grass or humus (Brune 2014). A fifth group of so-called moisture ants (Formicinae; one to two independent origins) uses fungi to build their "carton nests" in decayed wood (Schlick-Steiner et al. 2008).

The insect taxa involved in obligate farming mutualisms with fungi are usually among the first colonizers of freshly dead wood, which contains only a few microorganisms (e.g., plant endosymbionts) and high concentrations of plant-defensive terpenoids and phenolics (Six 2012; Beaver 1989; Krokene 2015). These insects bore tunnel systems within the xylem and inoculate the tunnel walls with vertically transmitted fungi that the female parents carry in mycetangia (Francke-Grosmann 1967). Mycetangia thereby secure transmission of the species-specific fungus (or fungi) from the natal nest to the new nest/gallery. While adult bark and ambrosia

Fig. 12.9 Phylogeny of wood-boring weevil (Scolytina, Curculionidae) genera with speciation rates (courtesy of Jostein Gohli). All the ambrosia beetle genera that feed either solely on fungus (mycetophagy) or on fungus-infested wood (xylomycethophagy) are highlighted in yellow. These genera are obligately dependent on fungi for nutrition, which they farm in tunnels within xylem. This habit evolved several times independently from a facultative dependence on fungi by phloem-feeding bark beetles. Such transitions to an obligate mutualism with fungi (phloeomycetophagy) are still found in some of the phloem-feeding bark beetle genera that are depicted in red. Non-highlighted genera are mostly phloem feeders, but it is likely that more dependencies on fungi will be discovered among them as many of these taxa are still unstudied. Pictures of species from four major clades are shown (a) *Cryphalus rubentis* Hopkins, (b) *Dendroctonus frontalis* Zimmermann, (c) *Xyleborus ferrugineus* (Fabricius), and (d) *Scolytus multistriatus* (Marsham) (photos by Jiri Hulcr and Andrew Johnson)



beetle tunnel in the wood themselves inoculate the fungus and lay eggs there, the other two wood-boring taxa only deposit eggs coated with fungal spores on (ship-timber beetles) or under (wood wasps) the bark and their larvae tunnel and inoculate the fungus themselves.

The fungi fulfill various functions for the different insect taxa (Table 12.1). For bark beetles and ambrosia beetles, they help in overcoming tree defenses and are of nutritional importance (Six 2012). Nutrition is the primary function of the fungus for macrotermites (Aanen et al. 2002) and probably also the major role of fungi for the understudied ship-timber beetles (Francke-Grosmann 1967). In all these three groups, this function is reflected by the mutualistic fungi forming so-called ambrosial growth, (thickened "conidia" or yeast-like growth in ambrosia and ship-timber beetles) or "nodules" (unripe mushrooms in macrotermites) which are usually only formed in the presence of the insects (Neger 1909; Francke-Grosmann 1967). The ambrosial growth can form thick layers on the walls of tunnels especially in ambrosia beetles (Fig. 12.8c). The fungi of both beetle groups evolved from phytopathogenic ophiostomatoid (Ascomycota) fungi (Harrington 2005). The symbiotic fungi of wood wasps, on the other hand, are originally basidiomycete wood degraders (some are still found free-living; Gilbertson 1984) that do not form thick ambrosial layers on tunnels and whose hyphae are apparently quite nutrient poor (Thompson et al. 2013). Instead they serve as an "external rumen" for the insects by excreting enzymes into the wood that digest lignocellulosic compounds, which are then ingested by the growing larvae (Thompson et al. 2014; Kukor and Martin 1983). Ancestors of the *Termitomyces* species of macrotermitines are basidiomycete saprobes, but although most species retained the ancestral condition of regular sexual reproduction (i.e., cultivars are horizontally spread from one termite nest to another via sexual spores produced by fruiting bodies growing on the external surfaces of mature nests), *Termitomyces* species have no known free-living populations existing entirely independent of the termite farmers (Mueller et al. 2005).

Two theories have been proposed for the evolutionary transitions from a purely plant-based diet to obligate fungus mutualisms (Mueller et al. 2005). (1) In the "transmission first" model, a fungus makes use of an insect as a vector and then begins to supply extra nutrients (sterols, amino acids) to increase insect reproduction, which directly benefits its dispersal. Insects coadapt by developing fungus-specific mycetangia and specialized farming behaviors until they finally rely on the fungus as a food source. (2) In the "consumption first" model, an insect supplements its plant diet with fungi and then begins to vector the fungus as it is nutritionally profitable. Later the fungus coadapts to the insect traits. Both models are equally tenable for all four insect groups. Given that wood-boring insects typically vector a lot of fungal spores (even ones specialized for wind dispersal; e.g., [Seibold et al. 2018-submitted; Jacobsen et al. 2017) (see Sect. 12.5)], the transmission first model may have occurred in the oldest associations between Platypodinae (*Raffaelea*) fungi and Scolytoplatypodini (*Ambrosiella*) fungi, for example. As these fungal lineages evolved to be nutritionally ideal for the beetles, they could have been acquired by the Xyleborini several million years later via the consumption first model (Table 12.1).

12.6.4 Evolutionary Consequences of Obligate Mutualism for the Insects and the Fungi

Mutualism with fungi allowed insects to flourish in freshly dead wood—a nitrogen-poor, carbon-rich, and highly toxic environment that is unsuitable for most organisms. The insects and fungi exchange transport and nutrition, so the most striking adaptations to this mutualism are the spore-carrying mycetangia of the insects and the highly nutritional ambrosial growth or increased enzyme production in the fungi. All three traits probably evolved relatively rapidly, which is indicated by their repeated independent origins in various fungal and insect lineages (Six 2012; Hulcr and Stelinski 2017). In the same genera of ambrosia beetles, for example, mycetangia can differ between sexes or occur in different body regions, which indicates rapid and independent origins and probably also losses due to parasitism by other fungi (Farrell et al. 2001). Ambrosial growth also evolved several times in unrelated lineages of fungi (Harrington 2005; Hulcr and Stelinski 2017).

Another consequence of the mutualism with fungi was the selection for social farming behaviors in some bark beetles and probably all ambrosia beetles (Kirkendall et al. 2015). Subsociality (i.e., both parents stay within the nest and care for their brood throughout their life, but there is no worker caste) is an ancestral trait for both Scolytinae and Platypodinae, so it had been present already before the origins of the mutualism with fungi (Jordal et al. 2011). Interestingly, during the evolution of the mutualism, many brood-tending behaviors apparently got modified to fungus-tending behaviors (Biedermann and Taborsky 2011). The resulting prolonged maintenance of fungus gardens due to parental care allowed multiple generations to develop within one nest (Kirkendall et al. 2015; Biedermann 2012). This was followed by evolution of division of labor between adults and their offspring in fungus-farming tasks like weeding, tending, and fertilizing ("advanced fungiculture"; Table 12.1), which apparently increased fungal yields further. This positive feedback between mutualism and social evolution (Biedermann and Rohlfs 2017) finally led to the emergence of eusociality (i.e., a society with a queen and workers in a caste system) in at least one ambrosia beetle and intermediate social structures like communal breeding and facultative eusociality in many others (Biedermann and Taborsky 2011). The eusocial ambrosia beetle colonizes living trees without killing them, which indicates that social evolution in these beetle-fungus mutualisms can only progress toward eusociality in very stable habitats (Kirkendall et al. 2015). Nevertheless, social behavior is not a requirement for obligate mutualisms to evolve. Larvae of ship-timber beetles and wood wasps live solitarily within their tunnels and lack active care of their fungal cultures ("primitive fungiculture"; Table 12.1). Termites evolved eusociality before fungus farming, but division of labor might have facilitated the evolution of fungus farming in this lineage (Mueller et al. 2005).

The consequences the mutualism has for the fungal partners are the least studied part of the relationship. Two changes are apparent: (1) Most fungal associates became asexual during the evolution of the mutualism with the insects (except termites). Sexuality is probably selected against by the insect because it may increase conflict within fungal cultures and break up advantageous coadaptations between insects and fungi (Mueller et al. 2005). (2) There has been a strong selection pressure on the fungi for being or providing “good food” for the insects, probably reflected by increased content of nitrogen, vitamins, amino acids, sterols, and lipids or by increased production of wood-degrading enzymes. Studies comparing nutrient content or enzyme production of mutualistic fungi with other wood-inhabiting fungi are lacking, but investigations of the *Termitomyces* fungi have shown that they are the most palatable and nutrient-rich fungi currently known (Mueller et al. 2005).

12.7 Indirect Interactions Between Insects and Fungi

Insect-fungus interactions can take many different forms, spanning from tight-knit mutualistic relationships, via specialized or opportunistic direct interactions, to a range of indirect interactions including modification of a common habitat. Indirect interactions go both ways: Fungi can improve habitat conditions for saproxylic insects in general by killing trees, by softening the wood and making it more accessible, or by emitting volatiles that insects use as semiochemicals. Likewise, insects can change the physicochemical properties of dead wood by their comminution and tunneling or through nitrogen enrichment, e.g., by N_2 fixing gut symbionts (Ulyshen 2015), thus improving the conditions for exploitation by fungi.

Several studies have documented that fungal community composition and the entire insect community—not only fungivores—often correlate in dead wood. Fungal fruiting bodies (e.g., of polypores) are known to shelter a variety of insects and arthropods. Kaila et al. (1994) investigated the beetle community in dead birches (*Betula* sp.) in Finland and found that distinct beetle assemblages seemed to be associated with different polypore species. Similarly, Abrahamsson et al. (2008) found that the root-rot fungi *Heterobasidion* spp. affected the assemblage of saproxylic beetles in high stumps of Norway spruce (*Picea abies* (L.) H. Karst.), probably by disfavoring certain beetle species. Jonsell et al. (2005) found that occurrence of *Fomitopsis pinicola* or *Trichaptum abietinum* had a stronger influence on species composition of saproxylic beetles in high stumps of spruce (*P. abies*) than important characteristics of dead wood such as diameter, height, or bark cover. Several other studies have also found similar correlations between the species composition of fungi and insects in dead wood (Gibb et al. 2006; Johansson et al. 2007; Persiani et al. 2010; Jacobs and Work 2012), without identifying the underlying cause. These correlations could be due to a number of direct and/or indirect effects of both the insects and the fungi.

12.7.1 Fungi Change Wood Characteristics Relevant for the Non-fungivorous Insect Community

Fungi create habitats also for saproxylic insects that are not fungivorous. For instance, many saprotrophic fungi can colonize living trees as parasites and directly cause or at least expedite tree death (Boddy 2001), thus creating habitats for the entire community of saproxylic beetles.

The presence of fungi and the related abundance of fungivores will also affect the abundance of saproxylic predatory insects, which in turn may affect the entire insect community within dead wood. According to Persiani et al. (2010), predatory beetles, together with necrotrophic fungal parasites, may control the structure and dynamics of fungal and beetle communities in dead wood through top-down mechanisms. However, the previously mentioned fact that fungi can move nutrients into the wood (Sect. 12.3) and thus affect the cohabiting insect communities might cascade all the way up the food web to the predators in decaying wood.

The structural breakdown by fungi favors carpenter ants (*Camponotus* sp.), which excavate the wood for nesting facilities (Chen et al. 2002; Hansen and Akre 1985; Birkemoe 2002). The combined effect of structural breakdown and nutrition may also affect the development time of insect larval stage. For instance, in the case of the deathwatch beetle *Xestobium rufovillosum*, larval development is faster in wood already decayed by fungi (Fisher 1940, 1941), but the mechanism behind this effect is unknown.

Non-fungivorous insects also profit due to the breakdown of the physical cellular structure of wood and the detoxification of phenolics and terpenoids. One example is the creation of cavity-bearing trees (Fig. 12.10). The activity of heart-rot fungi, specialized in decaying the dead heartwood of mature living trees, is the first step in the creation of cavities in living or dead trees. The breakdown of polymers makes the heartwood softer and facilitates further excavations by insects or woodpeckers (Jusino et al. 2016). The nests of woodpeckers may later be inhabited by other birds or insects, and the frass, feces, and dead animals that build up in the cavity are turned into a nutrient-rich “wood mold,” which is an important habitat for a diverse community of saproxylic insects (Sverdrup-Thygeson et al. 2010; Ranius and Jansson 2000). Cavity-bearing trees often contain a high proportion of endangered saproxylic species, as a large number of insects are specialized to these rare microhabitats (Siitonen and Ranius 2015; Micó 2018; see Chap. 21). In warmer areas, like tropical forest or savanna woodland, termites are the key agents creating cavities in trees (N’Dri et al. 2011; Werner and Prior 2007).

Other indirect effects can include chemical communication and orientation in insects. Ethanol from fermentation of sugar-rich sap can function as an orientational cue for insects during the colonization of recently dead trees (Stokland et al. 2012; Allison et al. 2004; Beaver 1989). Also, several volatiles of fungal origin have been found to be specific to wood infected by certain fungi. These may act as potential semiochemicals for wood-inhabiting insects and may mediate specific interactions between fungi and insects (Leather et al. 2014).

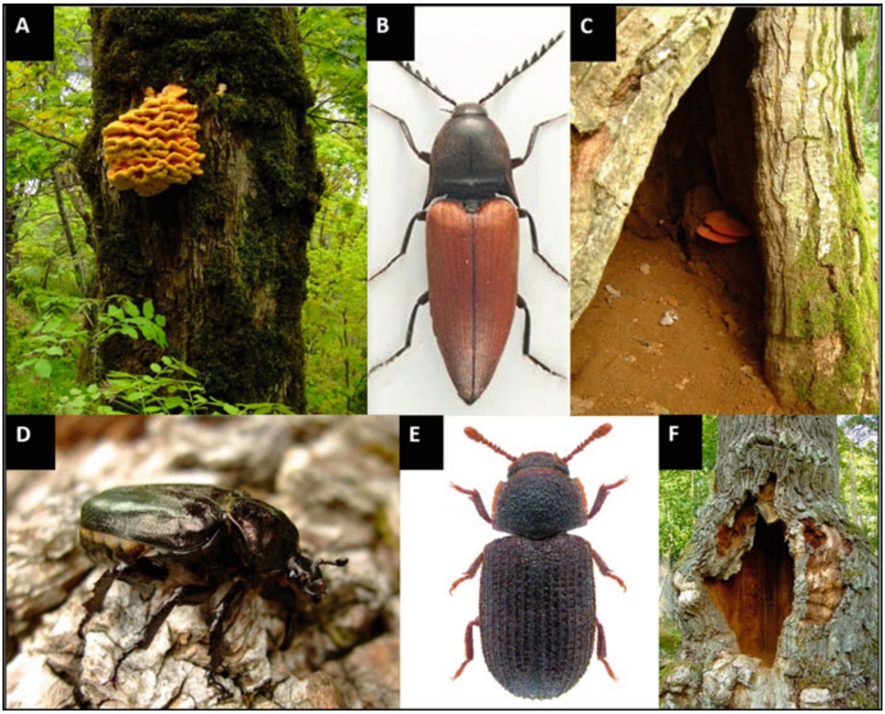


Fig. 12.10 Interactions between fungi and insects are important in creating the species-rich and endangered communities in tree cavities. (**a**) Old oak with fruiting body of chicken-of-the-woods, *Laetiporus sulphureus* (Bull.) Murrill, a brown heart-rot polypore in hardwoods and an important agent in softening the interior of the tree. Photo: Anne Sverdrup-Thygeson. (**b**) The beetle *Ampedus hjorti* (Rye) listed as Vulnerable on the IUCN Red List of threatened species. The species develops in wood mold in cavities in trunks and stumps of old oaks (*Quercus* spp.) in Europe. Photo Arnstein Staverløkk, Norsk institutt for naturforskning, CC BY 3.0. (**c**) Old oak with fruiting body of the beefsteak fungus, *Fistulina hepatica* (Schaeff.) With., a fungus found in many parts of the world. The species also causes brown heart rot and facilitates the colonization of the interior of, e.g., old oaks by a range of insects. Photo: Anne Sverdrup-Thygeson. (**d**) The hermit beetle, *Osmoderma eremita*, a large scarab entirely dependent upon veteran trees as it inhabits decaying heartwood, listed as Near Threatened on the IUCN Red List of threatened species. Photo: Anne Sverdrup-Thygeson. (**e**) *Eledona agricola* (Herbst), an uncommon tenebrionid beetle living in fruiting bodies of *L. sulphureus* in Europe. Photo: Udo Schmidt (CC BY-SA 2.0). (**f**) Old oak with a large opening into a cavity filled with nutritious wood mold. Photo: Anne Sverdrup-Thygeson

12.7.2 Insects Change Wood Characteristics Relevant for Fungal Community

Saproxylic insects can act as ecosystem engineers and modify the physical properties of the wood through their boring and tunneling activities. Wood often has a low surface area to volume ratio relative to other plant material, and the inaccessibility of the inner parts of a log may limit the availability of nutrients required by the fungal community (Cornwell et al. 2009). Through fragmentation and comminution of dead wood, insects reduce the particle size and increase the surface to volume ratio. This makes the woody tissue more susceptible to enzymatic activity (Walker and Wilson 1991). At the same time, smaller particles are more favorable for yeasts and bacteria than for filamentous fungi (Boddy and Jones 2008). Tunneling by wood-boring insects can increase access for fungi to the interior of the wood and improve aeration, which can result in greatly increased rates of decomposition (Dighton 2003).

By consuming the cambium, subcortical early-successional insects remove the layer that attaches the bark to the woody surface, and the bark will be more prone to falling off. This type of insect-mediated ecosystem engineering has been demonstrated for both Norway spruce (*P. abies*) (Weslien et al. 2011) and aspen (*Populus tremula* L.) dead wood systems (Jacobsen et al. 2015), with variable effects on the fungal community. Bark loss exposes the woody surface to wind-dispersed spores, which may increase the chances of fungal colonization. At the same time, removal of bark also leaves the wood exposed to sun and wind, which will reduce the moisture content in the wood (Ulyshen et al. 2016). These effects will therefore facilitate some species while inhibiting others and might shift competitive relationships within the fungal community.

Insects may also change the nutrient content of wood through their relationship with nitrogen-fixing bacteria. Evidence for nitrogen fixation in the gut has been found in several groups of insects, like termites, bark beetles of the genus *Dendroctonus*, the scarabs *Osmoderma eremita* Scop. and *Cetonia aurataeformis* Curti, the stag beetle *Dorcus rectus* (Motschulsky), and finally, in the guts of a wood-eating cockroach, *Cryptocercus punctulatus* Scudder [for references, see Ulyshen (2015)]. How this affects fungal communities in dead wood is not known in detail, but it has been shown that the addition of larval frass from the cerambycid *Monochamus scutellatus scutellatus* (Say) to mineral soils led to a significant increase in microbial activity (Cobb et al. 2010).

12.8 Concluding Remarks

12.8.1 Evolution and Adaptations

Adaptations to insect-fungus interactions are best known from the mutualisms between, for instance, bark beetles and fungi. There are competing theories as to how these mutualistic interactions evolved, but the main driving forces were probably dispersal of propagules for the fungi and nutritional benefits for the beetles. Fitness benefits from the interaction led to the evolution of adaptations such as pockets for transferring fungi (“mycetangia”) in insect exoskeletons and increased nutrient content in the fungi. The mutualism eventually became obligate as the fungi turned asexual and the beetle mycetangia developed toward high selectivity. Fungus farming has also been a driver for the evolution of eusociality in ambrosia beetles.

Adaptations to non-mutualistic insect-fungus interactions are far less studied. Potential adaptations have been documented, such as thick spore walls allowing passage through insect guts, mycetangia-like structures in insect exoskeletons, and fungal propagule structures that may increase chances of insect-vectored dispersal (reticuloperidia, spikes, or hooks on spores). However, further studies are required to verify the function of these structures.

Possible fungal adaptations to invertebrate grazing include physical or chemical defenses, changes in morphology (e.g., yeast-like growth), translocation of nitrogen to ungrazed mycelium, and compensatory growth. Fungi produce an almost endless diversity of organic compounds not required for growth and metabolism. Some of these secondary metabolites are highly toxic to animals and likely function as defense also against invertebrates. *Aspergillus* fungi have recently been demonstrated to respond to grazing by Collembola and fruit flies with an induced chemical defense. However, adaptations to grazing remain largely unstudied for fungi in dead wood.

Insect adaptations to fungal feeding might include behavioral attraction to fungal volatiles from polypores and collective feeding to overcome fungal toxin production, as demonstrated for collembolans. So far, physiological adaptations to fungivory in insects remain unstudied. Most remarkably, the close interactions between insect and fungi in dead wood may lead to horizontal transmission of fungal-derived genes for detoxification and degradation of wood, like those recently discovered in the genomes of certain wood-feeding beetles.

12.8.2 Specialization and Biodiversity

The insect-fungus interactions in dead wood range from highly specialized obligate mutualisms to opportunistic fungivory. For instance, whereas ambrosia and ship-timber beetles are dependent on their fungal mutualists as nutrition for their larvae, longhorn beetles and wood-feeding termites can benefit from fungi in their larval substrate but can also develop successfully in substrate without fungi.

Specialization of insect-fungus interactions in dead wood has recently been explored in two network studies. In the first study, where the insects were sampled or reared from polypore fruiting bodies, the degree of specialization was similar to that of pollinator-plant networks. In the second study, where wood-decay fungi was based on DNA isolated from insects sampled at fresh dead wood, specialization was lower and comparable to animal-mediated seed dispersal networks. Thus, networks in the first study might be dominated by specialized species with larval development in polypore fruiting bodies, while networks in the latter study might reflect spore feeding and subsequent dispersal.

Many of the same host characteristics that influence species richness in herbivore-plant and parasitoid-host systems are important for beetle communities in polypores;

abundant, large fruiting bodies with diverse growth forms host the highest species numbers. Thus, fungal species with these characteristics are particularly important for insect biodiversity in dead wood. Fungi might also contribute to insect diversity by indirect interactions. For instance, heart-rot fungi contribute to the creation of tree cavities, which are associated with a particularly diverse community of saproxylic insects. The importance of fungal species for species richness of hyphal grazers is practically unknown.

Insect grazing might potentially increase species richness of fungi by facilitating coexistence of inferior and superior fungal competitors. This mechanism has been demonstrated in the soil system. The effect of insect-vectored spore dispersal on species richness of fungi is unknown but might result in significant priority effects for the vectored fungi. On a larger scale, this effect might represent an additional element of stochasticity in dead wood colonization, which could contribute to the high beta diversity between dead wood objects and thus the high biodiversity in forest ecosystems.

12.8.3 Nutrient Flow and Decomposition

Fungi break down complex plant polymers and transport essential elements from the surroundings to the wood. Fungivores, and subsequently their predators, assimilate these nutrients. To what extent wood feeders get their nutrients directly from the wood or whether fungi (or bacteria) are involved through endosymbiosis or enzymatic digestion is a matter of great interest. Recent research suggests that many wood feeders do depend on fungi (and bacteria) to gain enough nutrients during the larval stage, although some beetles are capable of producing their own wood degradation enzymes.

Community composition of fungi can have significant effects on dead wood decomposition rates. As insects may affect fungal community composition through dispersal of propagules or grazing, they may indirectly affect decomposition rates. These causal relationships have been demonstrated in soil ecosystems but remain to be tested in dead wood. Insects dispersing fungal propagules, especially in early succession, might have particularly strong effects on the fungal community, as several studies have found that assembly history has strong influence on fungal community composition and rate of decomposition. Experimentally excluding insects from fresh dead wood significantly affects the fungal community and decomposition (Jacobsen et al. 2018b-Submitted), and at least part of this effect is likely to stem from the absence of insect-vectored fungi.

To conclude, insect-fungus interactions in dead wood are highly diverse and form an essential component of forest ecosystems. It is likely that there are hitherto unknown evolutionary adaptations to these interactions among both insects and fungi. At present, our knowledge of insect-fungus interactions is highly fragmented, but novel methodology such as DNA analysis presents new research opportunities that are already producing interesting results. Increased knowledge of insect-fungus interactions during decomposition of dead wood is necessary in order to conserve the diversity of species and functions involved in this ancient and essential process.

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Chapter 13

Nutrient Dynamics in Decomposing Dead Wood in the Context of Wood Eater Requirements: The Ecological Stoichiometry of Saproxylophagous Insects

Michał Filipiak

Abstract Dead wood is rich in sugars and can serve as an energy source when digested, but it lacks other nutrients, preventing the growth, development, and maturation of saproxylophages (saproxylic organisms that consume dead wood at any stage of decomposition). Split into atoms, sugars only serve as a source of carbon, hydrogen, and oxygen, thereby providing insufficient nutrition for saproxylophages and for their digestive tract symbionts, despite the ability of certain symbionts to assimilate nitrogen directly from the air. Ecological stoichiometry framework was applied to understand how nutritional scarcity shapes saproxylophage-dead wood interactions. Dead wood is 1–3 orders of magnitude inadequate in biologically essential elements (N, P, K, Na, Mg, Zn, and Cu), compared to requirements of its consumers, preventing the production of necessary organic compounds, thus limiting saproxylophages' growth, development, and maintenance. However, the wood is nutritionally unstable. During decomposition, concentrations of the biologically essential elements increase promoting saproxylophage development. Three mechanisms contribute to the nutrient dynamics in dead wood: (1) C loss, which increases the concentration of other essential elements, (2) N fixation by prokaryotes, and (3) fungal transport of outside nutrients. Prokaryotic N fixation partially mitigates the limitations on saproxylophages by the scarcity of N, often the most limiting nutrient, but co-limitation by seven elements (N, P, K, Na, Mg, Zn, and Cu) may occur. Fungal transport can shape nutrient dynamics early in wood decay, rearranging extremely scarce nutritional composition of dead wood environment during its initial stage of decomposition and assisting saproxylophage growth and development. This transport considerably alters the relative and total amounts of non-C elements, mitigating also nutritional constraints experienced by saproxylophages inhabiting such nutritionally enriched wood during

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later stages of decomposition. Additionally, C losses during later decomposition stages may further change non-C element concentrations beyond fungal enrichment. More detailed studies of the short-term nutrient dynamics in dead wood relative to the nutritional requirements of saproxylophages are needed to understand decomposition process and nutrient cycling in ecosystems. These studies should include a wide array of elements that may be limiting for saproxylophages (e.g., P, Na, K, Mg, Zn, and Cu in addition to commonly studied N). Studies on nutrient dynamics in dead wood should discuss obtained data in the context of nutritional needs of saproxylophages. To allow for this, data on multielemental ecological stoichiometry of saproxylophages of various taxa, inhabiting different wood species in various geographical locations, are needed.

13.1 Background: Nutritional Scarcity in Dead Wood and Why It Matters

Wood is composed of approximately 90–99% cellulose, hemicelluloses, and lignin (Parkin 1940; Pettersen 1984) and consists of 50% C, 44% O, and 6% H as well as trace amounts of other elements (Pettersen 1984). In temperate zones, elements other than C, H, O, N, and S may comprise approximately 0.1–0.6% of wood, but tropical wood may be more nutritious, containing up to 5% ash (Ragland et al. 1991; Pettersen 1984). Additionally, wood may consist of approximately 0.08–0.2% of N (Meerts 2002) and 0.003–0.03% of P (Pettersen 1984; Meerts 2002), which are extremely low concentrations that are insufficient for insects and other arthropods (they have one- to threefold higher N and P concentrations in their bodies (Fagan et al. 2002; Schneider et al. 2010; Filipiak and Weiner 2014; Filipiak 2016); see Sterner and Elser (2002) and Elser et al. (2000a, b) for discussions on how such nutritional imbalances may limit organisms and influence ecosystems). In dead wood, *C:N* and *C:P* ratios may be as high as 6500/7500 and 54,500/150,000 (dry mass ratio/molar ratio), respectively, which indicates severe nutritional scarcity for potential consumers (Filipiak and Weiner 2014; Filipiak et al. 2016). Therefore, the chemical composition of dead wood differs from that of other plant tissues because it is extraordinarily rich in C, H, and O atoms but scarce in other elements and thus extremely nutritionally unbalanced for its potential consumers. In this context, the growth and development of dead wood-eating beetles may be co-limited by the scarcity of non-sugar nutrients in dead wood, including essential bioelements such as N, P, K, Na, Mg, Zn, and Cu (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016). The limitations imposed by differences between nutritional demand (the nutritional needs of growing organisms) and supply (the availability of the nutrients required in an environment) can determine the fitness of an organism and may influence its ecological interactions (Haack and Slansky 1987; Sterner and Elser 2002; Pokarzhevskii et al. 2003; Cherif 2012; Kaspari and Powers 2016). A mismatch between the nutritional composition of food and the requirements of a consumer can limit the growth and development of the consumer even when potential foods are available in excess (Haack and Slansky 1987; Sterner and Elser 2002), which raises the following question: How do wood-eating insects obtain the nutrients required for growth and development?

The nutritional scarcity of dead wood may cause supplementary carnivory, which is observed among saproxylophages (Stokland et al. 2012), and cannibalism is a special kind of predation exhibited by some of saproxylic species. For example, larvae of the large wood-boring beetle genus *Monochamus* are highly carnivorous and will rapidly devour each other (Soper and Olson 1963), and these insects also feed on bark beetles they encounter within dead wood (Dodds et al. 2001). Furthermore, Thorne and Kimsey (1983) observed *Nasutitermes* termites feeding on a dead boa constrictor, a three-toed sloth, and a turtle, and in all cases, the termites had constructed carton foraging galleries over portions of the remains, beneath which feeding took place. Interestingly, carrion feeding was observed only during the dry season, when the demand for nutrients is highest due to the production of thousands of winged and reproductive adults. Termites are also known to feed on dead insect larvae and other corpses encountered while foraging in wood (Thorne and Kimsey 1983, and examples therein), which most notably includes cannibalizing dead (and in some cases living) nestmates, a behavior that is apparently exhibited by all termites (Wilson 1971). Apart from these examples, there are a number of saproxylophagous insects that apparently feed exclusively on dead wood and are able to survive and thrive on this low-quality food source (Wallace 1953; Hanula 1996; Grove 2002; Nadeau et al. 2015; Ulyshen 2016). How is this possible?

The activity of digestive tract symbionts is known to play a role in balancing the diet of insects that utilize suboptimal plant resources as their food (Ljungdahl and Eriksson 1985; Martin et al. 1991; Dillon and Dillon 2004; Douglas 2009), and in this context, xylophagous insects are believed to survive and thrive utilizing polysaccharides as either a direct food source or as a resource for their digestive tract symbionts (Mansour 1934; Parkin 1940; Martin 1983; Watanabe and Tokuda 2010). However, according to the law of the conservation of mass, this is insufficient because the constituent atoms of nutrients cannot be created by organisms from the available biomass. Therefore, the elemental composition of wood limits the available nutrients, although symbionts are able to increase the digestibility of woody matter and synthesize important organic compounds from nutrients furnished by dead wood (Ljungdahl and Eriksson 1985; Martin et al. 1991; Douglas 2009). Indeed, it has been suggested that the ability to feed on cellulose is rarely advantageous for insects (Martin et al. 1991). Polysaccharides and lignin, even when split into atoms, are a source of only three chemical elements (C, H, and O). This is not enough to enable the growth, development, and functioning of a living organism. Even considering the ability of symbionts to directly assimilate the fourth essential element (N) from the atmosphere, this is still not enough, since a source of other micronutrients is required to synthesize physiologically essential organic molecules (e.g., RNA, metalloproteins, enzymes, structural proteins, phospholipids, nucleotides, and vitamins). Therefore, wood alone may not be an appropriate food source for many saproxylic insects, even considering the activity of their digestive tract symbionts.

As reviewed by Swift and Boddy (1984), the colonization of dead wood by most arthropods requires, or is at least strongly favored by, prior microbial conditioning. Even species in close symbiotic relationships with microbes capable of breaking down wood often prefer wood that is already infested by fungi and other microorganisms (Kovoor 1964; Gentry and Whitford 1982). For example, Becker (1965) found that termites in dry wood consume approximately twice as much wood decayed by brown rot fungi as nondecayed wood, and after 18 months, colonies feeding on decayed wood were approximately five times larger than their counterparts in nondecayed wood. Research by Smythe et al. (1971) found the subterranean termite *Reticulitermes flavipes* (Kol.) to exhibit a similar preference for decayed wood, and Hendee (Hendee 1935) found *Zootermopsis* termites feeding on pine wood containing fungi to be healthier than those feeding on uninfested wood. According to Swift and Boddy (1984), there are four primary ways by which microbial activity may favor colonization and feeding by wood-dwelling arthropods: (1) production of attractant substances, (2) softening of wood through enzymatic activity, (3) destruction of allelopathic substances against wood-dwelling arthropods, and (4) improving the nutritional quality of the resource. Indeed, dead wood is not nutritionally stable, and microbial activity is responsible for the nutritional enrichment of dead wood (Filipiak et al. 2016). Nutritionally scarce dead wood may be highly enriched in nutrients during the first few years of decomposition, allowing saproxylophages to meet their nutritional needs (Filipiak and Weiner 2014; Filipiak et al. 2016). It has been suggested that dynamic changes in the nutritional composition of dead wood occur during the larval development of saproxylic beetles that promote their growth, development, and maturation (Filipiak and Weiner 2017a). These changes may be caused by decomposing fungi (Filipiak et al. 2016) and protists (Fukasawa et al. 2017).

As wood decomposes, it is colonized by a succession of microorganisms and saproxylic insects (Grove 2002), the majority of which are represented by three groups: beetles (Coleoptera), midges and flies (Diptera), and termites and cockroaches (Blattodea) (Hanula 1996; Grove 2002; Stokland et al. 2012) with beetles being among the first colonists of dead wood (Nadeau et al. 2015). Saproxylophages are also represented by butterflies (Lepidoptera), true bugs (Heteroptera), and hymenopterans (Hanula 1996; Stokland et al. 2012; Seibold et al. 2014). From these, beetles and termites have been studied most (see literature reviews by Grove 2002; Ulyshen 2016; Nadeau et al. 2015; Hanula 1996). To date, few data have been published on the nutrient dynamics of decaying wood associated with the nutritional needs of saproxylophages, and only three species of insects (beetles) have served as model organisms: *Stictoleptura rubra* (L.), *Arhopalus rusticus* (L.) (Coleoptera, Cerambycidae) and *Chalcophora mariana* (L.) (Coleoptera, Buprestidae) (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016).

This chapter will be presented within the framework of ecological stoichiometry (or biological stoichiometry), i.e., the study of the balance of energy and multiple chemical elements in ecological interactions (Sterner and Elser 2002; Filipiak and Weiner 2017b; Cherif et al. 2017). Ecological stoichiometry considers how the chemical composition of organisms differs from that of their food and the consequences of these differences for growth and development (Fraústo da Silva and Williams 2001; Sterner and Elser 2002). This concerns the organic chemistry of life but, in particular, the chemical elements that are the basic building blocks of all living matter from bacteria to wales. It is impossible to understand the nutritional constraints on the growth and development of individual organisms, colonies, and populations without considering these elements (see Cherif et al. 2017 for a discussion on how ecological stoichiometry may improve this understanding). Despite their diversity and complexity, all molecules, cells, tissues, organisms, and populations are composed of the atoms of approximately 25 elements and are maintained through the use of energy (Fraústo da Silva and Williams 2001; Sterner and Elser 2002; Kaspari and Powers 2016). Moreover, all are composed of specific sets of atoms selected from the environment in proportions required to create the organic molecules that form the bodies of organisms, which are built according to specific "elemental recipes" and thus must maintain "elemental" or "stoichiometric" homeostasis. Therefore, the active regulation of elemental body stoichiometry (proportions of atoms) is an essential trait of all organisms (Sterner and Elser 2002; Jeyasingh et al. 2017). In this context, the law of the conservation of mass predicts that the atoms of the approximately 25 elements composing all living things cannot be created from nothing. During growth and development, organisms achieve not only their final adult shape but also the size, condition, and fertility necessary for reproductive success. Adult bodies are fully formed, so their functionality is primarily limited by energy levels and, to a lesser degree, the availability of specific organic compounds (e.g., fatty acids and amino acids) and physiologically important ions such as K, Na, Mg, and Ca (Slansky and Rodriguez 1987; Cohen 2003). However, the ability to form a fully functional adult body may depend on the availability of body-building nutrients during the juvenile growth stages (Slansky and Rodriguez 1987; Sterner and Elser 2002). Thus, the growth and development of an organism may be compromised when food sources are nutrient limited, so adult fitness may be affected when deficiencies occur during the juvenile stage. Herbivores and detritivores rely on diets that are rich in energy but scarce in the components used for development and maintenance (e.g., metalloproteins, phospholipids, and amino acids, i.e., molecules rich in N, P, S, and metals), so the development and growth of these organisms may be limited by food quality, which is defined by the availability of (1) the nutrients required for growth and development and (2) the energy needed to fuel the biochemical processes contributing to growth and development as well as movement and foraging or, more simply, any action undertaken by an organism (Sterner and Hessen 1994; Sterner and Elser 2002; Pokarzhevskii et al. 2003; Cherif 2012; Kaspari and Powers 2016). Accordingly, saproxylophages (organisms that consume dead wood at any stage of decomposition) experience extremely severe nutritional limitations because their food (dead wood) almost exclusively consists of polysaccharides and lignin and therefore lacks other nutrients (Filipiak and Weiner 2014, 2017a). Sterner and Elser (2002) comprehensively discussed the nutritional needs of organisms relative to *C:N:P* stoichiometry, and more than these three extensively studied elements are needed to form the cells and bodies of organisms (Fraústo da Silva and Williams 2001; Kaspari and Powers 2016). The multielemental stoichiometry of saproxylophages, dead wood, and the fungi inhabiting the wood are considered in this chapter.

13.2 Nitrogen Fixation in Dead Wood and Saproxylophage Nutrition

Much attention has been given to the limiting effect of N scarcity on saproxylophages and the mechanisms underlying N dynamics in decomposing dead wood (e.g., Cowling and Merrill 1966; Swift et al. 1979; Roskoski 1980; Higashi et al. 1992; Varm et al. 1994; Vega and Blackwell 2005; Douglas 2009; Ulyshen 2015, 2016; Johnston et al. 2016). Herbivores and detritivores generally face N scarcity, which influences their fitness, consumer-driven nutrient cycling, and the fate of primary production in ecosystems (Elser et al. 2000b; Fagan et al. 2002; Sterner and Elser 2002; Martinson et al. 2008; Evans-White and Halvorson 2017). Dead wood is especially N scarce, but N may be utilized from external sources (Roskoski 1980; Douglas 2009; Ulyshen 2015). Two major mechanisms contributing to the N enrichment of wood have been suggested: transport in fungal hyphae and fixation from the air (Stenlid et al. 2008; Ulyshen 2015, 2016). The role of the transport of N, as well as other nutritional elements, by fungi will be discussed in further detail since such transport seems to be an important factor for mitigating the general nutritional scarcity (of all nutrients and not just N) of dead wood (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016). Therefore, I would like to briefly discuss only N fixation in this subsection. There are two types of N-fixing organisms that may mitigate N scarcity in the dead wood consumed by saproxylophages: (1) organisms that inhabit the wood and may therefore directly enrich the dead wood environment (e.g., Ulyshen 2015; Roskoski 1980; Spano et al. 1982) and (2) organisms that inhabit the digestive tracts of saproxylophages and may therefore mitigate the N scarcity experienced by saproxylophages regardless of that in the external dead wood environment (e.g., Ulyshen 2015; Douglas 2009). Both types of N-fixing organisms may play different roles in mitigating N scarcity for saproxylophages, and I will first focus on the first type (1) of organisms. Mycorrhizal fungi and N-fixing bacteria deliver up to 80% of all the N acquired by plants in temperate and boreal forests (Baldrian 2017), and half of the bacterial isolates from living trees may be able to fix atmospheric N (Aho 1974). Similarly, N fixation by bacteria and translocation of N by mycelial networks during decomposition increase the N content in dead wood with approximately 2 kg N-fixed ha^{-1} per year, which is an important contribution to the N cycling in the whole ecosystem (Stenlid et al. 2008; Baldrian 2017). A recent study (Rinne et al. 2017) showed the major role of N fixation in increasing the N content of dead wood during the late stage of decay in a Norway spruce-dominated forest; it accounted for 60% of the total N accumulation in the most decayed of the studied wood. It is known that N-fixing organisms play an important role in N cycling in ecosystems, and the amounts of N that they fix have been estimated (Roskoski 1980; Spano et al. 1982; Ulyshen 2015; Baldrian 2017; Rinne et al. 2017). However, this knowledge is taken out of context, since it was not related to the nutritional needs of saproxylophages, and the degree to which the amount of N fixed by microorganisms contributes to balancing the diet of saproxylophages is not known. Therefore, despite knowing that bacteria may fix 1–2 kg N ha^{-1} per year and that these amounts are comparable to inputs from precipitation and dry deposition (2–3 kg N ha^{-1} per year) (Ulyshen 2015), what these amounts mean for the nutritional needs of growing and developing saproxylophages is not understood. Future studies should take qualitative data on the N dynamics in dead wood into account since the quality of food may affect the growth, development, life histories, and fitness of consumers regardless of quantity (Sterner and Hessen 1994; Pokarzhevskii et al. 2003; Kaspari and Powers 2016; Filipiak and Weiner 2017b). The contribution of N-fixing bacteria to the N dynamics in dead wood has been shown to be temperature dependent and may therefore vary with geographical region (Rinne et al. 2017), which should be considered in future studies. Considering the other type (2) of organisms, the microbial symbionts in arthropod guts have been proposed as important vectors contributing to the growth of their hosts as well as to nutrient cycling in ecosystems, with N fixation rates of 10–40 kg ha^{-1} per year (ten times more than that of type 1 organisms) (Nardi et al. 2002). There is no doubt that N-fixing symbiotic microbes contribute to the supplementation of termite diets with N. Additionally, there is some scarce and nonconclusive evidence of similar diet supplementation mechanisms in wood-boring beetles (Higashi et al. 1992; Nardi et al. 2002; Kneip et al. 2007; Ulyshen 2015). Microbial N fixation may account for >60% of the N in the colonies of the termite *Neotermes koshunensis* (Shiraki) (Täyasu et al. 1994), but it is worth noting that there are species of saproxylophagous insects that naturally lack N-fixing gut symbionts (e.g., *Hylotrupes bajulus* (L.), Cerambycidae) as well as insects that contain such symbionts but whose use of the provided N has been impossible to prove (Bridges 1981). Douglas (2009) stated that the nutritional significance of microbial N fixation for insects is uncertain because the product of N fixation by bacteria is ammonia, which is potentially toxic to insects but may be metabolizable by animals to a small degree. Since most insects lack the ability to assimilate ammonia, they must rely on sources of high-quality N compounds (e.g., fungal hyphae) even if they live in symbiosis with N-fixing microorganisms (Vinet and Zhedanov 2010). In their review, Crotti et al. (2010) stated that there has, to date, been no clear demonstration of the function of the gut bacteria in ants feeding on N-scarce diets. However, ants have been shown to utilize different types of N-fixing organisms (other than N-fixing bacteria) and may rely on N fixed from the air by ant-cultivated fungi (Pinto-Tomás et al. 2009). Nardi et al. (2002) noted that the range of arthropod taxa that harbor N-fixing symbionts is not known and that only a limited number of reports have confirmed utilization of fixed N by the few insect taxa known to have these symbionts in their guts. It is possible that newly emerging symbionts of insects relying on sugar-based diets, i.e., acetic acid bacteria, could contribute to insect N metabolism or recycling, but this issue requires further investigation (Crotti et al. 2010). Symbiotic interactions between saproxylophagous insects and microorganisms are known in the vast majority of termites and cockroaches, but there are limited data on the contribution of N-fixing organisms to balancing the diets of Coleoptera and Hymenoptera (e.g., Vinet and Zhedanov 2010; Kneip et al. 2007; Lilburn et al. 2001; Ulyshen 2015). Furthermore, the available knowledge has been obtained using termites as model arthropods (Nardi et al. 2002; Dillon and Dillon 2004). In a literature review on insect-mediated N dynamics in decomposing wood, Ulyshen (2015) presented evidence of N fixation in insects that included data on 66 taxa of wood-feeding insects, including both saproxylophages and those in living wood, from 51 publications. Of the 66 taxa considered, 55 (83.3%) were termites; 10 (15.2%) were beetles, and 1 taxon (1.5%) was a wasp. Similarly, of the 51 publications reviewed, 42 (82.3%) concerned termites, 8 (15.7%) concerned beetles, and 1 (2%) concerned a wasp. Considering that approximately 2600 species of termites (Bignell et al. 2011) and 357,000 species of beetles (Bouchard et al. 2009) are known, one could conclude that the knowledge of the symbiosis between saproxylophagous insects and N-fixing organisms is strongly biased toward specific social isopteran taxa, whose symbiotic associations may differ from those of other insects, so this information should be applied to other insects with caution. As noted by Dillon and Dillon (2004), studies of termites and cockroaches have shown the extent to which microbes may contribute to balancing the diets of their insect hosts. However, the class Insecta is diverse, even if considering only saproxylophages, and there are groups of insects whose relationships with their microbiotas are undefined (Dillon and Dillon 2004; Nardi et al. 2002; Kneip et al. 2007) even if the specific groups of microbes inhabiting their guts are known (Baldrian 2017). Future studies should investigate the degree to which N-fixing organisms mitigate N scarcity in the food of the different taxonomical groups of insects that inhabit different ecosystems and feed on specific species of dead wood.

The knowledge gaps concerning both the types of microbes and the variations in the significance of their actions for saproxylophages should be considered in future research, which should explore the N dynamics in wood in the context of the life history, nutritional physiology, and fitness of wood consumers. This may be done using the multidimensional view of the ecological stoichiometry framework proposed by Reiners (1986) and postulated by Elser et al. (1996) and by Sterner and Hessen (1994) and described in detail in the book by Sterner and Elser (2002) [the ecological stoichiometry framework will be briefly introduced in Sect. 13.4, but for more detailed reviews, see, e.g., Sterner and Elser (2002), Hessen et al. (2013), Elser et al. (2000a), Moe et al. (2005), Klausmeier et al. (2008), Sardans et al. (2012), Lemoine et al. (2014), Sperfeld et al. (2016a, 2017), Filipiak and Weiner (2017b), Cherif et al. (2017)]. To elucidate the function that insects and their microbiota play in N cycling in ecosystems, future research should consider consumer-driven nutrient recycling (*CNR*), in which the flow of matter through the food chain is regulated by the elemental body composition of species that compose particular links in the chain (for reviews on *CNR*, see, e.g., Elser and Urabe 1999 and Atkinson et al. 2016).

13.3 Nitrogen Is an Important, but Not the Only Important, Element: The Role of Dead Wood Enrichment During Decomposition in P and Other Non-C Elements

Nitrogen is not the only physiologically important element, and co-limitation of the growth and development of animals by a set of elements that are scarce in food is more probable than limitation by a single or the most limiting element (Kaspari and Powers 2016; Filipiak and Weiner 2017b). Atoms of approximately 25 chemical elements are required to build an organism, and a shortfall in any can limit the development, performance, and fitness of an individual, thus altering population growth and, eventually, ecosystem function (Sterner and Elser 2002; Cherif 2012; Kaspari and Powers 2016; Fraústo da Silva and Williams 2001). To maintain stoichiometric homeostasis, growing individuals must collect specific proportions of atoms to form adult bodies according to a specific "elemental recipe" (Sterner and Elser 2002; Cherif 2012; Kaspari and Powers 2016; Jeyasingh et al. 2017), so their growth, development, and fitness are likely co-limited by a set of food-borne elements found in limited quantities (Kaspari and Powers 2016). This phenomenon has received limited attention in studies focused on the nutrient dynamics of decomposing wood (e.g., Swift et al. 1979; Boddy and Watkinson 1995; Laiho and Prescott 2004; Strukelj et al. 2017; Yuan et al. 2017), and although changes in the concentrations of elements during decomposition have been studied, they have not been related to the nutritional needs of saproxylophagous insects. Some studies have focused on long-term patterns of nutrient mineralization, mobilization, input, and accumulation (e.g., Swift et al. 1979; Boddy and Watkinson 1995; Laiho and Prescott 2004; Strukelj et al. 2017; Yuan et al. 2017), and their emphasis on C sequestration and nutrient availability in entire ecosystems leaves open the possibility of deeper investigation of the nutritional relationships between wood and saproxylophagous insects. These relationships may be central to the decomposition of dead wood and nutrient cycling in ecosystems (Chen and Forschler 2016).

Phosphorous is one of the most limiting elements for organisms feeding on dead plant matter, and this limitation is considerably mitigated by decomposing fungi (Filipiak 2016; Filipiak et al. 2016). Concentrations of P may be related to the amount of RNA in an organism (Sterner and Elser 2002). The growth rate hypothesis (*GRH*) postulates that P concentrations, growth rates, and body sizes are positively correlated (Elser et al. 1996, 2000b; Sterner and Elser 2002; Elser and Hamilton 2007; Hessen et al. 2013), so organisms feeding on food with high *C:P* and *N:P* ratios relative to the required ratios experience reduced growth, reproductive output, and survival (Sterner and Hessen 1994; Sterner and Elser 2002; Elser and Hamilton 2007; Danger et al. 2013; Hessen et al. 2013). Additionally, P limitations can affect ecosystem functioning and result in decreased litter decomposition rates (Kaspari and Yanoviak 2008; Čapek et al. 2016; Liu et al. 2016; Purahong et al. 2016). However, P is not the only element that is scarce in wood and limiting for wood eaters. Therefore, co-limitations on the growth and development of consumers with access to a limited number of elements through their food should be considered (cf. Kaspari and Powers 2016; Jeyasingh et al. 2017). Our understanding of elemental limitations in heterotrophs in the sense of Liebig's law, by which only the most limiting nutrient shapes ecological interactions, is too simplistic. Rather, multielemental (or multi-resource if macronutrients are considered) co-limitation likely occurs and shapes these interactions (Marleau et al. 2015; Kaspari and Powers 2016; Sperfeld et al. 2016b; Wirtz and Kerimoglu 2016; Jeyasingh et al. 2017; Kaspari et al. 2017a, b; Welti et al. 2017) (see also Meunier et al. 2017 for context and discussion of the links between nutrient stoichiometry and organismal traits). However, only *C:N:P* ratios have been extensively studied to date within the framework of ecological stoichiometry and mainly in aquatic ecosystems (see Filipiak and Weiner 2017b for review). Of the other elements, Na appears to be particularly important for organisms feeding on plant matter (both dead and living), and since Na is rare in plant tissues (including dead wood) but highly concentrated in the bodies of herbivores and detritivores, it may be one of the elements that co-limit the growth and development of organisms feeding on either dead or living plant matter (e.g., Kaspari and Powers 2016; Kaspari et al. 2017a, b; Filipiak et al. 2017). Indeed, the Na concentration in a host plant has been shown to be a factor shaping the life history and fitness of butterflies (Swanson et al. 2016). Furthermore, a recent analysis of the literature related to ecological stoichiometry shows that data about elements other than C, N, and P are scarce, especially for terrestrial ecosystems (see Filipiak and Weiner 2017b for review). Currently, many researchers continue to focus on *C:N:P* stoichiometry (e.g., Sitters et al. 2017; Meunier et al. 2017; Welti et al. 2017; Zhang and Elser 2017; Cherif et al. 2017, but see Jeyasingh et al. 2017, which discusses shifts from single-nutrient models to more complex, multiple-nutrient models that predict co-limitation), so future studies should fill this gap. Considering a larger number of limiting elements may elucidate the mechanisms that shape ecological interactions and the functioning of food webs (Chen and Forschler 2016; Filipiak 2016; Filipiak and Weiner 2017b), thus illuminating the multielemental nutritional limitations imposed on the growth and development of saproxylophagous insects that include P, N, K, Na, Mg, Zn, and Cu (Filipiak and Weiner 2017a).

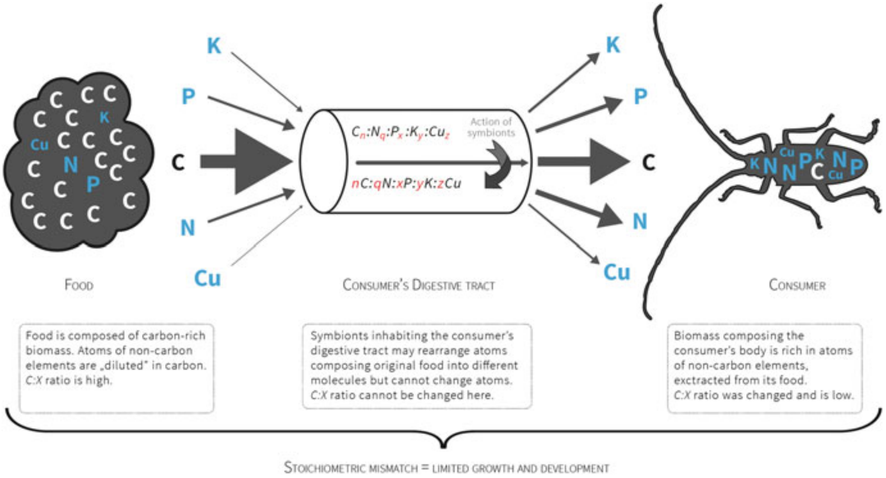
13.4 Ecological Stoichiometry of Dead Wood Eaters: An Elementary Approach to Balancing Energy and Matter

Chemical elements are the most basic and fundamental building blocks of all living matter, which, despite the diversity and complexity of its structure, consists of the same approximately 25 chemical elements that are obtained and assimilated with the use of energy (Sterner and Elser 2002; Cherif 2012; Kaspari and Powers 2016). Ecological stoichiometry considers organisms as sets of atoms selected from the environment in proportions required to create organic molecules. In this context of elemental (stoichiometric) homeostasis, the active regulation of elemental body stoichiometry is an essential trait of individuals (Sterner and Elser 2002; Jeyasingh et al. 2017) that influences the functioning of individuals as well as their ecological interactions, resulting in changes in populations and affecting communities and ecosystems as well as global levels of organization (Sterner and Hessen 1994; Sterner and Elser 2002; Cherif 2012; Cherif and Loreau 2013; Hessen et al. 2013; Galbraith and Martiny 2015; Wilder and Jeyasingh 2016; Zhang et al. 2016; Jeyasingh et al. 2017). Every species has a unique composition of chemical elements that must be homeostatically maintained (heterotrophs show lower levels of variability than autotrophs; Sterner and Elser 2002), which is the basis of the concept of the multidimensional stoichiometric niche that may expand our current understanding of how various biotic and abiotic factors regulate the abundance and distribution of organisms and how organisms utilize, affect, and compete for resources in the environment (Gonzalez et al. 2017).

The most influential feature of the elements that affect fitness is that specific atoms cannot be transformed into other atoms by an organism during processing. However, organic compounds composed of these atoms are changeable, and they can be procured from food or by symbionts that inhabit the digestive tract. This feature is consistent with the law of the conservation of mass, meaning that every developing organism has access to only the building materials offered by its environment. For saproxylic insects, this material consists of a few elements available in excess (e.g., C, H, and O) and others found in limited quantities (e.g., P, N, and Na; Sterner and Elser 2002; Kaspari and Powers 2016).

A mismatch between the elemental composition of a food and the requirements of a consumer, even when food is available in excess, limits the growth and development of the latter (Fig. 13.1; Sterner and Hessen 1994; Elser et al. 2000b; Sterner and Elser 2002; Schade et al. 2003), so maintaining a balance between the supply and demand of the elements needed for growth is crucial for development. Consequently, wood eaters must manage a high threshold of stoichiometric mismatching between their tissues and their food (Sterner and Hessen 1994; Sterner and Elser 2002; Denno and Fagan 2003; Fagan and Denno 2004; Hessen et al. 2013; Filipiak and Weiner 2017b). Incompatibility between the nutritional composition (including the elemental composition) of food and the needs of a consumer may result in limited energy budgets, slow growth rates, and decreased fecundity and survivorship (see Filipiak and Weiner 2017b for review). In other words, stoichiometric mismatches negatively influence the fitness of a consumer and must be overcome, regardless of the total amount of food available.

Previous studies (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016) have concluded that (1) during larval development, saproxylophagous beetles are confronted with a severe nutritional imbalance that is not solely caused by the poor digestibility of their food but mainly by stoichiometric mismatch; (2) the degree of stoichiometric mismatch between xylophagous larvae and decaying dead wood declines during larval development; (3) the relative proportion of nutritional elements other than C in wood increases substantially during decomposition, most likely because of the importation of nutrients by fungal mycelia; (4) nutritional



Food is composed of carbon-rich biomass. Atoms of non-carbon elements are „diluted" in carbon. C:X ratio is high.

Symbionts inhabiting the consumer's digestive tract may rearrange atoms composing original food into different molecules but cannot change atoms. C:X ratio cannot be changed here.

Biomass composing the consumer's body is rich in atoms of non-carbon elements, exctracted from its food. C:X ratio was changed and is low.

STOICHIOMETRIC MISMATCH = LIMITED GROWTH AND DEVELOPMENT

Fig. 13.1 Consumers that feed on nutritionally poor food (e.g., dead plant matter) consume a prepackaged ratio of atoms. For herbivores, detritivores, and saproxylophages, the food contains more C relative to other atoms, so these organisms must manage a diet with excess C that presents a stoichiometric imbalance that often limits their growth and development [consumer graphic source (changed): freevector.com; license: https://creativecommons.org/licenses/by-sa/4.0/]

elements that limit the development of xylophages include N, P, K, Na, Mg, and Cu; and (5) xylophage life history is shaped by elemental enrichment by fungal transfer of nutrients to dead wood. Particularly interesting and important for saproxylophage fitness are changes in the nutritional characteristics of dead wood that occur over time that correspond with saproxylophage larval development (i.e., the first several years of dead wood decay) and allow for saproxylophage growth, development, and maturation (Filipiak and Weiner 2017a). In this chapter, the nutrient dynamics of decomposing dead wood are discussed according to the nutritional needs of growing and developing saproxylophages under the framework of ecological stoichiometry, and the following section will explore (1) why the action of intestine tract symbionts does not solve the problem of an unbalanced diet; (2) how nutrient dynamics in decomposing dead wood may impact saproxylophage growth and development, thus influencing its fitness; and (3) how saproxylophage-fungi interactions can reduce stoichiometric mismatch, i.e., the limitations to growth and development experienced by a saproxylophage.

13.5 Limitations to the Growth and Development of Saproxylophages: What Symbionts Can and Cannot Do in Terms of Nutrient Dynamics

Similar to their hosts, digestive tract symbionts are limited by the poor nutritional quality of their food, so stoichiometric mismatches and the corresponding limitations to growth and development affect both the saproxylophage and its symbionts. Digestive tract symbionts can improve the digestibility of food, supplement diets with N, and synthesize organic compounds from the nutrients furnished by food, but the absolute content of every nutritional element, other than N, processed by microbial symbionts cannot be increased by those microbes. The role of symbiotic organisms in insect nutritional ecology, as described by Douglas (2009), includes the following: (1) enrichment of N-poor food via increases in the concentrations of N in nodules produced by cultivated fungi (termites), the use of N from insect waste compounds (symbionts: various bacteria and fungi; hosts: termites, cockroaches, and hemipterans), N fixation (symbionts: bacteria; hosts: termites, beetles, and flies) and the production of essential amino acids based on the available N; (2) the production of vitamins and sterols based on available matter (symbionts: various bacteria and fungi; hosts: all herbivorous and detritivorous insects); (3) the generation of available nutrients through the digestion of nearly indigestible matter (symbionts: protists, bacteria and fungi; hosts: saproxylic insects and insects using other cellulose-rich diets); and (4) detoxification (symbionts: fungi; hosts: ants). However, every atom processed by digestive tract symbionts remains in the digestive tract and can be either assimilated or excreted. Furthermore, the rearrangement of available atoms into chemical compounds can change the digestibility of food and may ease excretion of some of the surplus C, but it cannot influence the stoichiometric mismatches experienced by saproxylophages (Fig. 13.1). Thus, although digestive tract symbionts can alleviate N limitations for xylophages (as described in Sect. 13.2) and can make the diet more digestible, these symbionts cannot alleviate nutritional limitations independent of the digestibility of the diet, which is tied to the scarcity of elements other than C, H, O, and N.

13.6 Nutritional Requirements of Saproxylophages Relative to the Nutritional Scarcity of Dead Wood

Stoichiometric mismatch between the elemental composition of an organism and its food limits the organism's growth and development and negatively impacts its fitness, independent of the amount of food consumed; i.e., food quality may be limiting for the consumer regardless of quantity (Sterner and Elser 2002; Sterner and Hessen 1994; Cherif 2012; Kaspari et al. 2017a, b; Kaspari and Powers 2016; Pokarzhevskii et al. 2003; Denno and Fagan 2003; Fagan et al. 2002; Elser et al. 2000b; for review, see Filipiak and Weiner 2017b). In this context, I will calculate the index illustrating stoichiometric mismatch between various saproxylophages and different species of dead wood to relate the existing data on dead wood nutrient dynamics to the nutritional needs of saproxylophages. As a result, I will illustrate the meaning of the nutritional scarcity of dead wood for saproxylophages and the nutrient dynamics in decomposing wood.

The fundamental index in ecological stoichiometry is the threshold elemental ratio (*TER*), which allows the limiting effect imposed on an organism by stoichiometric mismatches to be calculated. The threshold elemental ratio is the lowest *C: other element* atomic ratio in food at which the development of the consumer is not limited by the availability of C (i.e., energy) but is limited by the non-C element (Urabe and Watanabe 1992; Sterner and Elser 2002; Denno and Fagan 2003; Fagan and Denno 2004; Hessen et al. 2013). The basis for calculating the *TER* represents the requirement of the consumer for any non-C element during growth and development that is represented by utilizing the consumption rates, assimilation rates, and respiration rates of C and the non-C element of the consumer. Hence, both (1) the energy budget, measured as the C balance, and (2) the budget of any non-C element are considered.

The *TER* is understood as follows (Urabe and Watanabe 1992; Sterner and Elser 2002; Denno and Fagan 2003; Fagan and Denno 2004):

$$\mathrm{TER}_x = (\mathrm{GGE}_x/\mathrm{GGE}_C) \times (C:X)_{i+1} \tag{1}$$

where GGE_x is the gross growth efficiency of element x, GGE_C is the gross growth efficiency of carbon, i is the trophic level, C is the concentration of carbon, and X is the concentration of element x.

If

$$(C:X)_i \geq \mathrm{TER}_x \tag{2}$$

then element x may become a limiting factor for growth at trophic level $i+1$.

Following Hessen et al. (2013), the *TER* for any *C:X* ratio, where X is any element other than carbon, may be calculated as follows:

$$\mathrm{TER}_X = \{A_X/[(I_C A_C - R_C)/I_C]\} \times (C:X)_{i+1}, \tag{3}$$

where A_X and A_C are the assimilation rates for elements C and X, respectively, I_C is the carbon ingestion rate, R_C is the carbon respiration rate, and $(C{:}X)_{i+1}$ is the atomic ratio of *C:X* in the body of the consumer.

However, in the case of herbivorous invertebrates, utilizing this index is technically impossible for certain elements. The gross growth efficiencies should be experimentally measured through laboratory feeding trials using growing animals. Such data are extremely scarce, particularly for elements other than N and P. For organisms that feed on extremely nutritionally poor food and present low growth rates and larval development that can take several years (e.g., wood eaters), obtaining all the necessary data is practically impossible. Thus, the *TER* index for invertebrates can only be estimated based on arbitrary assumptions (Fagan and

Denno 2004; Frost et al. 2006; Doi et al. 2010). To allow for the identification of multiple elements that co-limit the development of an organism and facilitate comparisons between various taxa, habitats, food, and life histories, the trophic stoichiometric ratio (*TSR*) was developed, which is a simplified version of the *TER* that solely utilizes the elemental composition data of an organism and its food and does not require feeding experiments (Filipiak and Weiner 2017a). The *TSR* is based on the following relationship:

$$(C:X)_i/(C:X)_{i+1} \geq \mathrm{GGE}_x/\mathrm{GGE}_C \tag{4}$$

The minimum balanced ratio of $\mathrm{GGE}_x/\mathrm{GGE}_C$ can be estimated as $1/0.25 = 4$ assuming that 75% of the consumed carbon is released as CO_2 while the other consumed elements are incorporated with 100% efficiency. Hence, it is conservatively assumed that for $(C{:}X)_i/(C{:}X)_{i+1} \geq 4.0$, the element x may impose a constraint on growth (Filipiak and Weiner 2017a). Therefore, the *TSR* is calculated as follows:

$$\mathrm{TSR}_x = (C:X)_{\mathrm{food}}/(C:X)_{\mathrm{consumer}} \tag{5}$$

where C is the concentration of carbon and X is the concentration of element x.

A $\mathrm{TSR}_x \geq 4$ indicates a possible limitation on the growth and development of an organism caused by the scarcity of element X in its food; the higher the *TSR* value, the more severe the limiting effect. The *TSR* is not meant to represent the actual measured *TER* of a given element, but it instead serves as a relative index indicating a potential stoichiometric mismatch. Various elements may be differentially acquired, assimilated, reused, and excreted, and the *TSR* index compares the elemental composition of the body of an animal and the food it consumed (not the food assimilated). The absorbed matter has a different elemental composition than the ingested matter, whose nondigestible surplus must be voided, and the physiological effort this requires is proportional to the difference between the food eaten and the food assimilated, which is proportional to the stoichiometric mismatch represented by the *TSR* index. Because the *TSR* index assumes that non-carbon elements are assimilated from food at a maximum rate (100%), the actual mismatches in natural situations cannot be less than the estimated *TSR* values. Therefore, the *TSR* index serves as a conservative but convenient tool that facilitates the detection of elements that co-limit development and can be used to compare the severity of the limitations imposed by various foods on different consumers.

In the present study, the *TSR* index was used to investigate (1) the constraints imposed on the growth and development of saproxylophages because of the nutritional scarcity of dead wood and (2) a possible strategy for mitigating the constraints resulting from nutrient dynamics in decomposing dead wood. To this end, I calculated the *TSR* for various saproxylophagous and detritivorous insects that may use dead wood as a food source. The calculation was based on data on the elemental composition of arthropods compiled by Filipiak (2016; data collected worldwide based on reported mean concentrations of elements for approximately ten species of every taxon used, although the number of reported concentrations varied by element and taxon due to the scarcity of the reported data; see Supplemental Table 3 in Filipiak (2016) for details). The *TSR* was calculated based on the elemental composition of the bodies of adult saproxylophages ($C{:}X_{\text{consumer}}$) and the elemental composition of the food eaten during their larval growth and development ($C{:}X_{\text{food}}$). I used the mean values for element concentrations reported by Filipiak (2016) to calculate $C{:}X_{\text{consumer}}$ considering three taxa: beetles (Coleoptera), ants (Hymenoptera; Formicidae), and dipterans (Diptera). Exact values are presented in Filipiak (2016, see supplemental Table 3). To calculate the $C{:}X$ ratios for exemplary food sources of these insects, which constitute the numerator in the *TSR* index, I applied data on variously decomposed dead wood of different species of angiosperms and gymnosperms based on data collected worldwide (Grier 1978; Lambert et al. 1980; Foster and Lang 1982; Harmon et al. 1986; Preston et al. 1998, 2009; Palviainen et al. 2010a, b; Filipiak and Weiner 2014; Johnson et al. 2014; Köster et al. 2015; Palviainen and Finér 2015; Pearson et al. 2017). Considering all the above studies, the wood was aged 0–64 years after tree death. Based on every study, I utilized data on the elemental composition of the least decayed dead wood (or the youngest if the decay stage was not given) and the most decayed dead wood (or the oldest if the decay stage was not given) for every species investigated in a study. The least decayed wood was aged 0–2 years after tree death depending on the study, and the most decayed wood was aged 6–64 years after tree death. The least decayed wood in a single study is hereafter called undecayed, and the most decayed wood is termed highly decayed. I calculated *TSRs* for undecayed and highly decayed wood to investigate whether and to what degree the stoichiometric mismatch experienced by saproxylophages might be mitigated by feeding on nutritionally enriched decomposed wood compared to undecayed wood. In other words, I asked the question: “Can the dead wood of various tree species be sufficiently enriched during decomposition to allow saproxylophages to nutritionally balance their diets and thus overcome the limitation to growth and development posed by the nutritional scarcity of pure, undecayed wood?” Some of the analyzed studies did not contain data on C concentrations in the dead wood under study, for which C concentrations were assumed to be 50% dry mass based on Johnson et al. (2014), who did not find statistically significant differences from $C = 50\%$ in various species and ages (0–16 years of decay) of dead wood. Concerning concentrations of C reported in all the considered studies, for all the wood species, age, and the stage of decomposition, the mean value was 49% and minimal, 45% and maximal, 57%.

The scarcity of seven elements (N, P, K, Mg, Fe, Zn, and Cu; Fig. 13.2) in dead wood may limit the growth and development of saproxylophagous insects regardless of the stage of wood decay and the insect taxa (exceptions: Zn tended to be not limiting for dipterans feeding on decayed wood, and Mg tended to be not limiting in decayed wood of *Tsuga heterophylla* (Raf.) Sarg.). This limitation occurred even though the *TSRs* calculated for N, P, Fe, and Cu for feeding on decayed wood tended to be 10–100 times lower than those for feeding on undecayed wood (exception: Fe for feeding on *Tsuga heterophylla*; Fig. 13.2). Also for Zn and Mg, the calculations showed a tendency to mitigate stoichiometric mismatch during wood decomposition but to a lesser degree (Fig. 13.2). Magnesium limitation tended to be lower in

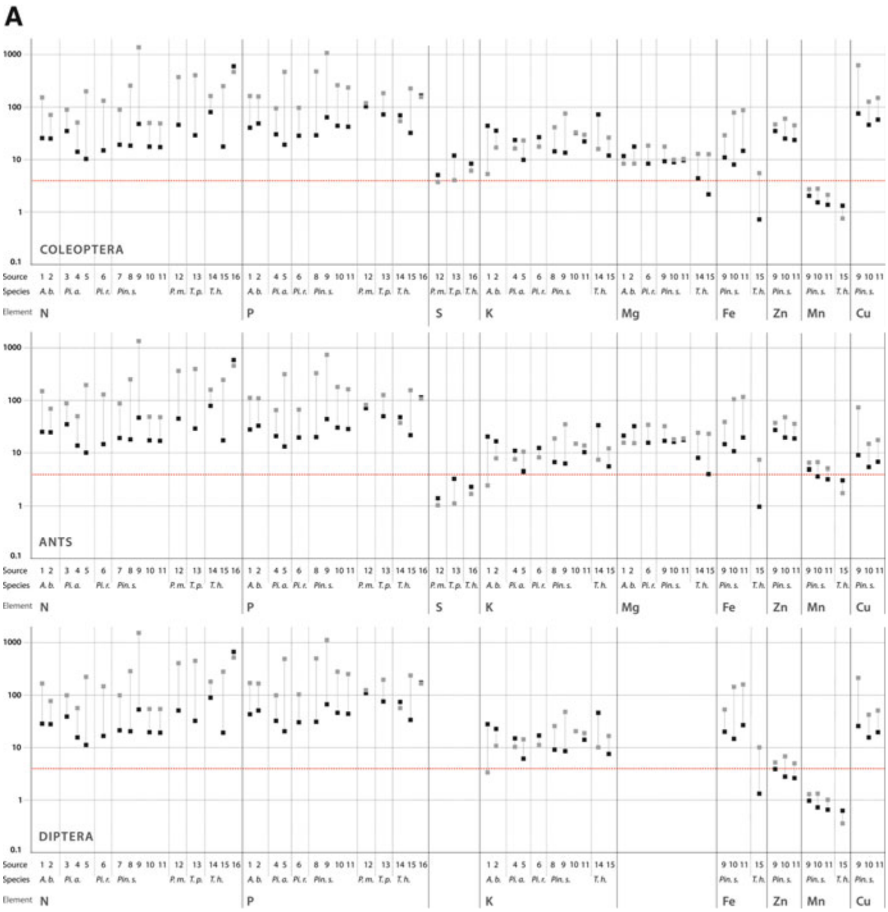


Fig. 13.2 Stoichiometric mismatches (trophic stoichiometric ratios, *TSR*s) calculated for detritivorous/saproxylophagous insects feeding on various species of dead wood: (**A**) gymnosperms and (**B**) angiosperms. *TSR* values were calculated based on data from the literature (means) on the elemental composition of dead wood and the elemental composition of the adult bodies of insects. Undecayed wood (gray squares)—the least decayed/youngest dead wood investigated in a single study; highly decayed wood (black squares)—the most decayed/oldest dead wood investigated in a single study. Corresponding squares connected by a line, dead wood investigated in a single (the same) study. Species symbols of gymnosperms, *A. b.*, *Abies balsamea*; *Pi. a.*, *Picea abies*; *Pi. r.*, *Picea rubens*; *Pin. s.*, *Pinus sylvestris*; *P. m.*, *Pseudotsuga menziesii*; *T. p.*, *Thuja plicata*; *T. h.*, *Tsuga heterophylla*; *and* angiosperms, *Ac. s.*, *Acer saccharum*; *Al. g.*, *Alnus glutinosa*; *Al. i.*, *Alnus incana*; *B. a.*, *Betula alleghaniensis*; *B. pe.*, *Betula pendula*; *B. pe* and *B. pu.*, *Betula pendula* and *Betula pubescens*; *F. g.*, *Fagus grandifolia*; and *P. t.*, *Populus tremula.* Source literature for the elemental composition of dead wood: Foster and Lang (1982), 1 and 6; Lambert et al. (1980), 2; Köster et al. (2015), 3, 7, 18, 19, 22, and 24; Palviainen and Finér (2015), 4; Filipiak and Weiner (2014), 9; Pearson et al. (2017), 10 and 11; Preston et al. (1998), 12, 13, and 16; Grier (1978), 14; Preston et al. (2009), 15; Johnson et al. (2014), 17, 20, and 23; and Palviainen et al. (2010a, b), 5, 8, and 21. Data source for insect elemental compositions: literature review by Filipiak (2016). The red, dashed line shows $TSR = 4$, and values below this threshold indicate the limiting effect on the growth and development of an insect by the scarcity of a given element in the food consumed during its larval period. The scarcity of N, P, K, Mg, Fe, Zn, and Cu in the dead wood of different species may limit the growth and development of various saproxylophage taxa, and the power of this

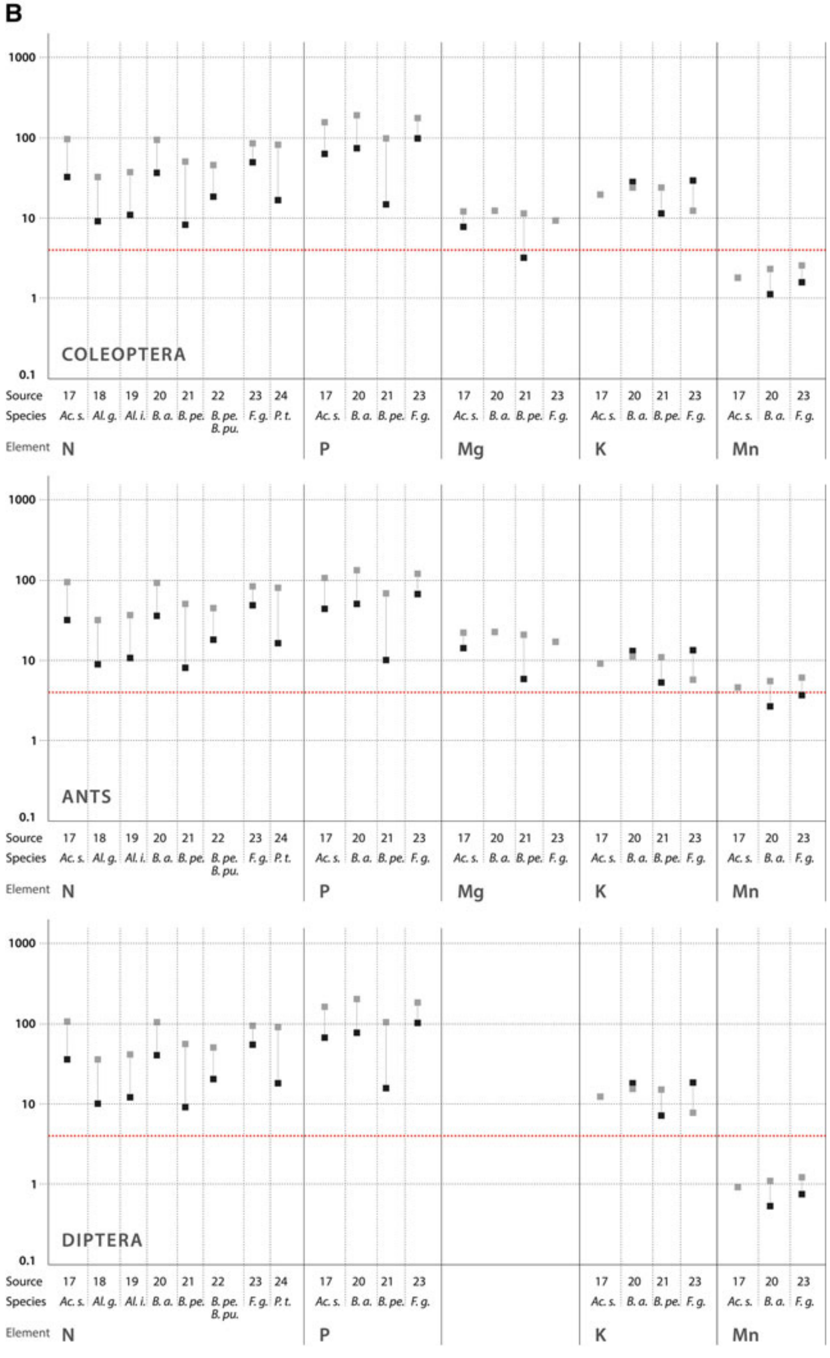


Fig. 13.2 (continued) limitation depends on the species and decay stage of the wood and the insect taxa. In most cases, the nutrient dynamics in decomposing dead wood are not sufficient to overcome the limiting effects, which persist even if mitigated by the nutritional enrichment of decomposing wood. Therefore, diet supplementation with non-woody compounds is required

decayed than undecayed wood for all the investigated species except *Abies balsamea* (L.) Mill. (Fig. 13.2). Sulfur may be limiting for beetles but not for ants, and Mn may be a limiting element for ants but not for beetles and dipterans (Fig. 13.2). The effect of the limitations posed by K and Mg scarcity tended to differ with the wood species. Furthermore, K limitation tended to be lower in decayed than in undecayed wood in *Pinus sylvestris* L. and *Fagus grandifolia* Ehrh., but for the other investigated species, K limitation tended to be higher in decayed wood or depended on the study (Fig. 13.2). The analysis of the limitations posed on the growth and development of insects by the multielemental stoichiometry of dead wood (Fig. 13.2) is simple and rough yet instructive; it shows the complexity of the relationship between the nutritional value of dead wood and its potential consumers. Several factors should be taken into consideration when discussing this issue: (1) the general nutritional value of dead wood; (2) changes in the nutritional value of the wood that occur during decomposition; (3) differences between the behavior of atoms of various elements, particularly increasing/decreasing concentrations of different elements with wood decay; (4) differences between various species of wood (e.g., *Tsuga heterophylla* versus other investigated gymnosperms or angiosperms versus gymnosperms; Fig. 13.2). This analysis also shows the scarcity of the knowledge of the nutritional value of dead wood for saproxylophages and the bias toward gymnosperms (especially *Pinus sylvestris*). In the following sections of this chapter, I will summarize the existing knowledge on the nutrient dynamics in decomposing dead wood, and I will relate the data on the dynamic changes in wood stoichiometry with the nutritional needs of saproxylophages. The analysis (Fig. 13.2) revealed that the nutritional scarcity of dead wood limits the growth and development of saproxylophages because of imbalanced multielemental stoichiometry. In the following subsections, I will discuss the mechanism by which saproxylophages mitigate this limitation by utilizing a fungal network that connects nutritionally scarce dead wood with nutritionally rich patches of the outside environment.

13.7 Nutrient Dynamics in Decomposing Dead Wood: Short-Term (Several Years) vs. Long-Term (Dozens of Years) Changes

Pure wood is rich in polysaccharides but includes few of the other biomolecules required for saproxylophage growth and development (Parkin 1940; Pettersen 1984). The actions of insects and mites include bringing symbiotic fungi or soil into the wood environment, which may contribute to the nutritional enrichment of the internal dead wood environment (Ulyshen and Wagner 2013; Ulyshen 2016) but not to the wood itself. Similarly, the dead wood environment may be nutritionally enriched by the accumulation of loose organic material in tree hollows (Landvik et al. 2016) or by the accumulation of the feces of saproxylophages (Chen and Forschler 2016; Sánchez et al. 2017). Another source of nutritional enrichment may be the action of ants bringing nutrients in the form of harvested organisms and excreta from the outside environment (Pinkalski et al. 2015). Finally, fungi inhabiting dead wood may create mycelial networks that extend beyond the wood itself, allowing them to import nutrients from external sources, thus improving substrate quality for invertebrates (Filipiak et al. 2016; Filipiak and Weiner 2017a). However, the wood tissues themselves cannot be nutritionally enriched in this way, so it was assumed that the wood mainly becomes enriched via the digestion of polysaccharides and the loss of C through respiration as CO_2 by microorganisms during decomposition (Swift et al. 1979; Boddy and Watkinson 1995). This process should result in an increase in the percentages of non-sugar nutrients and non-C elements in wood (Swift et al. 1979; Boddy and Watkinson 1995), and the nutritional quality of wood can be represented as the ratios of the concentrations of C to other elements (i.e., *C:X* ratio, where *C* represents the concentration of carbon and *X* represents the concentration of any non-carbon element x) (Swift et al. 1979; Boddy and Watkinson 1995; cf. Elser et al. 2000a; Sterner and Elser 2002, where the atomic ratio is utilized instead of the mass ratio). Changes in this ratio during decomposition have been used to discuss nutrient dynamics in decomposing dead wood (Swift et al. 1979; Boddy and Watkinson 1995; Filipiak et al. 2016), and it has been noted that nutrient importation via fungal mycelium probably occurs in the early stages of wood decomposition (first few years of decomposition) and results in an increase in the absolute contents of certain non-C elements (Stark 1972; Swift 1977; Swift and Boddy 1984; Wells et al. 1990; Clinton et al. 2009). However, this phenomenon has received limited research attention, with studies primarily focused on the nutrient losses that occur during later stages of decomposition (5—several dozen years of decomposition; Foster and Lang 1982; Harmon et al. 1986; Dighton 2003, 2007; Palviainen et al. 2010a, b; Köster et al. 2015). Therefore, it was assumed that C loss is the main driver of the observed increase in the nutritional quality of dead wood, so the eventual transport of substances by fungi from external sources may be neglected (Swift et al. 1979; Harmon et al. 1986; Wells and Boddy 1995; Johnson et al. 2014; Köster et al. 2015; Clymans et al. 2016). In this chapter, the nutrient dynamics observed in decomposing wood will be discussed in the context of the nutritional needs of saproxylophages, so in contrast to most previous studies, the short-term (several years) changes in the nutrient concentrations in the dead wood environment will be discussed with a focus on elements that are physiologically important for saproxylophagous insects. Additionally, the mechanisms responsible for these changes will be further discussed in relation to the growth, development, and fitness of saproxylophages.

Studies of dead wood decomposition processes have reported various and sometimes opposing changes in the concentration of elements, and such conflicting results can be attributed to the different methods used to classify the stages of wood decay. Certain methods are based on measuring samples collected from dead boles or stumps that may not represent the stage of decay of the entire bole/stump, and differences may be related to variation in samples of dead wood collected from different tree species or from wood with bark, wood alone (sapwood and heartwood), sapwood alone, or heartwood alone. An additional source of variation may be the location of the decomposing wood, which would be related to differences in environmental conditions and decomposer communities (e.g., Rinne et al. 2017 showed the temperature dependency of N fixation). It is also possible that the dead wood of various species has specific nutrient dynamics (Fig. 13.2).

Lambert et al. (1980) studied mass loss and chemical changes in decaying boles of balsam fir (*Abies balsamea*; subalpine balsam fir forest, North America) and measured the concentrations of C, N, P, Ca, Mg, K, and Na, and these authors did not observe significant differences in the element concentrations among (1) standing dead trees, (2) fallen and slightly decomposed logs, and (3) fallen and moderately decomposed logs. Dead wood in advanced states of decay presented significantly increased concentrations of N, P, and Mg relative to less decayed wood, but the concentrations of other elements were not found to change significantly. Lambert et al. (1980) also studied changes in the absolute amounts of elements in boles aged 0–70 years over seven decades. Bole death spurred a continuous increase in the absolute levels of N, whereas the absolute P levels tended to increase over the first 10 years and then decrease. In contrast, the absolute levels of Ca, Mg, and K tended to decrease (Lambert et al. 1980). However, different results were reported by Grier (1978) in western hemlock-sitka spruce (*Tsuga heterophylla*) ecosystems (Central Oregon Coast, North America); in this case, fallen logs aged 2–38 years were studied, and the absolute levels of N, P Ca, Mg, and K tended to decrease between the 2nd and 5th years of decomposition. The long-term changes in the concentrations and absolute levels of N, Ca, Mg, and Na tended to increase while P and K tended to decrease during decomposition; the C content was not determined. In a northern hardwood forest in North America, Johnson et al. (2014) studied the nutrient dynamics of dead sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) wood over 16 years of decomposition and reported increases in N, P, and Ca concentrations in all studied species, decreases in K concentrations in two species, decreases in the *C:N* ratios in all species, decreases in the *C:P* ratios in two species, decreases in the *N:P* ratio in one species, and an increase in the *N:P* ratio in one species. The total amounts of K and Mn decreased in all species, and the total levels of N, P, Ca, and Mg increased over the first 2–10 years depending on the species and decreased after 10 years in all species. In Asia, Yuan et al. (2017) studied the decomposition of *Pinus armandii* Franch. and *Quercus aliena* Blume wood over an 18-year period, and a decrease in K concentrations and an increase in C, N, P Ca, and Mg concentrations were observed for both species. The *C:N* ratios tended to decrease over time, yet the pattern of change in elemental concentrations and *C:N* ratios differed between species. Laiho and Prescott (2004) concluded in their review, which was based on a dataset that considered a decomposition period spanning 100 years for various wood species worldwide, that N and P concentrations typically increase during decay while the concentrations of other elements tend to vary. However, all these studies failed to consider the nutritional needs of saproxylophagous insects that develop in dead wood over several years (during

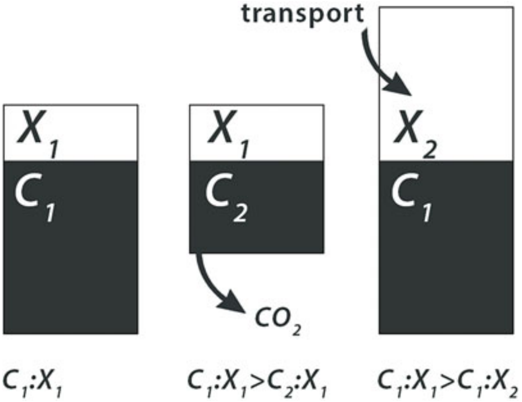


Fig. 13.3 Two mechanisms that contribute to the nutritional enrichment (an increase in elements other than C) of dead wood during decay: (1) C loss and (2) the transport of outside nutrients. A decrease in the *C:X* ratio during the initial stages of dead wood decomposition should favor the growth and development of saproxylophages. *X* represents the concentration of any non-carbon element *x* and *C* represents the concentration of carbon

which specific changes in nutrient concentrations may occur) that are not related to long-term changes. Therefore, the mechanisms contributing to the changes in the nutritional quality of decaying wood that occur during the time corresponding to saproxylophage growth and development cannot be interpreted reliably. Concentrations of non-carbon elements (*X*) can increase as decay proceeds because either the absolute amounts of C decrease or the absolute amounts of element x increase (Fig. 13.3), and lower *C:X* ratios indicate better nutritional conditions for saproxylophages (Filipiak and Weiner 2014; Filipiak et al. 2016; Filipiak and Weiner 2017a; Fig. 13.3). Assuming CO_2 loss from dead wood during decomposition is the main factor that contributes to wood nutritional enrichment, a similar increase in the concentrations of all non-carbon elements should be observed. Table 13.1 shows the estimated decrease in *C:X* ratios in decomposing wood calculated from the decrease in the density of decaying wood in which there is no net import of nutrients; the estimations were adapted from Boddy and Watkinson (1995). For comparison, Table 13.1 also shows the measured concentrations of non-carbon elements in decomposing wood. The measured concentrations changed to differing degrees during the first 4 years of decomposition, leading to different decreases in *C:X* ratios during decomposition depending on the non-carbon element (Table 13.1). This change suggests that at least in the initial stages of decomposition, mechanisms other than C loss via respiration may highly contribute to the observed nutrient dynamics and the rearrangement of *C:other element* ratios. During the very early stages of decay, the nutritional composition of dead wood may be dramatically rearranged (Filipiak et al. 2016), so the processes that occur during the early stages of decomposition that nutritionally enrich wood and allow saproxylophages to grow, develop, and reach maturity should be clarified. The few studies conducted on the nutritional changes in dead wood during early stages of decomposition (0–5 years)

Table 13.1 Decrease in the *C:X* ratios (*C*, concentration of carbon; *X*, concentration of any non-carbon element *x*) in decomposing wood

Mass loss (%)	**Decrease in estimated *C:X* ratios** (Boddy and Watkinson 1995)									
	C:N	***C:P***	***C:K***	***C:Ca***	***C:Mg***					
	***n*-fold decrease from the original mass**									
29	1.41	1.41	1.41	1.41	1.39					
46	1.86	1.85	1.85	1.85	1.85					
64	2.78	2.78	2.79	2.76	2.78					
82	5.61	5.56	5.53	5.63	5.55					
Decay stage	**Decrease in measured mean *C:X* ratios** (Filipiak and Weiner 2014)									
	C:N	***C:P***	***C:K***	***C:Ca***	***C:Mg***	***C:Na***	***C:Fe***	***C:Zn***	***C:Mn***	***C:Cu***
	***n*-fold decrease from the undecayed dead wood**									
Moderately decayed	4.45	5.41	2.01	1.13	1.14	1.02	2.27	1.18	0.92	8.12
Highly decayed	27.12	16.87	5.60	1.48	1.90	1.53	2.65	1.35	1.33	8.15

Theoretical and measured values are compared based on theoretical data estimated under the assumption that the loss of wood mass is only caused by the release of CO_2 during respiration and that a net loss or importation of minerals does not occur during the decay process (Boddy and Watkinson 1995), and the measured values are the means for pine stumps aged 0–4 years after tree cutting (Filipiak and Weiner 2014). The theoretical values show similar *C:X* ratios declines for all elements x considered, and the measured values show differing decreases in *C:X* ratios for various elements x.

suggest that nutrient transport by fungi from external sources plays a crucial role in the nutritional rearrangement of wood during the time of saproxylophage developmental requirements (Filipiak and Weiner 2014; Filipiak et al. 2016; Filipiak and Weiner 2017a; temperate deciduous forest, Europe). The further changes in dead wood nutrient dynamics may depend on the changes during the first few years of decomposition, when dead wood may be considerably enriched in several nutrients. For pine stumps in Central Europe, concentrations of N, P, K, Na, Mg, Fe, and Cu may increase by approximately 2 to 25 times, depending on the element, during the first 4–5 years of wood decay (Filipiak and Weiner 2014; Filipiak et al. 2016). The increase is considerable and reflects the increase in the absolute amounts of these elements in the wood (Filipiak et al. 2016), and such a nutritionally supplemented wood may be further exploited during later stages of decay by various taxa of saproxylophages. A 16-year study of the nutrient dynamics in the wood and bark of three tree species indicated that the net amount of N, P, Mg, and Ca increased in a species-dependent manner during the first 2 years of decomposition. However, detailed analyses of the observed patterns are impossible because of the small sample size and variability in element concentrations (Johnson et al. 2014). One could ask whether the age of decomposing wood is a good proxy for its nutritional characteristics. If changes in the nutrient concentrations of dead wood can result from microbial action with fungi being responsible for enrichment via the transport of outside nutrients, then fungal infection of dead wood may better explain the

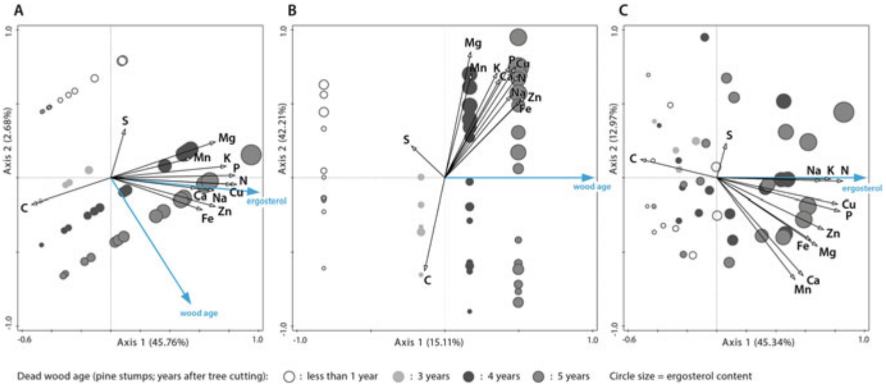


Fig. 13.4 Multivariate analysis of the stoichiometric relationships between the ergosterol content, dead wood age, and 12 studied elements. The RDA plot and the first two axes are shown. (**A**) Plot considering ergosterol content and wood age; (**B**) plot considering wood age alone; and (**C**) plot considering ergosterol content alone. Circles denote single pine stumps in various stages of decomposition, and the size of the circles denotes the ergosterol content of the stumps, $n = 45$. For all axes in **A**, **B**, and **C**, $p < 0.05$

observed variation in nutrient concentrations than the age of the wood. For this reason, I compared the relationship between (1) dead wood age and the concentration of nutritional elements and, for the same wood samples, between (2) levels of fungal hyphae and the concentrations of nutritional elements to examine whether the variation in the elemental concentrations of dead wood with age was attributable to fungal nutrient transport (Fig. 13.4). I examined the data from 45 pine stumps of known age in various stages of decay (a few months to 5 years after tree cutting) that included the concentrations of 12 elements (C, N, P, S, K, Na, Ca, Mg, Fe, Zn, Mn, and Cu) and a known concentration of ergosterol, which is a proxy for the levels of fungal hyphae, from Filipiak et al. (2016). A redundancy analysis (RDA) was performed to simultaneously compare the composition of multiple elements in wood and the relationship between ergosterol levels and wood age (Fig. 13.4). An analysis of the ergosterol content and wood age (Fig. 13.4A) suggested that concentrations of elements in wood (except S) are closely correlated with ergosterol levels (amount of fungi) and may be slightly correlated with wood age. The first two axes explained 48.44% of the total variance. Relationships between ergosterol content and the concentration of elements are denoted by vectors that symbolize the contents of ergosterol and the elements around the first axis, which explained 45.76% of the total variance (C concentration declined, and the concentrations of other elements, except S, increased as did that of ergosterol). A vector symbolizing wood age positioned between axes 1 and 2 was situated closer to the 2nd axis that explained only 2.68% of the total variance. High variation was observed in ergosterol content, and it was not related to wood age. Element concentration was strongly correlated with ergosterol content, and because fungi translocate nutrients to the wood, the amount of fungal tissue may be assumed to be responsible for the variation in the element concentrations in the wood. Thus, the variation in element concentrations was not dependent on the age of the dead wood, but it was dependent on the amount of fungi inhabiting the wood. Indeed, an analysis that focused strictly on wood age revealed a weak correlation between wood element concentrations and wood age (Fig. 13.4B). Axis one in Fig. 13.4B is related to wood age and explained only 15.11% of the total variance. The element concentrations were positioned closer to the 2nd axis and explained 42.21% of the total variance (Fig. 13.4B). The concentrations of Fe, Zn, Na, and N were correlated with wood age to the highest degree, but they were not strong for any of these elements. The analysis of ergosterol content alone revealed a random distribution of stumps by age in the RDA plot (Fig. 13.4C), and axis 1, which is related to ergosterol content and the element concentrations (except S), explained 45.34% of the total variance. Carbon concentrations decreased, while the concentrations of other elements (except S) increased along with ergosterol content. The elements most closely correlated with ergosterol were N, K, Na, Cu, and P, and these correlations were strong. Of these elements, the transport of N, K, Cu, and P to dead wood by fungi was reported in a previous study (Filipiak et al. 2016).

Thus, the age of dead wood is not a good proxy for its nutritional characteristics, while measures of fungal hyphae inside the dead wood environment are related to the observed pattern of *C:X* decline during decomposition. Previous studies have shown that fungal transport increases the total amount of N, P, K, Cu, and Fe, and potentially Na and Mg, in wood infested by fungi, and this may be the main factor explaining decreases in *C:X* during the initial stages of decomposition (first several years; Filipiak et al. 2016). Therefore, the age of dead wood may not be related to its nutritional quality, and the amount of fungal hyphae within dead wood may be a better proxy for nutritional quality and thus usability by saproxylophages.

13.8 Nutrient Dynamics Related to the Requirements of Saproxylophages: A Case Study Utilizing Existing Data on the Ecological Stoichiometry of Saproxylophagous Insects

To date, some data have been published on the nutrient dynamics of decaying wood associated with the nutritional needs of saproxylophages that use three species of beetles as model organisms: *Stictoleptura rubra*, *Arhopalus rusticus* (Coleoptera, Cerambycidae), and *Chalcophora mariana* (Coleoptera, Buprestidae) (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016). The goal of this chapter is to discuss the nutrient dynamics in dead wood in the context of the requirements of wood eaters, so in this subsection, I will focus on the three model species of beetles for which relevant data exists. All three beetles inhabit the same environment (dead pine wood) and exploit the same resources, but they belong to two families (Cerambycidae and Buprestidae) and have different life histories, resulting in different adult body sizes

(Filipiak and Weiner 2014). Therefore, the beetles differ in their nutritional needs and must collect different amounts of nutrients during larval growth to compose the adult body. In the literature (Dominik and Starzyk 2004), the development times for these species are reported to be 3 years in the smallest beetle, *S. rubra*; 2–4 years in *A. rusticus*, which is of intermediate size; and 5–6 years in the largest of these beetles, *C. mariana*. Their mean body sizes are as follows (species, female and male in grams dry mass): *S. rubra*, 0.07 and 0.03; *A. rusticus*, *0.13* and *0.08*; and *C. mariana*, 0.22 and 0.18 (Filipiak and Weiner 2014). I shall start by relating the available data on the body composition of various groups of insects (Coleoptera, Diptera, and ants) to the nutritional composition of dead wood in different stages of decay and that of fungi to investigate the possible nutritional mismatches experienced by various groups of saproxylophagous insects, the limitations to their growth and development posed by these mismatches, and the possibilities for mitigating these mismatches.

I used the *TSR* index (described in Sect. 13.6) to investigate (1) the constraints imposed on the growth and development of saproxylophages as a result of the nutritional scarcity of dead wood and (2) methods of mitigating the constraints resulting from these nutrient dynamics. Thus, I calculated the *TSR*s for various saproxylophagous and detritivorous insects that may feed on dead wood and performed two analyses. Analysis 1, illustrated in Fig. 13.5, was performed to answer the question: “How do fungi contribute to mitigating the stoichiometric mismatch and nutritional limitation experienced by various insects feeding on dead wood?” In this analysis, I utilized data available from the literature on the elemental composition of various insects, fungi, and dead wood collected worldwide. Analysis 2, which is illustrated in Fig. 13.6, was performed to investigate how dead wood nutrient dynamics are related to the nutritional requirements of saproxylophages inhabiting the wood. In this analysis, I focused on the example of trophic relationship between saproxylophages, dead wood, and fungi, utilizing the data on the three species of wood-boring beetles (*Stictoleptura rubra*, *Arhopalus rusticus*, and *Chalcophora mariana*) inhabiting pine stumps. The data used for both analyses contained precise average, variability and minimal and maximal values for C and other elements, which allowed for the potential mean and minimal and maximal values of the *TSR* index to be calculated.

The analysis of the literature related to the nutrient dynamics in dead wood and the elemental compositions of saproxylophagous insects revealed a lack of data associated with the nutritional needs of the organisms that inhabit wood, and the estimates are incomplete due to an absence of data on several physiologically important elements (atoms of 25 elements should be considered; Cherif 2012; Kaspari and Powers 2016) as well as the different saproxylophage taxa and various species of dead wood. Nevertheless, the extrapolation of such calculations to generalize the interactions between dead wood and wood eaters is highly instructive and may lead to important and testable hypotheses.

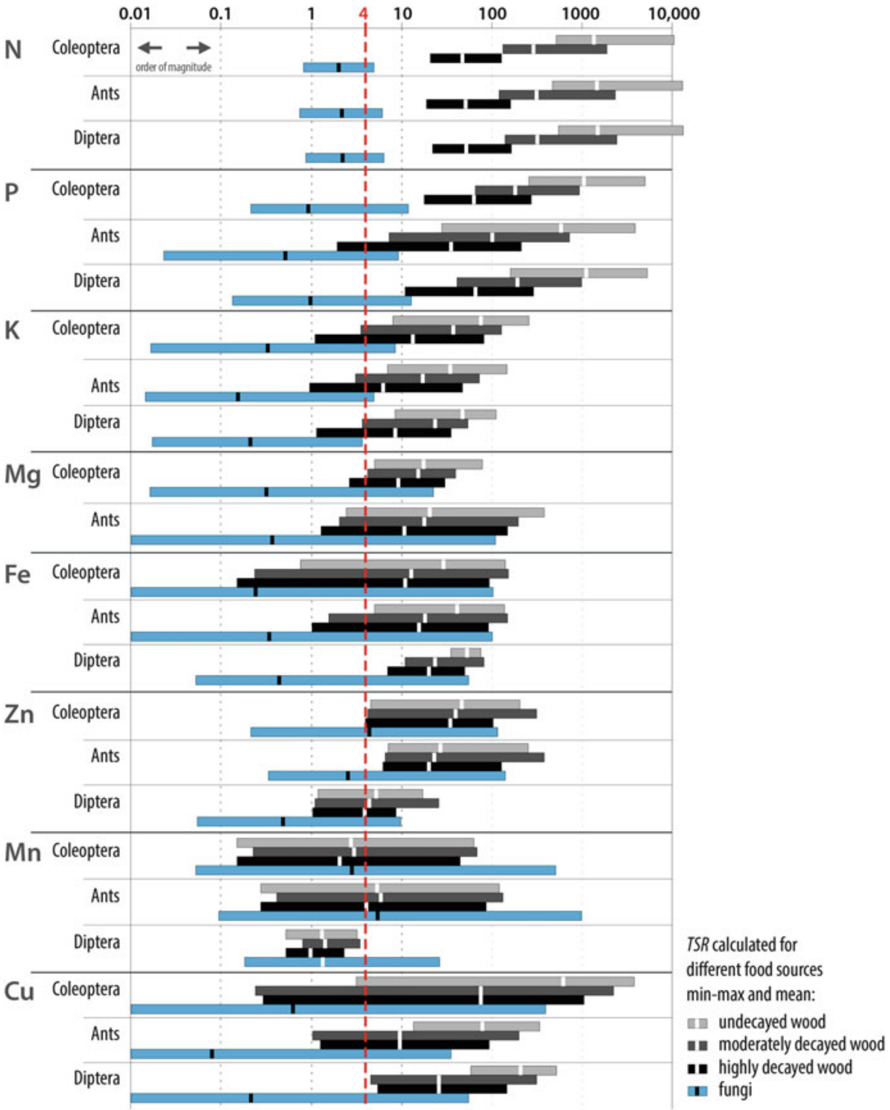


Fig. 13.5 Stoichiometric mismatches (*TSRs*) calculated for detritivorous/saproxylophagous insects that may use dead wood and fungi as food. *TSR* values were calculated for four sources of food: variously decomposed wood divided into three decay classes (source: Filipiak and Weiner 2014) and fungi (source: Filipiak 2016). Bars denote the minima and maxima, and white and black dashes denote means. The Y-axis scale is logarithmic. Source of insect elemental composition data: Filipiak 2016. *TSR* values ≥4 denote limitations on growth, and the dotted red line denotes the threshold value (*TSR* = 4). The growth and development of insects feeding on dead wood may be co-limited by N, P, Cu, K, Mg, Zn, and Fe scarcity, and the strength of this limitation is mitigated as wood is decomposed by one or two orders of magnitude during the first 4 years of decomposition. This limitation may be completely mitigated using fungi as a food source

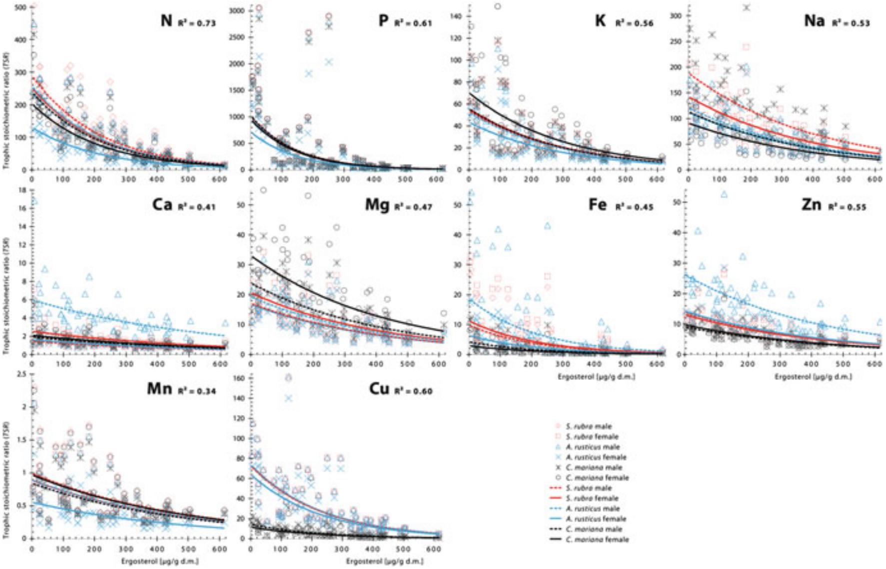


Fig. 13.6 Relationships between ergosterol content (proxy for fungi) in dead wood and the nutritional limitations imposed on the growth and development of saproxylophagous beetles inhabiting the wood expressed as *TSRs*. *TSR* values ≥ 4 denote the limitations caused by a scarcity of atoms of the considered element, and these limitations are more severe for *TSR* values substantially different than 4. Calculations were based on the mean element concentrations in beetle bodies (source: Filipiak and Weiner 2014) and the element concentrations and ergosterol content of dead wood inhabited by the studied beetles (aged a few months to 5 years) (source: Filipiak et al. 2016)

13.8.1 Analysis 1

I calculated the *TSR* index based on data on the elemental compositions of insects compiled by Filipiak (2016; data collected worldwide based on reported mean concentrations of elements for approximately ten species of every taxon used, but the number of reported concentrations varied by element due to scarcity of data on the elemental composition of the insects). The *TSR* was calculated based on the elemental compositions of adult bodies ($C{:}X_{\text{consumer}}$) and the food eaten during the growth and development of these bodies ($C{:}X_{\text{food}}$). To calculate the $C{:}X$ ratios for exemplary food sources for these insects, which constitute the numerator in the *TSR* index, I applied data on (1) variously decomposed dead wood aged 1–4 years and divided into three decay classes that differed in the amounts of fungal hyphae growing inside the wood (Filipiak and Weiner 2014; pine stumps collected from the Puszcza Niepołomicka Forest, Lesser Poland; $N = 8$–26 depending on the decay class and the element) and on (2) the elemental compositions of fungi that may grow inside dead wood and be used by saproxylophages as food instead of wood (Filipiak

2016; data collected worldwide based on reported mean concentrations of elements for a species, utilizing from 4 (C) to 69 (Fe, Zn, Mn) mean values).

The analysis revealed (Fig. 13.5) that limitations of seven elements (N, P, Cu, K, Mg, Zn, and Fe) had the greatest effect on insect development (Zn may not be limiting for Diptera), with calculated *TSR* values above the threshold of 4 (Fig. 13.5). For P and N, the *TSR*s calculated for feeding on moderately decayed wood were approximately ten times lower than those for feeding on undecayed wood, and the *TSR*s calculated for feeding on heavily decayed wood were approximately 100 times lower than those for feeding on undecayed wood. For Cu, the *TSRs* calculated for feeding on both (1) moderately decayed wood and (2) heavily decayed wood were approximately ten times lower than those for feeding on undecayed wood. For K, the *TSR*s decreased almost tenfold from undecayed to heavily decayed wood, and for Mg and Fe, the *TSRs* declined approximately two- to threefold from undecayed to heavily decayed wood. All the elements were considered limiting to insect growth and development, even for the most nutritious wood sample (heavily decayed wood). These limitations, however, are mitigated when insects feed on fungal hyphae that overgrow wood during decay. Therefore, the nutrient dynamics found in decomposing wood may mitigate the nutritional limitations on the growth and development of saproxylophagous insects, but these dynamics provide insufficient nutrients. Thus, selective feeding on fungal hyphae might supply saproxylophages with their required nutrients. Therefore, wood ingested by saproxylophages as they form corridors in dead wood may not be a major source of body-building nutrients for these organisms, and growing insects likely rely on fungi as a source of nutrition.

13.8.2 Analysis 2

During the first few years of dead wood decomposition, the transport of nutrients from the external environment through fungal hyphae shapes nutrient dynamics and transforms nutritionally scarce wood environments into niches that are nutritionally adequate for saproxylophagous insects (Filipiak et al. 2016; Filipiak and Weiner 2017a). It has been suggested that the transport of nutrients from the environment may continue during latter stages of wood decomposition, but the leaching of nutrients from wood into the environment may also occur. However, the *C:X* ratios continue to decrease, potentially because of C loss (Boddy and Watkinson 1995; Laiho and Prescott 2004; Johnson et al. 2014), so long-term C losses from decomposing wood initially enriched by fungi with non-C elements may further mitigate the nutritional limitations experienced by insects inhabiting dead wood during later stages of decay. Hence, the initial enrichment of the wood environment with nutrients transported by fungi from the outside may be an important mechanism that further shapes the long-term nutrient dynamics in dead wood. Therefore, I utilized the available data from the literature to investigate the degree to which the nutritional enrichment of dead wood during the first few years of decay might mitigate the nutritional constraints of saproxylophagous insects feeding on dead wood. For the three species of saproxylophagous beetles examined, I was able to determine the relationships between nutritional limitations and the amounts of fungi (expressed as the concentrations of ergosterol) within dead wood over the first 5 years of decay (Fig. 13.6). I used data published on variously decomposed dead wood aged from a few months to 5 years (Filipiak et al. 2016; 77 pine stumps collected in Puszcza Niepołomicka Forest). The *TSR* values for these stumps could be related to the ergosterol content (proxy for fungus levels) that was measured by Filipiak et al. (2016), and these stumps were inhabited by three species of saproxylophagous beetles that differed in their life history characteristics: *Stictoleptura rubra* (Cerambycidae), the smallest one with a larval development time reaching 3 years; *Arhopalus rusticus* (Cerambycidae), which is intermediate in size with a larval development time reaching 4 years; and *Chalcophora mariana* (Buprestidae), the largest beetle with a larval development time reaching 6 years (Filipiak and Weiner 2014, 2017a; Filipiak et al. 2016). Based on these data, I calculated *TSRs* for ten elements (N, P, K, Na, Ca, Mg, Fe, Zn, Mn, and Cu) and for the three species of the beetles (females and males separately) feeding on wood in various stages of decomposition and containing various amounts of fungi (expressed as ergosterol content) to show the nutrient dynamics in decomposing dead wood in the context of wood eater requirements. The calculated *TSRs* involved approximately 4 to 600 μg of ergosterol per g of wood (dry mass), and they decreased with increasing ergosterol content (Fig. 13.6) by approximately 100-fold for P (from 3000 to 30), 30-fold for N (from 450 to 15), 45-fold for Fe (from 30 to 0.7), 30-fold for Cu (from 160 to 5 for cerambycids and from 30 to 1 for buprestids), 13-fold for K (from 110 to 8.5), and 10-fold for Na, Mg, Zn, and Ca (Na, from 200 to 24; Mg, from 30 to 3; Zn, from 30 to 3; and Ca, from 7 to 0.7). Although the *TSR* levels decreased by almost tenfold for Mn, this element was not limiting ($TSR < 4$). These results suggest that fungal infection of dead wood during decomposition allows saproxylophagous insects to develop, grow, and reach maturity, and the strength of these limitations might be sex and taxon dependent, especially for Cu (Fig. 13.6). This analysis, similar to Analysis 1, revealed that even the most nutritious wood is not an adequate food source for its consumers; stoichiometric mismatches persisted even if considerably mitigated via fungal infection of dead wood. Supplementary feeding on fungi may additionally mitigate nutritional limitation. Prolonged development time, which is observed in the beetle species under consideration, may be the result of stoichiometric mismatch and thus limit growth and development as suggested by Filipiak and Weiner (2017a).

The comprehensive analysis of the nutritional limitations experienced over 3–4 years of larval development by *Stictoleptura rubra* and *Chalcophora mariana* in dead wood (Filipiak and Weiner 2017a) shows that the life cycles of these beetles are shaped by the importation of N, P, K, Na, Mg, Zn, and Cu by fungi into this nutritionally harsh environment at the start of the decay process. The strategy used by saproxylophages to overcome the nutritional limitations of dead wood involves (1) fungal rearrangements of dead wood stoichiometry during the first years of decay and (2) prolonged growth supported by a low mortality risk. Because the ecological stoichiometry of saproxylophagous insects has not attracted sufficient attention, global trends based on a multi-taxa analysis cannot be determined. Additional studies on the limiting elements (e.g., P, N, K, Na, Mg, Zn, and Cu) and different taxa of dead wood and saproxylophages are needed to elucidate the important interactions between saproxylophages and dead wood as well as the dependencies of saproxylophages on the nutrient dynamics of decomposing wood associated with fungi.

An experimental study of the interactions described above may not be possible because of the long-term and expensive feeding trials required to study growing, wood-eating animals (that require several years of larval development) and to perform long-term terrain studies of decomposing wood. However, the *TSR* index was developed to identify multiple elements that co-limit the development of an organism and facilitate comparisons between various taxa, habitats, food sources, and life histories (cf. Filipiak and Weiner 2017b). This index may be used as a convenient tool in future studies.

13.9 Limitations on the Growth and Development of Saproxylophages Are Mitigated During Dead Wood Decomposition via Contributions by Fungi

The nutritional quality of dead wood changes over the first several years of decomposition, and this is important for the first species of saproxylophagous insects that colonize a dead piece of wood (e.g., the three species of wood-boring beetles presented above). However, the other species that colonize dead wood after this initial stage of decomposition also rely on the nutritional rearrangement of the wood that happens over the first several years of decomposition (Figs. 13.2 and 13.4 suggest how this mechanism may work). As discussed earlier (Sect. 13.6; Fig. 13.2), pure dead wood is too poor nutritionally to be a sufficient source of food for saproxylophagous insects. The nutrients required for insects to properly develop are transported to dead wood by fungi, resulting in a rearrangement of the nutritional composition of the wood during the first few years of decay (Filipiak et al. 2016; Filipiak and Weiner 2017a). Fungal hyphae in dead wood are connected to nutritional patches of organic matter or minerals in the external environment. Rocks can be weathered by fungi and are sources of specific atoms used to build fungal mycelia, and these atoms are further translocated within the ecosystem (Burford et al. 2003; Gadd 2007, 2017a; Gadd et al. 2012; Li et al. 2016). Fungi can consume soil fauna and exchange acquired nutrients for C from trees (Klironomos and Hart 2001); the acquired nutrients are translocated to dead wood through the fungal mycelium (Stark 1972; Swift et al. 1979; Lodge 1987; Boddy and Watkinson 1995; Dighton 2003, 2007; Cairney 2005; Watkinson et al. 2006; Clinton et al. 2009; Mooshammer et al. 2014). Depending on the size of the adult, saproxylophages can grow, develop, and reach maturity by consuming wood rich in fungal hyphae over the course of several years (Filipiak and Weiner 2017a), and during this period, they are able to gather all the building blocks (atoms) required to develop their adult bodies. This prolonged developmental time is feasible because the interior of the dead wood is a safe environment that provides superior climatic conditions, thereby reducing mortality compared with that of insects in the surrounding environment (Walczyńska 2010; Filipiak and Weiner 2017a; Walczyńska and Kapusta 2017).

13.10 Conclusions and Avenues for Future Research

The nutrient dynamics of decomposing dead wood have rarely been studied in relation to the specific nutritional needs of saproxylophagous insects. Incorporating an ecological stoichiometric framework could be used to (1) directly relate the nutrient dynamics in dead wood to saproxylophage nutrition; (2) detect specific limitations imposed on the growth and development of insects; (3) identify a set of nutritional elements that co-limit the growth and development of insects; (4) discuss how nutritional limitations influence the growth, reproductive output, survival, fitness, and life histories of dead wood eaters; and (5) better understand wood decomposition rates and standing stocks of wood in different age classes. Points 1–4 could be discussed in relation to the decomposition process as influenced by saproxylophagous insects, which could (6) elucidate the role of dead wood nutrient dynamics in nutrient cycling in ecosystems. Although the nutritional composition of dead wood (including the species-specific concentration of elements in wood) has been studied over the past 50 years, limited information is available on the needs of growing and developing saproxylophagous insects. These insects must extract elemental atoms in the correct proportions to develop and maintain stoichiometric homeostasis. Studies of the elemental compositions of various saproxylophagous insect taxa are needed to identify the nutritional requirements for various elements and relate these needs to the elemental composition and nutrient dynamics of dead wood. Relating the multielemental stoichiometry of saproxylophage bodies to the nutrient dynamics in decaying wood is a prerequisite for understanding the dynamics underlying saproxylophage nutritional balance and identifying nutritional constraints experienced by saproxylophages and potential methods to overcome such constraints. The *TSR* index could serve as a convenient and easy-to-use tool for analyzing nutritional constraints. The identified limitations should be further studied via feeding experiments, but the long larval development periods of certain species of saproxylophagous insects may render such studies technically impossible.

To date, the application of ecological stoichiometry to the nutrient dynamics of dead wood has led to the following conclusions:

1. The growth and development of dead wood-eating beetles is co-limited by the scarcity of essential elements, such as N, P, K, Na, Mg, Zn, and Cu.
2. Fungi use dead wood as a source of energy and nutritionally rearrange it while growing in dead wood during the first 4–5 years of decay. Thus, fungi can fill a

nutritional niche for dead wood eaters that facilitates insect growth, development, and maturation.

3. In turn, xylophages affect dead wood by fragmenting, shredding, and producing frass, thereby contributing to further wood decomposition and nutrient cycling.
4. Because of the complex ecological interactions among dead wood, fungi, and dead wood eaters, large masses of organic matter in terrestrial ecosystems (wood) are continuously being decomposed in forests. Much remains to be learned about the multielemental co-limitation of saproxylophagous insect growth and development and its role in shaping wood decomposition and nutrient cycling in ecosystems.

Wood stoichiometry and stoichiometric mismatches between wood and saproxylophages might vary with latitude. As was noted in Sect. 13.1, tropical wood seems to be more nutritious than temperate wood (Ragland et al. 1991; Pettersen 1984), but it is not known whether this difference is large enough to be important for saproxylophage nutrition. It is also not known whether the nutritional needs of tropical saproxylophage assemblages differ from those of similar, temperate assemblages. Considering the differences in size between tropical and temperate insects, it may be hypothesized that tropical insects require larger amounts of nutrients to build their bodies. Therefore, a simple comparison of the nutritional quality of dead wood originating from different geographical regions is not sufficient, and such a comparison should be performed that considers the wood-saproxylophage relationship.

It is possible that wood stoichiometry differs between angiosperms and gymnosperms, imposing different stoichiometric mismatches on potential consumers (see Fig. 13.2 and Sect. 13.6). A quick analysis of already available data (Fig. 13.2) has shown that angiosperms indeed impose slightly lower limitations on saproxylophages growth and development than gymnosperms, which results from the generally lower *C:other elements* ratios in angiosperm wood than in gymnosperm wood. However, even if it is slightly lower, the limiting effect still exists, and it is not known whether the observed difference between angiosperms and gymnosperms is of any importance for saproxylophages (i.e., if the difference might influence their biology). As in the case of geographical differences, elucidating this question requires considering not only the difference between the nutritional value of gymnosperm vs. angiosperm wood but also the nutritional needs of the specific saproxylic assemblages that feed on different types of wood.

Analysis of the data in the literature related to nutrient dynamics in decomposing wood has shown that studies are biased toward temperate regions (mainly Northern Europe) and especially toward the wood of *Pinus sylvestris*. Additionally, the concentrations of C in dead wood, which are necessary to calculate stoichiometric mismatches, are rarely considered. Therefore, future studies should focus on sampling more taxonomically and nutritionally diverse data. Furthermore, data on the nutritional needs and stoichiometry of saproxylophages are extremely rare, and without such data, it is impossible to discuss the nutrient dynamics in dead wood, which can be clarified only by considering the nutritional needs of the organisms feeding on this wood. Therefore, studies are needed of the nutritional needs and stoichiometry of various saproxylophages inhabiting different wood species that originate from geographically diverse locations.

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Chapter 14
Biotic Interactions Between Saproxylic Insect Species

Antoine Brin and Christophe Bouget

Abstract A better understanding of biotic interactions in species-rich saproxylic insect communities can provide essential information for biodiversity conservation and ecosystem functioning enhancement. Evidence in the literature mainly relates to beetle species, in particular scolytines, at tree—or even smaller—spatial scales and mostly refers to antagonistic interactions. We here present an overview of competition, predation/parasitism and facilitation among saproxylic insects. We first underline segregation patterns between wood consumers, resulting from competition processes, such as spatial and temporal resource partitioning, competitive displacement via interference and even enemy-mediated "apparent competition." Considering natural history facts about prey-predator and host-parasitoid relationships, we then emphasize processes regulating the pressure of top-down influences on prey/host population dynamics. Facilitative interactions, including mechanisms of habitat location, creation, and improvement, are thereafter considered. The implications of some findings for pest management strategies (biocontrol, semiochemical-based methods) and for ecosystem functioning (deadwood decomposition) are highlighted meanwhile. Approaches based on life-history traits or indirect mediated interactions finally move the focus from the responses of paired species to multispecific community-level changes. Ecological network analysis should help increase our understanding of biotic interactions and investigate the consequences of environmental changes for those interactions and ecosystem functioning.

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14.1 Introduction

Biotic interactions have lain at the heart of community ecology since the beginnings of the discipline. Through a better understanding of biotic interactions, community ecology can provide essential information for biodiversity conservation (Jordano 2016; Tylianakis et al. 2010), community stability and ecosystem functioning enhancement (Thébault and Fontaine 2010; Peralta et al. 2014), and evolutionary processes (Fontaine et al. 2011).

A saproxylic insect community can be very species rich in a very restricted location because trees or logs form a distinct, patchy and transient habitat in a landscape. Competition is therefore expected to be a key driver of these communities. However, a recent meta-analysis on the importance of competition in phytophagous insect community structure (Kaplan and Denno 2007) revealed a more complex picture: interactions may be negative or positive, direct or indirect, and are highly variable. Unfortunately, we are far from being able to conduct such an analysis with the literature on saproxylic insects, notably due to the paucity of material in respect of the huge diversity of species and habitats but also to inherent methodological difficulties. The relative influence of different antagonistic interaction types, e.g., predation/parasitism vs intra−/interspecific competition, on the dynamics of saproxylic insect populations has seldom been properly and experimentally assessed (Aukema and Raffa 2002; Maynard et al. 2015; Miller 1985). Most interpretation remains highly speculative.

In this chapter, we present an overview of some of the observed or suspected biotic interactions between saproxylic insect species, without claiming to be exhaustive. Intraspecific interactions are not treated here due to space limitations. We begin with some information about the origin and nature of the evidence that has been gathered to date. Following the chronological order of appearance of the concepts in the literature, we then develop into three sections, the evidence for competition, predation and parasitism, and facilitation (see Fig. 14.1 for a broad overview).

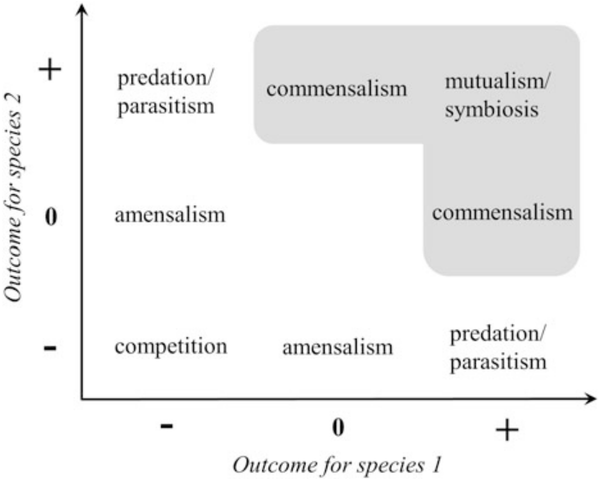

Fig. 14.1 Landscape of interspecific interactions. Facilitative interactions are outlined by the gray area

Competition will be restricted to primary consumer guilds (xylophagous, saproxylophagous, mycophagous). We draw research perspectives in a final section.

14.2 Overview of the Origin and Nature of Evidence

We combined database searches and searches of literature cited within published works to identify relevant scientific papers for this review, without any date restriction, but mainly from literature written in English. We performed keyword searches on Web of Science and Scopus using various combinations of the following terms: biotic interaction, deadwood, saproxylic insects, competition, facilitation, predation, and parasitism. Evidence in the literature comes equally from experimental and observational data and spans a broad spectrum of types (Fig. 14.2a). Logically, abundance or other demographic parameters of performance (survival, development time, relative growth rate, body size, fecundity) are the most widespread response variables. Approaches using niche overlap or the niche breadth [i.e., realized niche width (Colwell and Futuyma 1971)] are rare (see Sect. 14.2 on competition). Antagonistic interactions are by far the most investigated ones, with competition

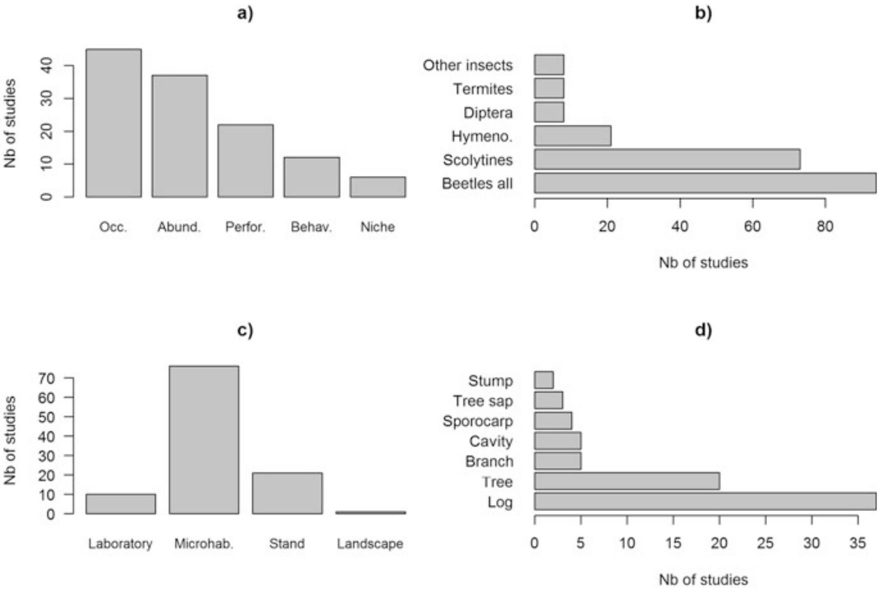

Fig. 14.2 Distribution of studies on biotic interactions between saproxylic insect species by (**a**) type of data collected (*Occ* occurrence, *Abund* abundance, *Perfor* breeding performance, *Behav* behavior), (**b**) the taxa under investigation, (**c**) the spatial scale of investigation, from local to landscape scales; and (**d**) detailed information about the substrate type for the microhabitat scale. Categories are not mutually exclusive

concerning 58% (out of 108 studies) and predation/parasitism 43% of the studies. Positive interactions are only treated in 12% of the references.

In respect to the taxonomic diversity of saproxylic insects, there is a taxonomical bias toward beetle species, in particular bark beetles (Fig. 14.2b), with respectively 86 and 67% of the references. Some species-rich orders such as Hymenoptera and Diptera have been studied far less than Coleoptera, and because most works are restricted to one order, it is hard to get a precise picture of the relative contribution of each order. Data by Savely (1939) from rearing experiments with downed logs allow us to make some rough estimates. Beetle species represented from 53 to 72% of the insect species found (depending on tree species and decay stages). However, Savely (1939) pointed out that Hymenoptera and Diptera were necessarily undersampled due to the method employed. Even so, those orders may respectively make up around 25% and 12% of the saproxylic species richness (but see Chap. 5).

Three bark beetle species have received much more attention: *Dendroctonus frontalis*, *Ips pini*, and *I. typographus* with respectively 18, 17, and 16% of the studies. This is obviously related to their economic importance as potential pest species and their value as well-known biological models. By contrast, biotic interactions involving threatened species such as *Osmoderma eremita* (two papers) or *Cerambyx cerdo* (one paper) have been scarcely investigated. This may arise from the taxonomical difficulties inherent to such a diverse group. The development of molecular analysis tools might help overcome this hurdle (see Chap. 25).

In line with the classical view that confines the importance of biotic interactions in insect community structures to local scales (Hortal et al. 2010; Soberón 2010), the studies on saproxylic insects have mainly been undertaken at tree—or even smaller—spatial scales (Fig. 14.2c, d). One can study microhabitat at the landscape scale. But this was not the case in the literature we gathered about biotic interactions. This raises the question of how to extrapolate results from local to larger scales. Indeed, there is an increasing interest toward more realistic predictions on species distribution by incorporating biotic interactions (Araújo and Rozenfeld 2014; Godsoe and Harmon 2012; Staniczenko et al. 2017; Wisz et al. 2013).

Lastly, the communities under investigation have mainly been species-poor compared with natural communities. To illustrate this point, let us consider beetles, the most studied order. About 80% of the references deal with communities made of only two to eight species. In natural conditions, the species richness in objects such as logs, cavities, or stumps ranges from 1 to 62 and reaches 234 when the meta-community level (sum of all sampling units) is taken into account (Table 14.1). For an example at an even larger scale, in Sweden, 95 species of saproxylic Coleoptera are known to live in the cambial zone of Scots pine [Ehnstrom 1999, quoted by Victorsson (2012)].

Table 14.1 Species richness of local beetle communities (mean and range) or meta-communities (total) emerging after 1 year (or one flying season) (*N* number of sampling units, *Na* not available)

Substrate type	*N*	Species richness			References
		Total	Mean	Range	
Carpophore	195	194	11.0	1–26	Rose (2011)
Cavity (oak and ash)	87	177	*Na*	*Na*	Quinto et al. (2015)
Cavity (oak)	73	234	18.5	1–58	Gouix (2011)
Cavity (oak and beech)	127	35	*Na*	*Na*	Bußler and Müller (2008)
Cavity (oak)	94	32	1.9 to 3.2	*Na*	Ranius (2002)
Log (spruce and pine)	198	103	*Na*	*Na*	Boucher et al. (2016)
Log (oak)	22	179	20.7	6–64	Bouget et al. (2012)
Log (pine)	15	60	8.0	2–14	Brin et al. (2011)
Snag (oak)	22	223	26.9	6–73	Bouget et al. (2012)
Stump (oak)	10	134	37.1	24–62	Brin et al. (2013)
Stump (pine)	18	132	36.6	13–61	Brin et al. (2013)
Wooden box	43	91	10	*Na*	Carlsson et al. (2016)

14.3 Competition Between Primary Consumers: Patterns and Mechanisms

Interspecific competition occurs when two (or more) species inhibit each other's access to shared resources that are in short supply (Birch 1957). There are two ways in which species can compete: interference or exploitation. Interference competition is a direct interaction involving either aggressive behavior, chemical communication, or even predation (Amarasekare 2002; Schoener 1983). Exploitation competition occurs when resource consumption by one species reduces the supply of this resource for another species (Birch 1957).

Evidence of competition is not easy to observe in nature. Diverse types of observations have been used. We used a framework to organize the available results on saproxylic insects loosely inspired by Connell's (1975) typology of evidence for competition, ordered by increasingly strong inference: (1) observation of resource partitioning, (2) comparison of resource use in sympatry vs. allopatry, (3) observation of direct competitive displacement via interference and (4) manipulative experimentation. We thus hope to give the reader a feel for the diversity of approaches and the heterogeneity of evidence.

14.3.1 Observations of Resource Partitioning and Spatiotemporal Segregation

Resource partitioning is a mechanism which minimizes interspecific competition (Schoener 1986). For wood- and fungus-eating insects (see below), it is mostly inferred from observed species distribution.

For wood-eating insects, for instance, many observational studies have shown that various bark beetle species partition the phloem resource at a fine scale resulting in a spatial distribution of the species along the stem and branches of a tree (Amezaga and Rodríguez 1998; Borkowski and Skrzecz 2016; Flamm et al. 1987; Grunwald 1986; Paine et al. 1981; Rankin and Borden 1991; Schlyter and Anderbrant 1993). A partitioning of resources based on body size has been suggested for some xylophagous beetles (Hespenheide 1976; Satoh et al. 2016) and wood-dwelling ants (Satoh et al. 2016). In large logs, small as well as large species can breed, whereas in very thin branches, only the smallest species occur. However, it remains uncertain whether body size is relevant when modeling phloem-feeder partitioning of resources (Paine et al. 1981; Grunwald 1986; Amezaga and Rodríguez 1998; Borkowski and Skrzecz 2016). For termite species with similar physiological tolerances, food requirements and predators, Maynard et al. (2015) hypothesized that different optimal temperatures may explain colony abundances and range boundaries in regions where they co-occur.

For fungus-eating insects, Matthewman and Pielou (1971) found that some Canadian insect species dwelling on *Fomes fomentarius* are specific to certain regions of the sporophore. In New Zealand forests, Kadowaki et al. (2011) observed that three spore-feeding beetles co-occurring on the wood-decaying basidiomycota *Ganoderma* spp. displayed different spore consumption patterns on the hymenial surface, a very limited space. One species (*Holopsis* sp. 1) was a pore-tube specialist whereas the other two (*Zearagytodes maculifer* and *Holopsis* sp. 2) were surface grazers. Guevara et al. (2000) demonstrated a successional niche partitioning for two ciid beetles (*Octotemnus glabriculus* and *Cis boleti*) which feed on different developmental stages of *Coriolus versicolor* distinguished by the age-related chemical composition of the sporocarps.

Some of the authors cited above used the degree of niche overlap to infer potential competition between co-occurring bark beetle species, as Li et al. (2015) did for termites. However, overlap may indicate either competition or a lack thereof, depending on the supply and the relevance of the resource under investigation (Colwell and Futuyma 1971). According to Lawlor (1980), niche overlap estimates cannot even come close to accurately measuring competition.

In all the examples above, it is not known whether the observed patterns are mediated by contemporary interspecific competition (competitive displacement) or result directly from species preferences. Species preferences may result from an evolutionary divergence due to competition; this has been called the “ghost of past competition” (Connell 1980). Such a mechanism was mentioned by Azeria et al. (2012) to explain the segregation patterns of two ecologically similar congeners

(*Monochamus scutellatus* and *M. mutator*) that may have evolved preferences for different tree species from past competition. The evidence provided by Guevara et al. (2000) for a competitive displacement of *Octotemnus glabriculus* by *Cis boleti* is questioned by the authors themselves. Firstly, the abundance of the inferior competitor was lower in sympatric situations than it was in allopatric situations. Secondly, the reproductive activity of the two species appeared to be independent of the presence or absence of the so-called competitor. Guevara et al. (2000) therefore concluded that resource partitioning is probably mediated by preferential choices for different developmental stages the fungus host. Lee and Seybold (2010) hypothesized competitive displacement of *Scolytus multistriatus* by *S. chevyrewi*. And they also clearly stated that further investigations are required to elucidate the mechanisms involved. Competitor-avoidance behavior of female woodborers have been observed in Canada by Gardiner (1957): the *Monochamus scutellatus* females inspected logs by bark chewing and antennal scrutiny before laying eggs, and they actually avoided laying eggs on the bark of trees already heavily infested by bark beetles.

It is intriguing to highlight that no ecological evidence for competition among hollow-dwelling species has been published, even though interspecific competition could be enhanced in space-limited habitats like tree cavities. Hilszczański et al. (2014) and Chiari et al. (2014) found no evidence of interspecific competition between larvae of *Osmoderma* spp. and other co-occurring Cetoniinae species in tree cavities, although both taxa seem to have similar food requirements (wood mold). One may hypothesize that those species forage in different parts of the cavity. As noted by some authors (Elton 1966; Graham 1925), the occupancy patterns of a set of deadwood items are very patchy. In other words, at the scale of a cavity or a log, for example, species do aggregate rather than segregate. According to the competitive exclusion principle (Gause 1934), such a pattern cannot arise when competition is strong. One may therefore hypothesize that competition is not a significant mechanism for the structure of saproxylic insect communities at the local scale. However, based on a simulation work, Ulrich et al. (2017) pointed out that species interactions could not be inferred from spatial patterns (i.e., co-occurrence) because these patterns also depend on the dispersal of the species under consideration.

A large body of theory exists on spatial coexistence mechanisms for competing species (Amarasekare 2003), but empirical evidence is very scarce for saproxylic insect communities. We only found two tests, one for the aggregation model and one for the competition-colonization trade-off model.

For resources occurring in discrete patches, the aggregation model of coexistence stipulates that species are spatially aggregated in many patches, thus creating random spatial refuges for inferior competitors in the empty spaces (Atkinson and Shorrocks 1981; Ives and May 1985). In a study of the insect community inhabiting the wood-decaying bracket fungus *Cryptoporus volvatus* in Japan, the aggregation model of coexistence satisfactorily explained the stable coexistence of the species under study (Kadowaki 2010).

The competition-colonization model predicts that competitors can coexist if patch dynamics offers colonization opportunities for an inferior competitor and if the dominant competitor is dispersal-limited (Calcagno et al. 2006). By combining model-fitting with observational time-series data, Kadowaki et al. (2011) provided some evidence for spatial niche partitioning in the competitive coexistence of spore-feeding beetles on the wood-decaying basidiomycota *Ganoderma* spp. However, they also acknowledged that further mechanistic evidence of beetle dispersal is required to demonstrate the existence of competition-colonization trade-offs.

Reduced competition can also arise from seasonality, whereby one species tends to be active (dispersing and/or foraging) earlier or for a different length of time or whose voltinism differs from other species using the same resource within the same region. Here we speak of temporal niche partitioning (Chesson 2000). For instance, in North America, the niche overlap of the sympatric cambiophagous pine beetles *Ips pini*, *I. perroti*, and *I. grandicollis* is reduced by their differences in phenology and voltinism (Ayres et al. 2001). Another example is from Rankin and Borden (1991); they hypothesized that *Ips pini* and *Dendroctonus ponderosae* mainly interact through exploitation competition. With a short life cycle and two to three generations per year, *Ips pini* can monopolize the phloem resource before *Dendroctonus ponderosae* has access to it (Rankin and Borden 1991). Finally, in freshly dead spruce in Finland, three scolytines coexist (*Hylurgops palliatus*, *Trypodendron lineatum*, and *Dryocoetes autographus*). By occupying the space and modifying the substrate by seeding the mycelium they feed on, they may reduce, due to the priority effect, the colonization by *Ips typographus* whose flights occur later in the summer (Joensuu et al. 2008). This hypothesis still has to be tested. Indeed, one may wonder if competition is restricted to bark or ambrosia species pairs or if competition can occur between these two types of scolytines.

When manipulative experiments are ethically (rare species) or logistically (too many species) impossible, null models have been put forward as a useful tool to detect competitively induced patterns (Connor and Simberloff 1986; Gotelli and Graves 1996). These models generate patterns of species presence and/or abundance which would emerge in some metacommunity if each species had the same habitat preferences and the same level of occupancy and abundance in the metacommunity than derived from observations, but were not interacting with other species. They use randomization techniques. If generated patterns do not significantly differ from observations, it suggests that interactions (most often competition) do not contribute a lot to the metacommunity assembly. Null models are however hard to implement because they need to account for all known differences in the species' habitat preferences (Peres-Neto et al. 2001; Sanderson 2004). As far as we know, such an approach has only been undertaken once for saproxylic species (Azeria et al. 2012) and the interpretation of the pairwise results is delicate, notably for statistical reasons. However, Azeria et al.'s results have at least opened some perspectives for further investigation (see above).

14.3.2 Natural Experiments

Natural experiments exploit natural situations in which competitors occur in sympatry to compare them with situations where each species occurs in allopatry. In this way, one can evaluate how much their niche breadth contracts (or not) in the sympatric situation to infer that interspecific competition is at work (Colwell and Futuyma 1971; Diamond 1978).

The arrival of an invasive species provides such insightful situations. Surprisingly, though several cases of competitive displacement related to invasive species are suspected for beetles (Bybee et al. 2004; Lee and Seybold 2010) and termites (Perdereau et al. 2011), no investigations have yet been carried out.

There are very few documented cases which compare sympatric and allopatric situations at the tree level, and all of them concern bark beetle species. Most studies have found that the beetles occupy broader niches in the absence of their competitor than they do in sympatry with them. For instance, Paine et al. (1981) observed that in standing loblolly pines (*Pinus taeda*) in the southeastern United States, both *Dendroctonus frontalis* and *Ips avulsus* colonized less area in the presence of *Ips calligraphus* than would be expected if they had been alone. By contrast, *I. calligraphus* did not colonize less area when in sympatry with *D. frontalis* or *I. avulsus* alone. However, a reduction in the breeding area of *I. calligraphus* was observed when all three species were found together. Another example is that of *Ips pini* which often invades the entire bole of lodgepole pine (Reid 1955). On a *Dendroctonus ponderosae*-infested tree in the field, an induced attack by *I. pini* led to a strong reduction in the progeny production of *D. ponderosae* (Rankin and Borden 1991). Flamm et al. (1987) induced colonization of loblolly pine by *Dendroctonus frontalis* and *Ips calligraphus* by girdling the trees and baiting them with bark beetle pheromones. They observed a population-dependent regulation of egg densities. Indeed, both species produced fewer galleries per adult when adult densities were higher. This compensatory feedback mechanism reduced competition within and among the two brood species.

Hui and Xue-Song (1999) used the overlapping area occupied by two bark beetle species on the same trunk as the sympatric situation to compare with the other parts of the trunk where each species occurred alone. They compared larval densities and suggest that *Tomicus minor* has a negative impact on the reproductive level of *Tomicus piniperda*.

A key assumption in inferring competition from natural experiments is that the only relevant difference between sympatry and allopatry is the respective presence or absence of one of the putative competitors. Accurately measuring the resource levels between the two situations is of prime importance if we are to infer that the species lower each other's resource use (Diamond 1978). Unfortunately, this has not been done in the studies we surveyed.

14.3.3 Direct Observations of Interference Competition

Numerous bark beetles seem to segregate themselves within specific portions of the tree or between trees through chemical communication, a process known as synomonal inhibition (Birch et al. 1980; Byers and Wood 1980; Byers et al. 1984; Byers 1993, 2004; Coulson et al. 1980; Flamm et al. 1987; Light et al. 1983; Paine et al. 1981; Raffa 2001; Wagner et al. 1985), a synomone being beneficial to both the producer species and the different recipient species. Repelling can be reciprocal, as, for example, between *Dendroctonus ponderosae* and *Ips pini* (Hunt and Borden 1988), but this is not always the case (Byers 1993). Rankin and Borden (1991) acknowledged that the number of *Dendroctonus ponderosae* progeny could possibly also be reduced through interference competition with *Ips pini*. Among the mechanisms involved here, Rankin and Borden (1991) suggested the introduction by *I. pini* of fungal competitors be deleterious to the symbiotic fungal associates of *D. ponderosae*, but this deserves further experimental investigation according to the authors.

In insect communities attracted to fermented sap-exuding patches on trees, agonistic interactions such as fighting behavior or departures from the patches may occur. Such interactions result in the establishment of interspecific dominance hierarchies. Competitor-avoidance behavior in subordinate species play a significant role in their foraging success at sap sites (Yoshimoto and Nishida 2009). Fighting behavior between adult male stag and horn beetles feeding on sap-exuding patches on trees have been documented by Hongo (2014). An apparent superiority of the horn beetle (*Trypoxylus dichotomus septentrionalis*) over the two stag beetle species (*Lucanus maculifemoratus maculifemoratus* and *Prosopocoilus inclinatus inclinatus*) arose by comparing body mass and observing fighting behavior. The two stag beetle species also exhibit mate-securing tactics by emerging at the feeding sites early and late during the breeding season, respectively, which limits their encounter rates with the superior competitor. Hongo (2014) hypothesized that stag beetles shift their daily activity patterns to secure feeding sites and breeding females in areas where these three species occur synoptically.

Several laboratory bioassays on termites have documented mortality rates following interspecific encounters (Li et al. 2010; Perdereau et al. 2011; Shelton and Grace 1996; Springhetti and Amorelli 1982; Uchima and Grace 2009) with several cases of asymmetry in agonistic behavior. Thorne and Haverty (1991) compiled evidence for contingency in such behavior based on species, colony, nest, individual and climatic conditions. Interpretation of such bioassays should thus cautiously account for these contingencies to avoid erroneous conclusion about agonistic interactions [see Cornelius and Osbrink (2009), Polizzi and Forschler (1998); quoted by Li et al. (2010) for agonism responses].

Many organisms use predation as an interference mechanism (Amarasekare 2002). Intra-guild predation can be seen as a combination of competition and predation (Polis et al. 1989) and has been documented for saproxylic insects (Box 14.1). But according to the authors mentioned below, intra-guild predation should be distinguished from simple competition due to the immediate energetic gains for the predator.

Box 14.1 Intra-guild Predation Among Wood-Eating Insects

Among wood-eating insects, the wood-eating larvae of longhorn beetles, classified as resource competitors for bark beetles, can facultatively act as intra-guild predators of other phloem-inhabiting beetles. For instance, foraging by *Monochamus titillator* and *Acanthocinus aedilis* (Coleoptera: Cerambycidae) larvae significantly reduced the survival and fecundity of the bark beetles *Dendroctonus ponderosae* and *Tomicus piniperda*, respectively (Coulson et al. 1976; Schroeder and Weslien 1994). The mechanism involved still has to be elucidated. Dodds et al. (2001) further demonstrated that bark beetle larvae were not only killed but also ingested by *Monochamus carolinensis* (Col. Cerambycidae) larvae. From Schoeller et al. (2012), using PCR-based molecular gut content analyses, about 10% of the field-collected *Monochamus titillator* larvae tested positive for the DNA of at least one of the five co-occurring species of pine bark beetles in the southeastern USA. The authors hypothesized that this intra-guild predation may result from an adaptation of *M. titillator* for living in a nitrogen-poor habitat.

14.3.4 Evidence from Manipulative Experiments

Experimental manipulations of saproxylic insect communities are few and far between, probably due to the technical difficulties of this kind of investigation. Most of the existing studies are restricted to two species. Factors investigated include species ratio, the density of individuals, order of arrival and agonistic behavior—all of which appear to play a role in establishing a competitive interaction.

A key point which emerges from manipulative experiments is the asymmetry of the competitive interactions, as observed for two pairs of bark beetle species: *Ips pini-Ips paraconfusus* (Light et al. 1983) and *Dendroctonus ponderosae-Ips pini* (Davis and Hofstetter 2009; Rankin and Borden 1991). This asymmetry can be subtly influenced by order of arrival. *Rhagium inquisitor* suffers from competition with *Acanthocinus aedilis* only when it arrives in second position (Victorsson 2012).

Density dependence and sex ratio effects were evidenced by Light et al. (1983) for *Ips pini* and *I. paraconfusus*. Moreover, the nature of the competitive outcome can change from negative to positive depending on sex ratio. However, we currently know very little about how factors such as competing predator density or sex ratios determine the sharing of resources between natural enemies (Hougardy and Grégoire 2001).

In manipulative experiments, the strength of the competition is highly variable. Furthermore, effects can only be revealed by investigating the impact on offspring. Rankin and Borden (1991) observed severe reductions of between 72.5 and 92.8% in

Dendroctonus ponderosae progeny when the species co-occurred with *Ips pini*. Boone et al. (2008a) estimated a reduction of 22% in *D. ponderosae* progeny due to the presence of *I. pini*. In both studies, beetle densities and sex ratios were similar and had been selected to emulate field conditions. *Rhagium inquisitor* descendants showed a 39% weight loss under the influence of competition by *Acanthocinus aedilis* (Victorsson 2012).

The experimental removal of the giant hornets (*Vespa mandarinia*), one of the most dominant species in a sap feeder community, induced higher abundance for 5 out of 19 taxa (Yoshimoto et al. 2007). However, this manipulation showed no effect on either species richness or total abundance of the remaining insects. Interference competition induced by the fighting behavior of hornets seemed to be only a minor determinant in overall community structure, probably due to the short stay of the dominant species and to individual behavioral responses, such as competitor avoidance (Yoshimoto et al. 2007).

As shown by the evidence mentioned above, the relative importance of competition among saproxylic insects in structuring their communities and how competition intensity varies are open and challenging questions.

14.4 Prey-Predator and Host-Parasitoid Relationships in Saproxylic Food Webs

Saproxylic food webs include a wide diversity of insect predators [Coleoptera (Cleridae, Histeridae, Trogossitidae, Rhizophagidae, etc.), Diptera (Lonchaeidae, Dolichopodidae, etc.), Heteroptera (Anthocoridae, etc.)] and parasitoids [mainly Hymenoptera (Braconidae, Pteromalidae, etc.) and Coleoptera (Bothrideridae, Staphylinidae, Elateridae, etc.)], all of which feed on primary consumer guilds (Kenis et al. 2004). Compendia of the literature on relationships between bark beetles and their natural enemies are currently available [see, e.g., Kenis et al. (2004) and Raffa et al. (2015)].

In the following section, we consider natural history facts about prey-predator and host-parasitoid relationships and provide an overview of processes regulating the pressure of top-down influences (predation and parasitism) on prey/host population dynamics. The implications of some findings for biocontrol strategies are highlighted (Boxes 14.2 and 14.3).

14.4.1 Life-History Traits and Enemy-Prey/Host Relationships

Saproxylic insects spend most of their lifetime inside living trees, in deadwood tissues or in associated microhabitats, and only several groups have adult stages that live in the open air on tree bark or surrounding flowers. As a result, their predators and parasites face a challenge when trying to locate and catch their prey. Predators exhibit morphological adaptations to their specialized type of foraging: many deadwood-associated species are cylindrical shaped, which enable them to forage in tunnel galleries, or flat-shaped to better move through the subcortical space. Some predators have also developed adaptative behavioral strategies, such as trapping (e.g., lignicolous *Allomerus* ants; Dejean et al. 2013).

Several parasitoids enter the bark through entrance and emergence holes and directly oviposit in the galleries, though most female parasitoids oviposit through the bark onto host larvae. Bark thickness and parasitoid ovipositor length have a crucial effect on parasitism success rate: the percentage of *Dendroctonus pseudotsugae* larvae parasitized by the wasp *Coeloides brunneri* at any given height in a tree is influenced by the percentage of the tree circumference which has an outer bark thickness of less than the mean ovipositor length (Ryan and Rudinsky 1962). Similarly, two parasitoid wasp species (*Tetrastichus planipennisi* and *Atanycolus* spp.) were unable to parasite the emerald ash borer (*Agrilus planipennis*) in trees with bark thicker than 3.2 mm and 8.8 mm, respectively, due to ovipositor length limits (Abell et al. 2012).

Olfactory and optical cues are commonly used by natural enemies to locate their insect prey/hosts at both short and long distances. The first step in searching for prey is to locate a suitable foraging habitat, i.e., a host tree. Dark vertical silhouettes are known to attract bark beetle predators (*Thanasimus* sp., *Rhizophagus grandis*) in the field (Raffa et al. 2015). Beetle enemies also follow volatiles released by trees under attack by wood-eaters. For example, the camphor, fenchone, and verbenone emitted by Norway spruce colonized by *Ips typographus* (Curculionidae: Scolytinae) are attractive to female parasitoids of *Rhopalicus tutela* and *Roptrocerus mirus* (Pteromalidae) (Pettersson 2001a).

Volatile chemicals released by the prey/hosts themselves (from pheromones to larval frass) act as kairomones (Grégoire et al. 1991; Pettersson 2001b) and give specialist natural enemies such as egg-larval and adult parasitoids a more reliable signal of prey presence than do host tree volatiles (see, e.g., the differential response of *Dastarcus helophoroides* [Coleoptera: Bothrideridae] to substances emitted by host trees or the longhorn beetle host; Wei et al. 2008). *Elater ferrugineus*, a European click beetle whose larvae consume other saproxylic insect larvae in hollow trees, use the male-produced sex pheromone of *Osmoderma eremita* to locate its prey's microhabitat (Svensson et al. 2004).

How female parasitoids so precisely locate potential hosts beneath the bark is poorly known. It is however recognized that the complex and often taxonomically specific blends of long-chained cuticular hydrocarbons (CHC) on beetle hosts play a role as a semiochemical cue for host location by foraging female parasitoids, which find their hidden host by following its CHC trails (Fürstenau and Hilker 2017). Some experimental evidence from studies of bark beetles also suggests that parasitoids orient to sound (Wang et al. 2010), heat in the form of infrared radiation (Richerson and Borden 1972), chemical cues (Mills et al. 1991; Pettersson 2001a) or fungal cues (Boone et al. 2008b).

Predators attacking multiple bark beetle prey have antennal receptor cells keyed to many different pheromones. For example, *Thanasimus formicarius* has sensillae keyed to 22 bark beetle pheromones and conifer volatiles (Raffa et al. 2015). Although receptive to many signals, some predators can learn to respond to one particular signal after a first exposure. Early arrivers are also sensitive to signals indicating that a mass attack has reached its end. For instance, predators specializing on early successional bark beetles (e.g., *Thanasimus undulatus*, *Enoclerus sphegeus*, *Enoclerus lecontei*, and *Lasconotus* sp.) are repelled by verbenone, since this volatile, released by some bark beetles to indicate to their congeners that a tree is "full," indicates a late-stage attack. Generalist predators either do not respond to verbenone at all, or they may be attracted by it (Lindgren and Miller 2002). Late arrivers (larval ectoparasitoids) respond to odors produced by the larvae's microbial symbionts (Raffa et al. 2015).

The relative role of each signal (trunk silhouettes, synomones from host substrates, prey kairomones) and the extent of synergistic effects in multitrophic interactions are still active fields of research. The existence of a "generalist" (e.g., clerid beetles) and a "specialist" strategy (e.g., trogositid beetles) in olfactory perception has been suggested (Raffa et al. 2015).

The specificity, or exclusivity, of predators to prey species not only hinges on detection ability but also on other life-history traits. For instance, *Rhizophagus grandis*, a specific and exclusive predator of the bark beetle *Dendroctonus micans*, has developed relatively high tolerance to monoterpene toxicity, which allows it to follow its prey into living host trees. Its potential competitors, for example, *Rhizophagus dispar* (Paykull), do not have the same level of resistance to monoterpenes (Everaerts et al. 1988).

Predation/parasitism may be limited by the predator/parasitoid specialization. The ecological cost of specialization for natural enemies has deleterious demographic effects in case of prey/host scarcity. The natural enemies which live longer than their bark beetle prey could experience a shortage of resources during a part of their life cycle. It should however be acknowledged that bark beetles as hosts/preys often have several generations per year, despite their short-lasting development. Natural enemies may develop an opportunistic strategy to compensate for potential resource scarcity, by attacking a flexible range of prey/host species and/or developmental stages in order to be able to switch prey/host (broadening the feeding niche). Attacking many different species of prey may benefit predators that are partially asynchronous with their specialist prey. For instance, *Thanasimus formicarius* has a 2-year generation time (Schroeder 1999), and has been recorded attacking at least 27 different prey species (Tømmerås 1988) with overlapping phenologies during the same season. Many parasitoids seem to be able to attack other hosts if the preferred host is not readily available. This adaptability to switch from one host to another may be a survival-enhancing mechanism. Some models have described the shifts parasitoids make between two beetle hosts (*Ips* and *Dendroctonus frontalis*) as each host becomes relatively more or less abundant over time (Kudon and Berisford 1980). We do not yet know how the presence of alternative hosts determines the sharing of host resources among parasitoids (Hougardy and Grégoire 2001).

Box 14.2 Semiochemical-Based Methods of Deterring Bark Beetle Attacks

Semiochemical-based methods of deterring bark beetle attacks have been investigated. Host tree colonization by bark beetles actually depends on the relative amounts of attractant, e.g., aggregation pheromones, and anti-attractant compounds released. When beetles reach a maximum attack density on the host tree, some of them produce their own anti-attractant compounds that inhibit the attraction of new conspecifics. These studies have led to the use of anti-attractants such as verbenone, an anti-aggregation pheromone produced by several bark beetle species including the western pine beetle (WPB) *Dendroctonus brevicomis*, to minimize damage caused by beetle infestations. Tests of verbenone's efficiency in interrupting colonization by WPB were inconsistent, but recent investigations have identified and tested other anti-attractants such as acetophenone and fenchyl alcohol (Erbilgin et al. 2007). Erbilgin et al. (2007) suggested that acetophenone may play a role in intra- and interspecific interactions among sympatric species of bark beetles, and its use would not disrupt colonization of the natural enemy (*Temnochila chlorodia*, Coleoptera: Trogositidae).

Another proposed approach for biologically controlling bark beetles is to use semiochemicals to selectively manipulate predator movements without attracting the pests themselves in order to obtain the highest possible predator-prey ratio (Aukema et al. 2000). Using traps baited with frontalin, a semiochemical produced by a number of *Dendroctonus* species, selectively attracted the predator *Thanasimus dubius* without attracting the principal bark beetle in the system, *Ips pini* (Aukema and Raffa 2005).

14.4.2 Top-Down Influence of Natural Enemies on the Dynamics of Saproxylic Insect Systems

The impacts of natural enemies have been measured mostly on bark beetles (Raffa et al. 2015), occasionally on termites (Maynard et al. 2015), and very rarely on other saproxylic insects such as fungus-dwelling beetles (Paviour-Smith 1968). Data are collected through a variety of approaches, including direct laboratory observations under controlled conditions, short-term field sampling, and modeling.

The response of prey to predation or parasitism has been quantified through a wide range of metrics: predation/parasitism rate, killing rate, consumption per day (or per life cycle), induced larval/egg mortality, decreased fecundity, and reduced emergence. Available figures were scarcely provided by experiments that both strictly exclude natural enemies and measure effective demographic effects on prey populations. Life tables, which could facilitate the study of saproxylic insect population dynamics, are uncommon (but see Duan et al. 2014). Kenis et al. (2004) compiled killing or parasitism rates of bark beetles by insect predators and parasitoids but the rates vary widely, ranging from 0 to 100%. Studies of bark beetles in North America and Europe indicate low parasitoid mortality on average (Amman 1984; Feicht 2004; Hougardy and Grégoire 2001; Weslien and Schroeder 1999).

The relative importance among top-down influences (predation or parasitism) is poorly understood. During a post-storm surge in *Ips typographus* on Norway spruce forests in France and Switzerland, predators were more abundant and therefore the main cause of mortality in the first year of the study while parasitoids were more abundant and therefore caused higher mortality in the second year (Wermelinger 2002). The number of killed bark beetles by each antagonistic group was actually estimated using literature-based consumption rates. Additional generations of natural enemies would be required to significantly reduce host populations (Hougardy and Grégoire 2001). For other xylophagous insects, the relative role of parasitoids remains unclear (Kenis et al. 2004). For instance, Boone et al. (2008a) captured many more predators than parasitoids during the analysis of *Ips pini* populations in North America. For fungus-associated beetles, Paviour-Smith (1968) showed that a parasitic wasp, *Cephalonomia formiciformis* (Bethylidae), exerted high mortality on ciid beetle populations though population extinction did not occur.

Time series, spatially replicated if possible, can be informative when characterizing the local and regional processes affecting spatiotemporal dynamics of bark beetles and their key predators. The inherent tendency for predator-prey interactions to generate coupled oscillations in abundance has never been observed in real saproxylic insect populations. The "time-series" approach can be illustrated by the famous case study of *Dendroctonus frontalis* (the southern pine beetle, SPB), the most destructive insect pest on pine in the southern USA, and its key predator *Thanasimus dubius* (Col. Cleridae). A first time-series analysis of fluctuations in SPB suggested that *T. dubius* densities play a significant role in beetle dynamics, with a delayed reaction possibly because predators often have longer life cycles than do bark beetles (Turchin et al. 1999). The authors determined that SPB mortality associated with predation is negligible in the population growth phase, increases during the peak year of the bark beetle populations, and peaks during the decline of the bark beetle. Further long-term time-series analyses by Weed et al. (2017) indicated that the abundance of the key SPB predator responded almost instantaneously to changes in SPB abundance and that local dynamics of SPB and *T. dubius* are not cyclical. *T. dubius* does not typically go locally extinct when SPB is absent or rare, since it is able to maintain a stable population on other conifer-attacking bark beetle species (e.g., *Ips* spp.; Martinson et al. 2013). In line with the debate about bottom-up versus top-down regulatory mechanisms (Hunter and Price 1992), spatial variation in the long-term forest-scale abundance of both *Ips* spp. and SPB was more linked to the bottom-up effect of the density of pine habitat than to top-down predation effects. Geographically broad exogenous effects such as resource availability (e.g., following climatic patterns) are presumed to be stronger than predation effects in SPB population dynamics.

Other case studies have highlighted this limited top-down influence compared with stronger bottom-up effects in saproxylic insect system dynamics. Marini et al. (2013) analyzed demographic time-series data for *Ips typographus* and *Thanasimus* *formicarius* in Sweden from 1995 to 2011 and found no clear influence of *T. formicarius* on the bark beetles' demography. Increased breeding material after storm damage was the principal trigger of the outbreaks, with intraspecific competition as a density-dependent negative feedback. The mechanisms underlying *Ips typographus* declines after outbreaks are not fully understood up to now.

The insurance model predicts that the top-down control of wood-dwelling insects increases with enemy richness, due to synergistic interactions among natural enemies covering a wider range of forest conditions (Jonsson et al. 2017). However, in their meta-analysis, Letourneau et al. (2009) did not find mention of any significant effect of enemy richness on top-down control of herbivorous arthropods in nonagricultural habitats. Nor did we find any published results to support or invalidate the insurance model hypothesis.

Box 14.3 Successful Biocontrol Case Studies: *Dendroctonus micans* and *Agrilus planipennis*

Regarding the biocontrol of xylophagous insect pests, one classical and one emerging technique are mentioned below. First, *Rhizophagus grandis*, a specific predatory beetle, is widely used for the biological control of its prey, the greater Eurasian spruce beetle, *Dendroctonus micans* (Grégoire et al. 1989). Mass reared in insectaries, *Rhizophagus grandis* has been released on thousands of hectares of infested stands in Russia, France, the UK, and Turkey (Grégoire et al. 1989). Using chemical signals, the predator rapidly locates and colonizes *D. micans* brood chambers advancing at a rate of about 200 m/year, with exceptional movements of 1 km or more occurring (van Averbeke and Gregoire 1995). The proportion of colonized brood chambers is used to measure the predator's expansion. In a French experiment, 54% of the broods in a 2 km radius had been colonized by *R. grandis* 3 years after release. Practice has taught us that, several years after a release, the rate of *D. micans* infestation will always fall to, and remain at, a harmless level of 5–10% of infested trees and that 60–80% of the broods will eventually be colonized by *R. grandis* (Grégoire et al. 1989). Secondly, natural enemies have been introduced to control the emerald ash borer (EAB) *Agrilus planipennis*, an invasive phloem-feeding beetle originating from Asia, which has been responsible for the death of millions of ash trees in North America since 2002. A significant and sudden decline in EAB larval density in small-diameter trees was observed by Duan et al. (2014, 2015) after introduction of exotic natural enemies. Actually, the successful biocontrol of EAB involves both local, generalist natural enemies (such as *Atanycolus* wasps) and introduced specialist parasitoids (such as *Tetrastichus planipennisi*; Duan et al. 2015). The efficiency of this biological control is still limited by the length of ovipositors of the parasitoids that are too short to reach larvae under thick bark (Abell et al. 2012, see Sect. 14.3.1).

14.4.3 Ecological Processes Limiting Predation or Parasitism

The dynamics of enemy-prey/host relationships are influenced by a set of factors, including prey/host detection ability, contrasting dispersal abilities, life cycle duration, and fertility of both prey/host and enemy. Synchronism of activity cycles and specificity of prey/host preferences also play a role. As a consequence, several ecological processes have been advanced to explain the sometimes limited impact of predation/parasitism on prey/host population dynamics: (1) anti-enemy mechanisms, (2) spatial escape from enemies, (3) predator swamping, (4) density dependence, and (5) interference competition among natural enemies.

14.4.3.1 Antipredator and Anti-parasitoid Mechanisms

Saproxylic insect defenses against natural enemies include detection avoidance (e.g., camouflage), evasive behavior, microhabitat refugia, or mechanical defense. Thanks to highly dynamic interactions, bark beetles are known to sometimes modify their own communication system throughout their distribution range to avoid being located by their enemies (Raffa and Dahlsten 1995). Another line of defense consists of warding off attacks by advertising the presence of strong defenses like unpalatability (aposematism) or by mimicking animals which do possess such defenses. It has recently been demonstrated that North and South American cerambycid species (respectively, *Megacyllene caryae*, and *Callisphyris apicicornis*), which are conspicuously patterned yellow and black, are mimics of co-occurring vespid wasps. They also mimic their model's pungent odor by producing the common constituents of vespid alarm pheromones (Mitchell et al. 2017). Beetles of the saproxylic family Lycidae have long been known to use chemical protection strategies. The North American species of the lycid genera *Calopteron* and *Lycus* contain a systemic compound, lycidic acid, which was shown to actively deter predatory beetles during feeding tests. In addition, the lycid genera produce pyrazines that could be aposematic to predators (Eisner et al. 2008). The *Lycus* species are models of mimic species such as the cerambycid beetle genus *Elytroleptus*, which prey upon the model lycids (Eisner et al. 2008). Prey species can use both passive and active chemical strategies to avoid and prevent predatory attacks. The first form is typical of insects whose tissues are saturated with toxic substances. The active strategy is exemplified by species which produce and store noxious substances in the hemolymph or in special glands and then eject them onto predators. The musk longhorn beetle (*Aromia moschata*) attacks its predators by releasing large amounts of salicylaldehyde and iridodial produced in the metasternal gland (Unkiewicz-Winiarczyk and Gromysz-Kałkowska 2013). Besides chemical deterrents, defensive behavior also includes active sound emissions, for example, the Passalidae squeak when disturbed (by rubbing the undersides of their wings across their abdomen; Buchler et al. 1981).

Several wood-dwelling social insects defend their colonies by recruiting suicidal soldiers among a special caste of female workers equipped with mandibular glands filled with a sticky substance (Asian *Camponotus* ants, *Globitermes sulphureus* and *Anoplotermes* sp. termites). The substance is released when the kamikazes explode their own body through violent muscle contractions. The defensive liquid solidifies in the air and impairs the movements of intruding predators. Finally, some species are able to directly attack the predator. The heads of *Nasutitermes corniger* termite soldiers resemble a glue tube filled with a toxic terpenoid substance which is shot at the predator (Unkiewicz-Winiarczyk and Gromysz-Kałkowska 2013).

14.4.3.2 Spatial Escape from Enemies

The hypothesis of escape in space from enemies was originally proposed to explain the rapid growth in *Ips typographus* bark beetle populations in windthrow gaps during the first summer after a storm (Schroeder 2007). The idea was that prey are more effective at colonizing and establishing local populations than are their predators when the resource is highly aggregated in space and time.

Fresh-deadwood-associated species, which depend on a resource whose natural distribution is spatially and temporally fragmented, are considered to be good dispersers which rapidly and efficiently colonize newly emerged habitat patches despite weak initial populations. For several species of bark beetles, dispersal abilities have even been evaluated at several kilometers (e.g., for *Ips typographus*; Forsse and Solbreck 1985). It is assumed that dispersal ability is lower for enemies than for their prey/hosts (but see Costa et al. (2013) for reverse trends). Beetle predators' movement patterns also appear to be more restricted by fragmentation (Costa et al. 2013). Komonen et al. (2000) demonstrated that habitat fragmentation truncated the food chains of fungus-dwelling species in boreal spruce forests in eastern Finland. Ryall and Fahrig (2005) highlighted the differential impact of habitat loss at the landscape scale on scolytine predators and their prey (*Ips pini*), with a reduction in the predator-prey ratio as habitat isolation increased. The authors hypothesized that it may change the population dynamics of the scolytine leading to higher outbreaks hazards. It should also be noted that long flight periods and frequent long-distance flights have been observed for some predators (Cronin et al. 2000), thus suggesting that the cumulative dispersal capacity of these predators is greater than that of their prey (Schroeder 1999).

Other parameters than dispersal ability have been invoked in the spatial escape concept. Activity asynchronism and the difference in life cycle duration actually limit initial predation pressure. Predators are often more active than their prey at the end of winter (Kenis et al. 2004). In Sweden, Weslien and Schroeder (1999) showed that the predator *Thanasimus formicarius* of the spruce bark beetle *Ips typographus* initiates its flights early in spring, about a month before its prey, at a time when the main available prey is a pine bark beetle, *Tomicus piniperda*. As a result, many of the first-generation *Thanasimus* individuals leave spruce stands and settle in Scots pine stands. Moreover, one generation of *Thanasimus* lives 2 years, while *Ips typographus* lives only 1 year in Sweden (Schroeder 1999).

The idea that enemies and prey exhibit contrasting dispersal abilities and that wood-feeding beetles may benefit from decreased predation pressure is also associated with another ecological concept, the enemy release hypothesis (Schultheis et al. 2015). The absence of keystone predators from a community can result in a secondary increase in competitors elsewhere in the food web and consequently extirpate other competing species. However, empirical case studies of these processes are scarce. As mentioned by Jonsson and Nordlander (2006), the lack of colonization of *Fomitopsis pinicola* fruiting bodies by the polyphagous predator *Medetera apicalis* caused an overall decrease in the average number of colonizing fungivore taxa per fruiting body. This mechanism is also thought to contribute to the success of invasive species in their introduced range; they undergo less damage from enemies compared to co-occurring native species (Schultheis et al. 2015). For instance, invasive termite species have been shown to display higher-than-normal levels of interspecific antagonism and lower-than-normal levels of intraspecific antagonism (Perdereau et al. 2011), thus allowing them to become competitively dominant by minimizing the energy lost in competitive interactions among conspecifics (Maynard et al. 2015).

14.4.3.3 The Risk of Predator Swamping

Wood-eating prey may adopt a group-colonization strategy to face generalist predators in the absence of emergent multiple enemy effects. Mass emergence or mating aggregations are known to be used by periodical cicadas as survival strategies involving predator satiation, i.e., the saturation of predator feeding abilities (Williams et al. 1993). In the saproxylic context, such a process of predator dilution (or predator swamping) was demonstrated by Aukema and Raffa (2004) in an experimental test with a prey bark beetle, *Ips pini*, and two predators, *Thanasimus dubius* (Coleoptera: Cleridae) and *Platysoma cylindrica* (Coleoptera: Histeridae). Each predator alone decreased *I. pini's* net replacement rate by approximately 42%, while their combined effect was approximately 70%, and was therefore neither additive (in case of predator saturation) nor synergistic. The fact that the proportional impact of the predators decreased with increased bark beetle densities suggests that prey aggregation dilutes predation effects.

14.4.3.4 Density-Dependent Relationships in Enemy-Prey/Host Dynamics

Most parasites and predators show a typical density-dependent response in relation to prey density. For instance, Weslien (1994) observed that *Thanasimus* density was related to host *Ips* gallery density. The fact that the degree of regulation of saproxylic insect populations by predation/parasitism depends on prey/host population size was scarcely demonstrated (Weslien 1994), sometimes as a delayed density-dependent process (Turchin et al. 1999). The mechanisms controlled by prey/host density differ between predators and parasitoids due to contrasts in specialization and to the fact that predators usually arrive before parasitoids (Kenis et al. 2004). Beaver (1966–1967 in Kenis et al. 2004) described more complex processes for spruce bark beetle populations. Predation pressure is important when the beetles have only recently become established, so that predator response increases when prey density is low and decreases when prey density is high. Parasitoids become important later on when damage to trees is already advanced. They have a density-dependent response only above a certain host density threshold. This decreases the importance of parasitoids for the first generation of bark beetles, but suggests stronger parasitism in the second generation when bark beetle populations peak, as Feicht (2004) demonstrated in the Bavarian National Park and as Wermelinger (2002) found in Swiss spruce forests after the storms in 1990.

14.4.3.5 Interference Competition Between Natural Enemies

A possible form of interference competition among natural enemies is facultative cleptoparasitism, i.e., when one parasite differentially attacks and steals host-insect already infected by another parasite (Holt and Hochberg 1998). Mills (1991) reported female *Cheiropachus quadrum* and *Eurytoma morio* (primary parasitoids of various bark beetles) stealing *Leperisinus varius* larvae from *Coeloides filiformis*. Hougardy and Gregoire (2003) observed similar behavior in *Rhopalicus tutela*, the females of which displace *Coeloides bostrichorum* females from their oviposition sites and steal the hosts (*Ips typographus*) previously located by the first parasite through the bark.

An asymmetry of competitive interactions was observed for two parasitoid species of the emerald ash borer. Both Hymenoptera species exhibited similar parasitism rates when they independently occurred with host beetle larvae. However, *Spathius agrili* nearly excluded *Tetrastichus planipennisi* in field trials when the two species coexisted with host larvae (Ulyshen et al. 2010). This asymmetry can be influenced by order of arrival. *Rhagium inquisitor* suffers from competition with *Acanthocinus aedilis* only when it arrives in second position (Victorsson 2012). The same occurs for two bark beetle predators: fewer *Enoclerus lecontei* adults were produced when the species arrived after *Temnochila chlorodia* (Boone et al. 2008a).

14.4.3.6 Extreme Antagonistic Interactions Between Natural Enemies

Other phenomena which can limit the regulation pressure of natural enemies on saproxylic insects are intra-guild predation (IGP; Vance-Chalcraft et al. 2007) and hyperparasitism (Kenis et al. 2004), the most extreme versions of interference competition within the guild of natural enemies.

IGP occurs when one predator species consumes another predator species with whom it also competes for shared prey, e.g., *Thanasimus formicarius* larvae feeding on *Medetera* larvae and *Temnochila chlorodia* larvae attacking *Enoclerus lecontei* larvae (Boone et al. 2008a). IGP can cause shortfalls in the additive effects of multiple predators (see above); in this case, multiple predators actually suppress fewer prey than the addition of two single predator species occurring alone.

In addition to cleptoparasitism, antagonistic interactions may occur between parasitoids of saproxylic insects. Facultative hyperparasitism of primary parasitoids may be a compensatory solution to local host scarcity. This process has been poorly studied and never quantified (Kenis et al. 2004), but has been observed among bark beetle parasitoids. For example, the primary parasitoid of *Ips typographus*, *Dinotiscus eupterus*, has been observed facultatively hyperparasitizing the other primary parasitoid, *Dendrosoter middendorffii* (Sachtleben 1952 in Kenis et al. 2004). Kenis and Mills (1994) observed that *Calosota aestivalis* and *Eupelmus urozonus*, the most often cited eupelmid parasitoids of bark beetles in Europe, parasitized cocoons of parasitoid wasps (*Dolichomitus terebrans* and *Coeloides*, respectively) in galleries of *Pissodes castaneus* in pine logs.

It should also be kept in mind that many generalist bark beetle predators, such as clerid beetles and dolichopodid flies, feed indiscriminately on both hosts and their embedded parasitoids; however, the cascading impacts of this on the overall pressure of natural enemies have never been measured.

14.5 Facilitations

Facilitative interaction is defined as an interaction that benefits one or both of the participants and harms neither (Stachowicz 2001). Positive interactions can occur either directly when one species makes the environment more favorable for others or indirectly when removing competitors or deterring predators (Bruno et al. 2003).

Several cases of facilitation among saproxylic insects are suspected and some have even been demonstrated. At least four types of mutually nonexclusive, facilitative interactions can be considered: locating a suitable host substrate, creating habitat, increasing habitat quality, and swamping predators. Predator swamping has already been dealt with in Sect. 14.3 (enemy-host/prey relationships in saproxylic food webs).

14.5.1 Locating a Suitable Host Tree

Using heterospecific compounds like kairomones to locate host trees is a well-documented mechanism that minimizes the foraging costs for some cerambycid species (Allison et al. 2001) and can explain the high degree of synchrony among species in bark beetle infestations (Allison et al. 2013; Birch et al. 1980). This interaction may be seen as a form of commensalism (Ayres et al. 2001). The presence of host tree volatiles can have synergistic effects in some cases (Pajares et al. 2004). Chemical communication among bark beetles is part of a complex interactive olfactory system, with differences in species response to heterospecific lures and host tree volatiles (Birch et al. 1980; Hofstetter et al. 2012) which result in either avoidance or attraction. Cross-attraction can be both symmetrical and asymmetrical. For instance, *Ips grandicollis* is attracted to trees colonized by *Dendroctonus frontalis*, but the reverse is not true. The attraction between *Ips avulsus* and *I. grandicollis* is reciprocal (Birch et al. 1980). A large guild spectrum of kairomonal responses to *Ips* spp. aggregation pheromones was observed by Allison et al. (2013); 13 species belonging to the guilds of meristem feeders, woodborers, or predators were attracted by the compounds. The attraction of natural enemies is discussed in detail in the section "predation and parasitism," as it may have implications in biological control. As an aside, the attraction of several *Monochamus* spp. to bark beetle pheromones opens up opportunities for improved monitoring of some pest species (Allison et al. 2001; Pajares et al. 2004).

Another way for late-arriving species to locate a suitable host is to use the penetration holes of bark- or wood-boring beetles for oviposition (Escherich 1923, quoted by Grunwald 1986; Schroeder 1997; Victorsson 2012). Schroeder (1997) suggests that the presence of *Tomicus piniperda* egg galleries indicates that a tree is a suitable reproductive substrate for *Acanthocinus aedilis*. No effect related with the quality of the habitat was suspected. Indeed, the number of individuals and their body length was affected neither by the presence of the bark beetle nor its abundance. Colonization by *Rhagium inquisitor* also seems to have a facilitative effect on *Acanthocinus aedilis*, though the reverse is not true (Victorsson 2012). The author suggests that oviposition enhancement is a potential facilitation mechanism as Schroeder (1997) already observed preference of *Acanthocinus aedilis* females to oviposit in entrance holes made by other saproxylic species.

14.5.2 Creating Habitat

Few saproxylic species can kill living trees, but if they do, e.g., during outbreak events, they can provide habitat for many other species. The bark beetle *Ips typographus* can be viewed as a keystone species in mountainous forested areas of Central Europe (Müller et al. 2008). Forest gaps created when this scolytine kills trees harbor significantly higher species densities of saproxylic beetles, including endangered species, compared with the forest interior. About half of the 60 insect species with a statistically significant preference for one specific habitat type (gap, edge, meadow, or closed forest) are associated with gaps. In their presentation of a conceptual framework for the dynamics of bark beetle outbreaks, Raffa et al. (2008) emphasize that these species have ecological effects across a broad range of spatial scales (from the portion of the tree used for oviposition to the landscape scale), highlighting in this way their potential for ecosystem engineering (Jones et al. 2010).

Bark beetle attacks increase the resin flow in trees as well as concentrations of allelochemical that can inhibit aggregation and be toxic to beetles and their microbial associates (Raffa et al. 2008). Interspecific aggregation may therefore help overcome host tree defenses (Ayres et al. 2001; Økland et al. 2009). Through simulations, Økland et al. (2009) showed that relatively nonaggressive bark beetles benefit from interaction with the most aggressive bark beetle species, i.e., the most abundant or which can kill living tree. Their results are in line with several observations. For instance, *Pityogenes chalcographus*, a bark beetle restricted to weakened or dying trees, has significantly higher reproductive success in trees colonized by *Ips typographus* (Hedgren 2004), which is more aggressive and able to kill trees, thereby increasing the amount of suitable habitat for *P. chalcographus* in the landscape (Hedgren 2004). Bark beetle activity is suspected to favor *Monochamus titillator* by expanding its resource (Flamm et al. 1989). Davis and Hofstetter (2009) consider that *Dendroctonus brevicomis* and *D. frontalis* engage in facultative cooperation.

Other species can also have indirect beneficial effects for the community by creating habitat without necessarily killing the tree. The positive impact of stem-borer *Oncideres albomarginata chamela* activity on the arthropod community living in detached branches of *Spondias purpurea* (Anacardiaceae) has been experimentally shown by Calderón-Cortés et al. (2011) in tropical dry forests. Females of this longhorn species girdle and detach branches with high nutritional quality and then make incisions and gnaw egg niches along the detached branches for oviposition. Those physical modifications have strong positive effects on the colonization, abundance, species richness, and composition of the arthropod community living in the branches, across all trophic levels.

Another longhorn species, *Cerambyx cerdo*, may also play a key role in structuring saproxylic communities colonizing oak trees. Saproxylic beetle catches from flight interception traps on oaks colonized by *C. cerdo* were compared with catches from uncolonized oaks in Lower Saxony, Germany (Buse et al. 2008). The trees colonized by *C. cerdo* were significantly more species rich and harbored more red-listed species. According to the authors, this pattern was probably due to the tunneling activity of the *C. cerdo* larvae, which created extensive accessibility to deadwood material. Buse et al. (2008) suggested that *C. cerdo* should be reintroduced into regions where it has become extinct to restore its strong physical influence (i.e., tunneling) on oak trees. This would benefit many saproxylic beetles, even threatened ones, and possibly other taxa as well.

A last example comes from an experiment on *Picea abies* logs where holes and galleries made by bark beetles facilitated the entrance of other beetles and other deadwood fauna (Isopoda, Diplopoda, and Annelida) (Zuo et al. 2016). The positive influence of the surface area of inner bark consumed by bark beetles on the abundance of invertebrates was even more important in the nutrient-rich site compare with the nutrient-poor site. The authors speculate about a difference in decay rates with a faster decomposition in the moist and rich site leading to a more favorable microclimate and higher resource availability for other invertebrates.

14.5.3 Improving Habitat Quality

Facilitation may also occur through an improvement in habitat quality. Such interactions are suspected between the scarabid beetle *Osmoderma eremita* and associated beetles living in hollow trees (Jönsson et al. 2004; Ranius et al. 2005). Its larvae feed on the deadwood forming the wall of the cavity and may enrich the mold with their frass. Evidence of facilitation has been provided for *Cetonia aurataeformis*, another cavity- and log-dwelling scarabid beetle. Its larvae produce a feeding residue richer in nutrients than the original substrate by digesting polysaccharides and lignin (Micó et al. 2011). The authors concluded that this could facilitate the use of the woody substrate by other saproxylic organisms. In another study, observations of a positive relationship between cetoniine activity and the presence of saprophagous syrphid species under natural conditions were confirmed by laboratory experiment (Sánchez-Galván et al. 2014). The substrate enriched with *Cetonia aurataeformis* larval feces improved both larval growth rate and adult fitness for *Myathropa florea* (ibid).

The ability of saproxylic insect species associated to symbiotic bacteria to fix atmospheric nitrogen has been proven in termites (Breznak et al. 1973), bark beetles (Bridges 1981; Morales-Jiménez et al. 2009), the cockroach *Cryptocercus punctulatus* (Breznak et al. 1974), the scarabid beetle *Cetonia aurata* (Citernesi et al. 1977), and the stag beetle *Dorcus rectus* (Kuranouchi et al. 2006). This could be important for species communities living on poor diets like wood. However, to our knowledge, the consequences of nitrogen-fixing ability on species presence or performance have not yet been investigated for any of the species mentioned above.

Finally, there are other examples where a facilitative effect through habitat quality improvement might be at work. For instance, in lodgepole pine (*Pinus contorta*) occupied by *Pseudips mexicanus*, the offspring of another bark beetle, *Dendroctonus ponderosae*, emerged earlier compared with trees infested only by *D. ponderosae* (Smith et al. 2011). Furthermore, when in sympatry with *P. mexicanus*, the *D. ponderosae* larvae required a significantly lower amount of resource to complete their development, without any loss in size (ibid.). Another example is the facilitative effect of *Rhagium inquisitor* on *Acanthocinus aedilis*, mentioned above (see "creating habitat"); this may also be a case of resource enhancement. Indeed, *A. aedilis* had 161% more offspring per female when colonizing logs inhabited by *R. inquisitor* (Victorsson 2012). However, the mechanism still has to be elucidated.

14.6 Research Perspectives and Challenges

This section will open up three lines of investigations. First, in many insect systems, multispecies interactions yield outcomes that would not be predicted based on paired biotic interactions alone (Boone et al. 2008a; Kaplan and Denno 2007). Scaling up from pairwise species interactions to ecological networks is therefore necessary to understand species interactions among saproxylic insects. Second, as suggested by recent advances in theoretical community ecology, building on life-history traits of the species is a promising avenue. Lastly, wood decomposition is accompanied by a succession of species that has been well documented (Graham 1925; Hammond et al. 2004; Hövemeyer and Schauermann 2003; Saint-Germain et al. 2007; Savely 1939; Vanderwel et al. 2006; Wallace 1953), but biotic interactions have not been taken into account, either as drivers or as consequences of this successional process. This is our third research perspective.

14.6.1 Scaling Up the Ecological Network

Like we mentioned earlier, most of the studies addressing interactions among saproxylic insects focus on two interacting species. We therefore advocate that an insightful first step toward understanding multispecific interactions would be more research about the indirect interactions which arise when the effect of one species on another is mediated by the action of a third species.

The holistic view given by ecological network analysis can be useful in reframing descriptive questions into the testing of specific hypothesis (Poisot et al. 2016). For instance, by assessing the robustness of the network to species extinction, such analysis can reveal keystone species (Petchey et al. 2004). Quinto et al. (2012, 2015) and Wende et al. (2017) provide examples of network analysis with saproxylic insects. They particularly showed that woodland site characteristics act in concert with biotic complexity of the saproxylic network to confer resistance to the community in face of microhabitat loss. Ecological network analyses could also be helpful to understand whether and how outbreaks or invasive species may drive trophic cascades in saproxylic food webs (Vinstad et al. 2014).

14.6.1.1 How Are Between-Insect Interactions Mediated Through Shared Natural Enemies?

Shared predation is a widespread phenomenon in natural communities that can affect species abundance and coexistence through a variety of indirect effects (Chaneton and Bonsall 2000). The indirect enemy-mediated interaction (also called “apparent competition”) is one of them in which two victim species apparently compete, i.e., interact negatively, via their shared natural enemy (predator or parasitoid). For example, if a predator preys more heavily on one of two competing species, it can reduce the superior competitor’s impact on the less consumed species (Boone et al. 2008a). It is not currently known whether such interactions among competitor bark beetles and their associated natural enemy significantly affect the population dynamics of eruptive bark beetles. Raffa (2001) suggested that predators such as *Enoclerus lecontei*, *Thanasimus dubius*, and *Platysoma cylindrica*, which are pine specialists but generalist predators in the sense that they are attracted to several species of bark beetle, may induce apparent competition among sympatric *Ips* species on American pine trees (see Sect. 14.4.1 for details about multiprey generalist predators). Moreover, when the bark beetles *Dendroctonus ponderosae* and *Ips pini* were experimentally forced to simultaneously colonize pine trees, *D. ponderosae* suffered from higher parasitism and predation rates, because some of their natural enemies were attracted by the *I. pini* pheromones (Bergvinson and Borden 1991). Hanks et al. (1997) and Bybee et al. (2004) hypothesized a competitive displacement for *Phoracantha semipunctata* by *P. recurva*, potentially due to a difference in susceptibility to an egg parasitoid (Luhring et al. 2004).

Selective predation on deadwood-dwelling insect species by woodpeckers may alter the competition processes. It has been suggested that the excavating activity of woodpeckers facilitates predation or parasitism of wood-boring insects (Kroll and Fleet 1979 in Martin et al. 2006). As far as we know, the influence of vertebrate predation on between-insect interactions has been poorly investigated.

14.6.1.2 How Do Micro-Organisms Mediate Between-Insect Interactions?

Complex chains of species connections with intricate feedback structures, dependencies, and cascading effects contribute to interaction dynamics within deadwood-dwelling communities where multiple symbiotic relationships occur between deadwood-eating insects and their fungal and invertebrate associates.

The multiple mutualistic, commensalistic, and antagonistic relationships associated with bark beetles and woodwasps provide an outstanding example (Ryan et al. 2012; Yousuf et al. 2014a, b). This example illustrates how competition among wood-eating insects may be mediated by their fungal associates. Woodwasp larvae (*Hymenoptera*, *Siricidae*) commonly share the tree with subcortical bark beetles. The woodwasp *Sirex noctilio*, native to Eurasia and Northern Africa, has recently infested pines in eastern North America where it is competing with the beetle *Ips grandicollis*. This competition seems to be mediated by fungal symbiont associates. The woodwasp's symbiont *Amylostereum areolatum*, on which *Sirex noctilio* larvae feed (Ryan et al. 2012; Yousuf et al. 2014a, b), is outcompeted by the beetle-associated fungus *Ophiostoma ips*, thereby causing mortality during the woodwasp's early life stages.

Several interesting issues fall outside the scope of our review. In particular, biotic interactions between insect and noninsect species are crucial. For example, the mutualistic relationships between fungi and beetles (Floren et al. 2015) or between birds and beetles (Ranius and Nilsson 1997) have not been considered here.

14.6.2 Species Life-History Traits and Species Interactions

Understanding the rules responsible for biotic interactions is central to predicting community dynamics. Trait-based approaches typically move the focus from the responses of single species to community-level changes. Trait values may indeed affect a given interaction parameter, e.g., body mass (Berlow et al. 2009), and aggressiveness (tendency to attack and kill living trees; Økland et al. 2009) may determine the strength of trophic interactions or competition. Species traits sensu lato may determine species interactions through a two-step process (Bartomeus et al. 2016). First, ecological and life-history traits determine species co-occurrence, and therefore potentially interacting species, by governing species distributions. Secondly, the morphological or physiological traits of co-occurring partners should match for an interaction to occur. Only by elucidating which species traits are important in determining the establishment and strength of each interaction process can we better explain how species actually do interact (Bartomeus et al. 2016).

We have seen that knowledge of species life-history features is crucial to account for actual species niche breadth. Trophic specialization of predators/parasitoids, from generalists to prey/host specialists, may also strongly affect the strength of interactions (see, e.g., Sect. 3.3.2). Species' degree of specialization can also vary over its geographical range (Victorsson 2012). In addition, contrary to parasitoids, many predators actually have a mixed diet, being alternatively zoophagous, detritivore (frass-eating), or fungivore (e.g., *Corticeus* spp. gut analyzed by Smith and Goyer 1980), with resulting sharp changes in trophic level.

Building on life-history trait databases is therefore necessary and should take into account that both the magnitude and sign of species interactions are context- and life stage-dependent (Økland et al. 2009). Species interactions vary along geographic and abiotic context and can even vary as a function of the presence/absence of a third species (Berlow et al. 2009; Chamberlain et al. 2014). For instance, in the south-eastern US pinewoods, the low rate of parasitism of *Dendroctonus frontalis* (5–6% on average) appeared to be due to the low floral diversity of intensively managed forests, which provided a weak complementary resource to parasitoids (Stephen et al. 1997). The authors experimentally measured that the longevity and fecundity of bark parasitoids could be improved by combining other forest trophic resources (e.g., floral nectar or pollen) with host populations. Most parasitoid Hymenoptera of bark beetles are indeed synovigenic, i.e., females emerge with a small number of large oocytes but can produce others if the resources are available. Finally, landscape scale modifications such as habitat loss may translate into variation in the strength of interaction between species with different dispersal abilities (see Sect. 14.4.3.2).

14.6.3 Exploring Biotic Interactions in Time: Successional and Priority Effects

We mentioned earlier that temporal segregation could occur among species that share resources and thus lead to reduced competition. However, temporal segregation does not mean absence of interactions. Indeed, Kaplan and Denno (2007) reported interactions between species that are temporally segregated. As decomposition proceeds, habitat properties change, partly due to the action of saproxylic insects (Ulyshen 2016); therefore, one might expect indirect biotic interactions mediated by resource condition, as in the processing chain model (Heard 1994). Basically, this model considers two pathways for the transformation or processing of a resource. In consumer-dependent processing, some resource is processed as a consequence of the activity of the early-stage (or upstream) consumer. Consumer-independent processing, by contrast, occurs even in the absence of the early-stage consumer. The key point for predicting subsequent biotic interactions is the relative importance of the two pathways in providing resources for the late-stage (or downstream) consumer. According to this model, we would expect relationships to range from strongly amensal (resource preemption) through strongly commensal (resource dependence). This is a significant difference with the facilitation model of Connell and Slatyer (1977) which could be typically applied to heterotrophic successions such as the one associated with deadwood decomposition. Finally, contrary to the facilitation model, the processing chain model is concerned with resource processing. To our knowledge, the processing chain model has not yet been applied to any saproxylic system, though it is potentially relevant (Heard 1994).

The particular order and timing in which different species join a community may also affect biotic interactions and eventually community composition and ecosystem functioning (Chase 2003; Drake 1991; Fukami 2015). This phenomenon, known as the priority effect, has been scarcely documented for saproxylic insects (e.g., Weslien et al. 2011). Weslien et al. (2011) followed the colonization and succession of wood-living insects and fungi on high stumps for 15 years after cutting. The initial colonization of the stumps by either the bark beetle *Hylurgops palliatus* or the woodborer *Monochamus sutor* appeared to be highly random. However, after initial colonization, two successional pathways were verified in respect to the occurrence of a rare, wood-living beetle, *Peltis grossa*. Whereas *H. palliatus* had a positive effect on the occurrence of *P. grossa*, the presence of *M. sutor* was negatively correlated with the subsequent occurrence of *P. grossa*. These interactions were mediated by the saproxylic fungus species *Fomitopsis pinicola*. Weslien et al.'s results indicate that the "inhibition model" (sensu Connell and Slatyer 1977) may also be relevant for saproxylic succession. This is in line with experimental results on wood-decaying fungi (Fukami et al. 2010).

The influence of order of arrival on the outcome of competition has been documented for other saproxylic species and habitats (Rankin and Borden 1991; Boone et al. 2008a; Victorsson 2012) (see Sect. 14.2), and one might expect that such priority effects occur in other saproxylic insect systems. Moreover, evidence of priority effects for wood-living fungi have been found (Dickie et al. 2012; Fukami et al. 2010), and insects do contribute to the development of early fungal succession in deadwood (Strid et al. 2014) particularly as they can function as fungi vectors (Jacobsen et al. 2017). The priority effects of early successional insects on late successional fungi in aspen dead wood observed by Jacobsen et al. (2015) may extend on other saproxylic insects in the same way as Weslien et al. (2011) showed for *Picea abies* high stumps (see above).

Given this importance of successional and priority effects, we call for further investigation of historical contingencies in saproxylic systems. Such efforts would have at least two applied perspectives: biological conservation and ecosystem functioning enhancement. Indeed, Weslien et al. (2011) exemplified how a better understanding of saproxylic succession could open up new management options for the conservation of threatened species. For instance, leaving high stumps could be a way to favor *Peltis grossa*. By cutting trees after the flight of *Monochamus sutor* (inhibitor) and before the flight of *Hylurgops palliatus* (facilitator), one could guide succession in the desired direction. If the priority effect matters, the simple timing of an operation could determine the successful outcome of conservation actions (Seibold et al. 2015). It is also interesting to know whether priority effects affect the ecosystem functioning of saproxylic systems (see Box 14.4). Results from field tests on wood-dwelling fungi suggest that priority effects can have strong consequences on some ecosystem properties (carbon and nitrogen concentrations and decomposition rate) (Dickie et al. 2012).

Fukami (2015) provides a conceptual framework based on the ecological niche and species pool concepts to study the mechanisms and conditions of priority effects and their consequences on ecosystem functioning. Increasing our knowledge of species traits and spatial distribution is of prime importance if we are to make any progress in our understanding of priority effects in saproxylic systems. Another challenge lies in the ability to conduct long-term work since wood decomposition can take several decades (Ulyshen 2016).

Box 14.4 Biotic Interactions and Deadwood Decomposition Rate

Interspecific interactions among invertebrates have been identified as one of the key mechanisms influencing wood decomposition (Ulyshen 2016). Considering evidence of the influence of predators on litter decomposition rate through their impact on invertebrate populations (Gessner et al. 2010), one can expect saproxylic insect predators or parasitoids to play a similar role in the wood decomposition process (Ulyshen 2016). We found only one study evidencing such an effect. In southeastern US deciduous forests, the predation of termite colonies by ants resulted in an alteration of coarse woody debris decomposition; without ants, termites removed 11.5% more woody biomass (Warren and Bradford 2012).

There are several indications that further investigation of the relationships between biotic interactions and deadwood decomposition is needed. Indeed, the tunneling activities of phloem feeders and woodborers differ greatly, both in shape and in location, from just under the bark to the inner part of the heartwood. This leads to different types of impact on deadwood structure, which in turn can have consequences on fungi colonization and development, thus driving different successional pathways (Leach 1937; Savely 1939; Strid et al. 2014; Weslien et al. 2011).

Broadening our view will doubtless require innovative analytical and sampling tools in order to identify community modules and to describe network topology (Poisot et al. 2016). Progress in these two areas may help us to understand how species interactions contribute to food webs and ecosystem functioning in addition to describing species richness patterns (Brophy et al. 2017).

14.7 Conclusion

It should be borne in mind that this overview of saproxylic insect species interactions is partial. The field of exploration teems with open-ended questions. Investigating such species-rich communities is quite challenging. Indeed, research on saproxylic insect communities requires a wide perspective, including both antagonistic and facilitative interactions and direct and indirect effects. According to Gilman et al. (2010), species interactions can strongly influence how climate change affects species at every spatial scale. Unfortunately, since no investigation looked into the spatial scaling up of biotic effects on species distribution, our ability to predict the response of saproxylic insects to climate change is currently very limited. Besides, coevolution between saproxylic insects—i.e., reciprocal evolutionary change in interacting species—clearly lacks well-founded results. The evolutionary perspective will however deserve forthcoming attention with respect to theoretical and empirical findings coming from other taxonomic and trophic groups (Forister and Jenkins 2017; Thompson 2009).

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Chapter 15
Dispersal of Saproxylic Insects

Heike Feldhaar and Bastian Schauer

Abstract Dispersal is a key trait of species that is required to maintain gene flow between habitat patches. Furthermore, it allows the colonization of new habitats and thus affects population dynamics, extinction risk of populations, and species distributions. Dispersal enables species to persist in a changing environment. Saproxylic insects, depending on deadwood at some stage during their life cycle, must compensate local extinctions resulting from the decay of deadwood with colonizations of new deadwood structures locally and on the landscape scale. Their dispersal strategies are shaped by a suite of driving forces such as spatial and temporal variability of deadwood structures in the environment, feeding strategy, resource competition, kin competition, and inbreeding avoidance. The importance of each factor in selecting for a dispersal strategy will vary among species depending on their life history and interactions with the environment, such as the longevity of the deadwood habitat used. Species using a more transient habitat, such as freshly killed wood, have better dispersal abilities than those in more persistent habitats such as tree hollows that may exist for several decades. Dispersal abilities of only a few saproxylic insect species are known, and these comprise mostly pest species or flagship species of interest to conservation. Dispersal distances vary greatly from a few meters in passalids dispersing by walking to over 100 km in some flying bark beetles. Knowledge of dispersal abilities is of paramount importance though, as it can help to improve conservation strategies and forest management especially in terms of spatial distribution of suitable habitats to enhance species persistence. In this chapter we first review the factors driving dispersal ability and our current knowledge on dispersal distances of saproxylic insects. We provide an overview of different methods used to measure dispersal ability of saproxylic species. We discuss whether saproxylic species are rather dispersal or habitat limited and identify open questions in the study of dispersal of saproxylic insects.

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15.1 Introduction

Dispersal is defined as any movement of individuals or propagules with potential consequences for gene flow across space (Ronce 2007). Dispersal is a three-step process where individuals leave their birthplace and then cross a more or less hostile matrix before settling down in a new habitat patch to reproduce (Bonte et al. 2012). Most species live—at least to some degree—in spatially structured populations. Species with such a metapopulation structure are comprised of spatially discrete local populations in patches that are connected by the migration of individuals between local populations. Metapopulations are characterized by frequent extinction of local populations. For long-term persistence of a metapopulation, local extinctions and colonization through local dispersal need to be balanced (Hanski 1998). Dispersal ability (and propensity) is therefore an important life-history trait as it strongly impacts persistence of a species, especially in human-impacted landscapes. Anthropogenic habitat destruction often results in habitat fragmentation, reduced connectivity between suitable habitats, and a reduction in habitat size and quality. These transformations of ecosystems negatively impact many species, potentially driving them toward extinction. Therefore dispersal has received increasing attention by ecologists and conservationists.

As a result of habitat fragmentation, connectivity between suitable habitat patches is often reduced, and species with limited dispersal abilities may not be able to recolonize patches where they have become extinct or reach new habitat patches. In addition, smaller populations often release a smaller number of dispersing individuals, which may reduce not only demographic connectivity but also the genetic exchange between habitat patches even further. Additionally, the smaller the habitat patches, the smaller population sizes will be locally, which renders populations more prone to extinction by stochastic processes (Hanski et al. 1994). The strength of Allee effects (positive density dependence) may also become stronger in smaller populations, and, e.g., finding a mating partner may become more difficult, which may increase dispersal propensity of individuals (Kuussaari et al. 1996). Dispersal has consequences not only for the fitness of the respective individual moving from one habitat patch to another but also for population dynamics and genetic cohesion of species across their range (Bowler and Benton 2005). Spatially structured populations are largely dependent on dispersal for their long-term persistence. Immigrating individuals may rescue small populations by preventing local extinction events due to stochastic processes (Brown and Kodric-Brown 1977; Gotelli 1991) or enhance the fitness in small populations by genetic rescue (Whiteley et al. 2015). Empty habitat patches can only be (re-)colonized by dispersal (Fahrig and Merriam 1994; Hanski et al. 1994), and thus dispersal also determines the ability of populations to track favorable conditions or cope with habitat loss or fragmentation in a changing world (Travis et al. 2013).

Dead and decaying wood represents a spatially and temporally dynamic habitat for insects. Insects depending on deadwood structures at some point of their life cycle have been termed saproxylic insects (Speight 1989). Species depending on wood-decomposing fungi or other saproxylic species are also considered as saproxylic. These saproxylic insects constitute a large part of forest biodiversity and play a major role in nutrient cycling and ecosystem functioning (Stokland 2012; Ulyshen 2016), and diversity is driven by the range of decay stages and types of deadwood structures that provide habitat to different saproxylic insect assemblages (Grove 2002b; Schauer et al. 2018a; Ulyshen 2011; Ulyshen et al. 2004). Habitat patches for saproxylic insects can be as small as an individual deadwood structure, such as a tree, log, or fungal sporocarp, and can host several to many generations of a particular insect species. However, eventually the insect population will become extinct as the resource decomposes. Locally, new habitat patches will become available for colonization with the appearance of new deadwood structures. While forest management or natural disturbances alter patch dynamics and abundance locally, forest fragmentation determines connectivity and ecological continuity on the landscape level (Grove 2002b).

Saproxylic insects are adapted to their spatially and temporally dynamic habitat and have developed a range of dispersal strategies. In general, it is assumed that species inhabiting long-lived (e.g., specialists of tree hollows) or abundant habitat patches are poor dispersers (Nilsson and Baranowski 1997; Ranius and Hedin 2001) in comparison to those relying on more ephemeral or scarce habitat patches (e.g., scolytine beetles on wind- or fire-damaged trees) (Nilssen 1984; Saint-Germain et al. 2008).

Many saproxylic insect species can actively disperse on their wings, while others disperse passively by hitchhiking on dispersing animals (so-called phoresy). Phoresy as dispersal strategy is most often used by small-bodied and/or flightless saproxylic arthropods such as mites or pseudoscorpions (Karpinski et al. 2017; Katlav et al. 2014; Ranius and Douwes 2002; Zeh and Zeh 2013). As dispersal distances of phoretic saproxylic arthropods are determined by the dispersal abilities of the individual they hitchhike on, these often tiny arthropods may be able to disperse over relatively large distances (Ranius and Douwes 2002). Other flightless taxa reach new habitat patches actively by walking and are assumed to be strongly limited in their dispersal range in comparison to flying or phoretic saproxylic arthropods (Buse 2012; Horak et al. 2013; Janssen et al. 2016). A mixture of active and passive dispersal may be used by thrips. Saproxylic species may have rudimentary wings only (Kettunen et al. 2005). However, aside from active dispersal by walking, thrips as tiny insects may potentially sail with the wind and may thus cover larger dispersal distances passively without using energy for flight (Compton 2002).

Many saproxylic insect species are regarded as threatened worldwide due to fragmentation, loss of habitat, or degradation of forests resulting in reduced amounts of deadwood structures (Grove 2002a, b; Seibold et al. 2015; Siitonen 2001; Speight 1989). Aside from the absence of suitable habitat patches (habitat limitation), the entailing lower connectivity between those patches may result in dispersal limitation, i.e. the inability of a species to occupy all suitable patches in the environment or reach suitable habitat patches due to insufficient dispersal abilities. This is often invoked as a reason for the absence of a particular species within a habitat patch (Brin et al. 2016; Brunet and Isacsson 2009; Irmler et al. 2010; Schiegg 2000a, b).

Knowledge on dispersal biology of saproxylic insects is therefore of paramount importance to improve conservation strategies.

This chapter reviews the current knowledge of dispersal abilities of saproxylic insects (also in relation to habitat fragmentation). We first provide an overview of the factors influencing dispersal. As knowledge on dispersal abilities of saproxylic insects is based on different methods we will then compare the direct and indirect methods for measuring dispersal with advantages and drawbacks. We provide an overview of dispersal distances of various taxa. Lastly, we will discuss the role of potential dispersal limitation in population dynamics and colonization of new habitats by saproxylic insects.

15.2 Factors Influencing Dispersal Strategies: Why Disperse and How Far?

Dispersal strategies of organisms are shaped by a suite of driving forces such as environmental stochasticity, resource competition, kin competition, and inbreeding avoidance (Benton and Bowler 2012; Bonte et al. 2012; Bowler and Benton 2005; Matthysen 2012). The importance of each factor in selecting for a dispersal strategy will vary among species in accordance to their life-history traits and their interactions with the environment.

15.2.1 Longevity and Spatial Distribution of Habitats of Saproxylic Insects

Theory on dispersal suggests limited dispersal of species inhabiting long-lasting and stable habitats, while those inhabiting ephemeral habitats should have a higher dispersal propensity as suitable habitat is present for a short time only (Southwood 1962; Shaffer 1981; Roff 1994; Denno et al. 1996). The spatial distribution of suitable habitat should also have a strong influence on dispersal abilities. If habitat patches are rare and more isolated, then dispersal ability needs to be greater to colonize new habitat patches. Availability of habitat patches is also dependent on the range of habitats used per species. Habitat specialists potentially have fewer habitat patches available than species being able to use a broader range of habitats.

Habitats of saproxylic insects differ strongly in their persistence and spatial distribution. One habitat type with very short availability only is freshly burned wood. Pyrophilous insects, whose larvae require the nutritional conditions present in the very early decay stages, colonize it immediately after a forest fire (Hanks 1999; Heikkala et al. 2017). These specialists use the freshly burned wood as a habitat for a single to a few generations only before their populations decline again (Hanks 1999; Heikkala et al. 2017). In addition, burn sites are spatially and temporally unpredictable and may occur at relatively great distances from each other. Consequently, spatial separation and transience of the habitat should select for very good dispersal abilities of pyrophilous species. Indeed, pyrophilous species have been shown to colonize freshly burned forest stands quickly, and they do not seem to be dispersal limited if sufficient source populations are available on the landscape scale (Boulanger et al. 2010; Heikkala et al. 2017; Kouki et al. 2012; Ranius et al. 2014; Saint-Germain et al. 2013). Other early decay stages have also been shown to favor good dispersal abilities. For example, bark beetles colonizing stressed or freshly killed trees have excellent dispersal abilities (Forsse and Solbreck 1985).

Standing and downed dead trees or coarse woody debris are deadwood habitats of intermediate longevity. In contrast to early decay stages that are the result of forest fires or other stressors to trees, deadwood at intermediate and late decay stages is a resource that may have become available more gradually and continuously in comparison to the early decay stages (Nilsson and Baranowski 1997). In addition, these habitat types should be the most common within natural forests (Nordén et al. 2004), in contrast to the very early decay stages with limited temporal (and spatial) availability or hollows in living trees with a naturally patchy spatial distribution. Saproxylic insect species utilizing intermediate to late decay stages of deadwood should thus have more limited dispersal abilities in comparison to species utilizing ephemeral early decay stages. However, evidence for limited dispersal abilities of saproxylic species using deadwood structures of intermediate longevity is equivocal. Saint-Germain et al. (2013) did not find an effect of isolation in colonization patterns of burned forest sites by pyrophilous vs. non-pyrophilous beetle species. Other studies suggest that species requiring a more specific habitat may be dispersal limited, which is often the case for threatened species (Gibb et al. 2006; Schiegg 2000a, b; Seibold et al. 2015).

Hollows in living trees are considered an extremely stable habitat as they may persist for many decades (Ranius and Hedin 2001), potentially providing a suitable habitat for many generations of species inhabiting those hollows. Tree hollow specialists are therefore expected to have more limited dispersal abilities and a lower dispersal propensity than species inhabiting more transient deadwood habitats. Direct measurements of dispersal abilities of one specialist, the Hermit beetle *Osmoderma eremita* Scopoli, 1763, suggest more limited dispersal abilities in comparison to other saproxylic insects (Hedin et al. 2008; Ranius 2006). Likewise, Nilsson and Baranowski (1997) found the beetle fauna in hollow trees to be impoverished in previously disturbed stands and argue that this is due to dispersal limitation. On the other hand, the naturally patchy distribution of tree hollows should favor dispersal abilities. In addition, the potentially small population size of a particular species within a tree hollow may select for a high dispersal propensity of at least one sex to avoid inbreeding (Perrin and Mazalov 2000; Waldbauer and Sternburg 1979) and potentially competition among relatives (see below).

15.2.2 Influence of Feeding Strategies on Dispersal

Dispersal is defined as the movement from the natal or breeding site to another breeding site. This includes not only the departure from a patch and settlement in the (new) breeding site but also the movement between those patches (Clobert et al. 2009). The movement strategy and potential dispersal distance of saproxylic insects will be strongly influenced by nutritional and habitat requirements of the dispersing life stage—which are usually the adult insects.

While larvae of many saproxylic species are dependent on decomposing wood in some form, adult life stages may rely on very different food sources. At one extreme, adults may not feed at all, which will limit the maximum distance that can be covered during dispersal as only the stored biomass can be utilized for flight or movement and is traded off against reproduction. Nonfeeding species therefore tend to have a more sedentary lifestyle than those feeding as adults (Hanks 1999). A comparison of the life history and dispersal behavior of two cerambycid beetles, the Japanese pine sawyer *Monochamus alternatus* Hope, 1843 and the Sugi bark borer *Semanotus japonicas* Lacordaire, 1869, suggests that dispersal propensity is strongly influenced by adult feeding behavior. While *M. alternatus* Hope, 1843 adults must feed on the bark of twigs of healthy pine trees for maturation and then have to search for weakened or newly killed pine trees to oviposit, *S. japonicus* Lacordaire, 1869 is more sedentary as oviposition may take place on the same tree that larvae developed in and no maturation feeding of the adult is required (Shibata 1986a, b).

Other insects that have to undergo maturation feeding are many saproxylic species of syrphid flies that require protein-rich pollen in order to fully develop their reproductive organs and achieve egg maturation (Speight 2012). Saproxylic syrphid flies therefore require open stands with a rich herb layer within forests (Fayt et al. 2006) and are also frequently found in meadows (Branquart and Hemptinne 2000). In order to meet nutritional demands, they potentially need to cover quite a distance before entering deadwood structures again to reproduce or deposit eggs.

15.2.3 Inbreeding Avoidance

Mating between related individuals results in inbreeding. Inbreeding can occur in both large and small populations. In large populations, nonrandom mating of related individuals may occur simply due to geographic proximity of these individuals. In small populations however, the probability of inbreeding is much higher, even with random mating because most individuals within the population will be related.

Local population sizes of saproxylic insects may often be small, which may result in substantial levels of inbreeding if mobility of the species is low. A local population may comprise individuals within the same forest or forest fragment, but may be as small as the group of individuals living in the same habitat patch, which can be a deadwood structure like a tree hollow, a fallen log, or the sporocarp of a bracket fungus. Especially bark and ambrosia beetles show very high levels of inbreeding in some species when mating takes place among kin within the same galleries (Keller et al. 2011; Kirkendall 1983; Kirkendall et al. 2015). Other saproxylic insect species also show considerable levels of relatedness within the same breeding structure such as a particular tree hollow, e.g., the two cetoniine beetles *Osmoderma barnabita* Motschulsky, 1845 and *Protaetia marmorata* Herbst, 1786 (Oleksa et al. 2013) or the beetle *Anaspis ruficollis* Fabricius, 1792, the syrphid fly *Criorhina floccosa* Meigen, 1822, and the wood-soldier fly *Xylomya maculata* Meigen, 1804 (Schauer et al. 2018b).

As inbreeding has been shown to reduce fitness in many insects (Henter 2003), mechanisms to avoid inbreeding are expected to be selected in order to reduce negative fitness effects (Pusey and Wolf 1996). Inbreeding can be avoided either by dispersal (of at least one sex) from natal sites to reduce contact with relatives (Waldbauer and Sternburg 1979) or, when dispersal is not possible, inbreeding may be avoided by mechanisms that prevent breeding with close relatives (Blouin and Blouin 1988).

Sex-biased dispersal has been observed in several species of saproxylic beetles. In *Melandrya barbata* Fabricius, 1792 and *Melanotus villosus* Gmelin, 1789, a larger proportion of males was found to colonize recent forest fragments, suggesting male-biased dispersal (Bouget et al. 2015). In the stag beetle *Lucanus cervus* Linnaeus, 1758, both sexes disperse. However, females fly for shorter distances in comparison to males and then move around on the ground in search for an oviposition site (Rink and Sinsch 2007). Likewise, the sex ratio was more female biased at shorter dispersal distances and unbiased at larger distances in *Ips typographus* Linnaeus, 1758 (Dolezal et al. 2016), which can be explained by males being the pioneer sex. In contrast, tethered flight experiments on *Osmoderma eremita* Scopoli, 1763 suggest that females may have higher flight capacities (Dubois et al. 2010). Several authors point out the observed patterns with potential sex-biased dispersal may be due to differences in the likelihood of catching beetles of one of the sexes (often the males). Thus, recapture rate of male Rosalia longicorn beetles was higher than that of females, but no sex difference in cumulative dispersal distance was found (Drag et al. 2011).

15.2.4 Delayed Dispersal, Flightless Males, and Outbreeding Depression in Cooperatively Breeding and Social Saproxylic Insects

A special case of sex-biased dispersal can be found in ambrosia beetles (Scolytinae) where inbreeding polygyny has evolved repeatedly as mating system (Kirkendall 1983). Female ambrosia beetles mate with close kin (brothers) before they disperse (Kirkendall et al. 2015). Adult females often stay within natal galleries where fungus is grown and delay dispersal after mating in order to provide parental care to closely related offspring (Peer and Taborsky 2007). Dispersal of mated females is triggered by a low number of close kin dependent on alloparental care (Biedermann and Taborsky 2011). Males in such species are usually flightless, resulting in highly sex-biased dispersal patterns (Kirkendall et al. 2015). In addition, mating with related individuals may by now be favored in these species as outbreeding has been shown to reduce fitness (Peer and Taborsky 2005).

Likewise in the lower dry-wood feeding termite *Cryptotermes secundus* Walker, 1853, inclusive fitness gains that can be attained by individuals delaying dispersal. Individuals stay as helpers in the natal nest and delay dispersal to found a new colony themselves when the piece of wood they nest in is still large and food abundant. When food becomes scarce, workers develop into winged sexuals more readily and disperse (Korb and Schmidinger 2004).

15.2.5 Competition-Colonization Trade-Offs

Differences in dispersal ability among species may be selected by competitive interactions. Individuals of smaller species are often inferior competitors during scramble or interference competition, i.e., when they have to compete for resources directly and a superior individual can displace an inferior competitor or prevent access to the resource. However, if inferior competitors have better dispersal abilities, coexistence may be enabled. Such a competition-colonization trade-off seems to allow species coexistence of species of spore-feeding beetles on a wood-decaying bracket fungi *Ganoderma* spp. in New Zealand. Here the beetle *Zearagytodes maculifer* Broun, 1880 evades competition with the superior competitor *Holopsis sp.* by dispersing and colonizing distant habitat patches not yet colonized by the latter species (Kadowaki et al. 2011).

15.3 Measurement of Dispersal

While dispersal is an important life-history trait influencing the persistence of a species locally and regionally as well as its range, it is notoriously difficult to observe or measure, especially in rare species or those with a mainly cryptic lifestyle such as many saproxylic insect species. Dispersal can be measured either directly or indirectly. Direct measurement of dispersal implies that individuals (or a cohort) are observed during the whole dispersal process from the departure point to the point of settlement. This usually requires that individuals are marked in some way so that they can be identified. Direct measurements of dispersal have the advantage that exact dispersal distances and movement patterns of particular individuals can be measured. Based on the distribution of observed dispersal distances of many individuals, a dispersal kernel, i.e., a probability distribution of the distance traveled by any individual, can be calculated (Etxebeste et al. 2016). In addition to the distance traveled, information on movement behavior can be gained during direct measurements. In contrast, indirect measurement of dispersal is usually based on the interpretation of patterns generated by dispersing individuals. Indirect methods comprise population genetic analyses or patterns of occurrence of saproxylic insects (usually in relation to landscape structure and spatial distribution of potential habitat patches). Direct and indirect measures of dispersal are complementary and not redundant methods (Lowe and Allendorf 2010; Ranius 2006).

15.3.1 Direct Measurement of Dispersal: Radio Telemetry

Radio telemetry allows the measurement of exact dispersal distances and movement patterns of particular individuals of saproxylic insects (Chiari et al. 2013; Dubois and Vignon 2008; Hedinand Ranius 2002; Hedin et al. 2008; Moore et al. 2017; Svensson et al. 2011). By closely following movements of single individuals through the habitat, radio telemetry can uncover the use of hitherto unknown or cryptic breeding sites (Moore et al. 2017) or time spent in other habitats (Chiari et al. 2013), which may contribute to increased distances from the natal patch to a breeding site. The most important limiting factor in such studies is the trade-off between the weight of the transmitter that is attached to the insect and the power of the transmitter. Active transmitters used in radio telemetry are powered by batteries and are usually relatively heavy (200–1000 mg), but the signal is transmitted over larger distances of up to 500 m on the ground (Kissling et al. 2014). While a 500 m radius may be enough to monitor movements and short-distance dispersal by telemetry, those individuals that fly beyond the range of the receiver are lost (Moore et al. 2017), and therefore long-distance dispersal events are rarely (if ever) detected with this method. Another problem arises due to the relatively large weight of the transmitter, which precludes their use in studies with smaller saproxylic insects as their normal movement and dispersal behavior may be altered. Consequently, most studies using radio telemetry have been conducted on large beetles such as *Osmoderma eremita* Scopoli, 1763 (Chiari et al. 2013; Dubois and Vignon 2008; Hedin and Ranius 2002; Svensson et al. 2011), the stag beetle *Lucanus cervus* Linnaeus, 1758 (Rink and Sinsch 2007), or rhinoceros beetles (Moore et al. 2017). Passive transmitters (without a power source) such as RFID tags are much lighter than active transmitters (weighing only 0.9 to 100 mg) which would allow the study of small saproxylic insects. However, as the range of the signal is <1 m, landscape-scale studies using transmitters are currently impossible (Kissling et al. 2014).

15.3.2 Direct Measurement of Dispersal: Capture-Mark-Recapture

Another method measuring exact dispersal distances is capture-mark-recapture (or mark-release-recapture). This method allows the determination of dispersal distances of particular individuals and dispersal rates of released cohorts (Rossi de Gasperis et al. 2016; Torres-Vila et al. 2017). Recapture efficiency may be increased using odor traps with species-specific semiochemicals if available for the respective species (Meurisse and Pawson 2017; Torres-Vila et al. 2015; Zauli et al. 2014), or traps with fermenting baits (Torres-Vila et al. 2017; Torres-Vila et al. 2012), that are placed at different distances from the release site. Using fermented bait traps to recapture *Cerambyx welensii* Küster, 1846 and *C. cerdo* Linnaeus, 1758, recapture rate ranged from 36% to 66%, which permitted the study of the influence of parameters such as wind speed and direction, air temperature, temporal patterns, and impact of season on dispersal behavior (Torres-Vila et al. 2017). As the study was conducted in two species in parallel, this allowed a direct comparison of dispersal behavior. Nonetheless, capture-mark-recapture studies are often biased toward those individuals that are captured again—often relatively close to the habitat patch they emigrated from. Long-distance dispersal events are rarely observed (Vlasanek et al. 2013), but can be estimated by extrapolation from the dispersal function at shorter distances (Drag et al. 2011; Torres-Vila et al. 2017). Another caveat may be that—depending on the method of marking—the movement abilities and thus movement patterns of insects may be altered (Gall 1984) or make them potentially more conspicuous to predators. In addition, movement behavior may be influenced by the translocation, e.g., if individuals are released in unfamiliar or matrix habitat (Heidinger et al. 2009). Both problems may be overcome by using a passive marking method, where individuals become marked when leaving their breeding site and are then captured after dispersal. Bark beetles have been successfully marked by coating or dusting infested logs with fluorescent dye or powder. As emerging beetles walked on the surface of the logs before flight, they became marked passively as grains of fluorescent powder adhered to cuticular hairs. After recapture, beetles can be inspected for the presence of fluorescent marker using a UV light source (Cronin et al. 1999; Dolezal et al. 2016).

15.3.3 Direct Measurement of Dispersal: Assignment Methods Using Genotypic Data of Individuals

Genotypic data (such as multilocus genotypes based on microsatellites) can also be used for direct measurement of dispersal. Such studies may yield comparable results to mark-recapture studies. While the dispersing individual is not directly observed, a particular dispersal event of an individual may be detected and distances measured when offspring can be assigned to their source parents based upon multilocus genotypes unambiguously. This, however, requires some genetic divergence of potential source populations and that these source populations have been sampled (Lowe and Allendorf 2010). This method is best applicable for species where groups of related individuals represent source populations with only a few individuals leaving such a kin group to disperse. Such a scenario can be found in bark beetles with high levels of inbreeding or subsocial beetle colonies as well as in eusocial ants and termites. Genotypes of source populations (or mature colonies) can then be compared with genotypes of individuals that have just dispersed to start new kin groups or colonies (Türke et al. 2010). Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 could be assigned unambiguously to their parental colonies based on multilocus genotypes and have been shown to disperse over at least 500 m (Simms and Husseneder 2009).

15.3.4 Direct Measurement of Dispersal: Colonization Experiments

Colonization experiments, where empty habitat patches (or odor traps) are provided and distances to potential source populations of colonizing insects are known, can also be utilized to measure dispersal distances. This method has been used to estimate dispersal abilities of beetles associated with bracket fungi (Jonsell et al. 1999; Jonsson and Nordlander 2006) and also for bark beetles and bark weevils on a very large scale (Chase et al. 2017; Nilssen 1984). In the latter study by Nilssen (1984), trap logs of spruce were laid out and colonized by the large pine weevil *Hylobius abietis* Linnaeus, 1758 at a distance of 171 km to the nearest occurrence of spruce forest. Chase et al. (2017), in contrast, used black panel insect traps with α-pinene and ethanol to attract the two bark beetle species *Hylurgus ligniperda* Fabricius, 1787 and *Hylastes ater* Paykull, 1800. Both species were trapped up to approximately 25 km away from the nearest pine stands. Colonization of deadwood structures after a large-scale forest fire can be seen as a natural experiment as abundant resources are generated over a vast area with a clearly visible distinction of burned and unburned parts of the forest. The colonization of large recently burned forest sites by pyrophilous saproxylic beetles as well as non-pyrophilous secondary users suggested that these groups were not negatively affected by up to 8 km distance to the border of the burned area (Saint-Germain et al. 2013).

15.3.5 Indirect Measurement of Dispersal: Population Genetic Analyses

Population genetic analyses are frequently used to infer population connectivity, i.e., the degree of gene flow on larger spatial and temporal scales, which is not feasible with direct measurements of dispersal. Population genetic inference is based on the principle that genetic divergence among local populations due to genetic drift (which causes subpopulations to diverge) is counteracted by the cohesive effects of gene flow due to individuals migrating from one population to another (Lowe and Allendorf 2010). The degree of genetic divergence can be used as an indicator of dispersal capacity of a species as it reflects past gene flow and thus dispersal (or absence thereof). When populations are subdivided (e.g., by fragmentation of forest habitats), the number of migrants can be estimated using classical F-statistics approaches. In species distributed continuously over space, limited gene flow (i.e., limited dispersal distances) leads to an increasing genetic differentiation among individuals as geographic distance increases, an effect known as isolation by distance (Allendorf et al. 2013).

Population genetic analyses also allow hierarchical analyses of populations on very different spatial scales within the same analysis. The relatedness and level of inbreeding of a group of individuals collected from a single structure such as a tree hollow can be measured (Schauer et al. 2018b) as well as genetic variation on the local (e.g., same forest patch) to regional scale as described above (Oleksa 2014; Oleksa et al. 2013, 2015; Schauer et al. 2018b). Dispersal distances can be estimated from spatial patterns of relatedness within local populations, where spatial autocorrelation among genotypes at varying distances is estimated. When individuals disperse over short distances, this will result in positive spatial genetic autocorrelation, i.e., the genotypes of individuals that are spatially closer are genetically more similar than at random (Epperson 2005; Oleksa et al. 2015).

Recent studies using population genetic analyses have shown that several saproxylic insects may be able to disperse over much longer distances than expected as no isolation by distance or population substructure was found among populations sampled over a distance of several hundred kilometers. For example, the cerambycid beetle *Rosalia alpina* Linnaeus, 1758 showed only very little genetic substructuring on a range of 600 km and potentially a rapid expansion of one genetic lineage within this area (Drag et al. 2015). Likewise beetles associated with bracket fungi such as *Bolitophagus reticulatus* Linnaeus, 1767 or *Diaperis boleti* Linnaeus, 1758 showed no spatial genetic substructuring over sites up to 200 km apart (Jonsson et al. 2003; Oleksa 2014). When landscape features are included in population genetic analyses, potential barriers to gene flow can be identified (or the lack of dispersal barriers that had been assumed before), which allows some inferences of dispersal behavior (Schauer et al. 2018b). However, this is also a potential drawback of landscape or population genetic analyses as for population substructure to arise gene flow must be lacking or hampered for a number of generation among subpopulations (Epps and Keyghobadi 2015). Furthermore, genetic analyses do not provide information about dispersal rate and exact dispersal distances of single individuals or on dispersal periods and patterns. Another drawback of population or landscape genetic analyses is that they are only feasible when a significant number of individuals per species [>30 to 50 at least, but the more the better (Lowe et al. 2004)] can be analyzed. For very rare species where only a handful of individuals can be analyzed, statistical noise would be too high to produce meaningful results.

15.3.6 Indirect Measurement of Dispersal: Analysis of Morphological Traits Impacting Light Performance

Dispersal ability can also be inferred indirectly by measuring traits associated with flight performance such as wing load (body mass divided by wing area) or wing aspect ratio (measure for shape of wings as wing length is divided by wing width) of the insect (Berwaerts et al. 2002). A lower wing load (i.e., less body weight per mm^2 of wing) supposedly translates into better flying ability because flight becomes energetically more efficient with decreasing wing load (Angelo and Slansky 1984). Relatively longer wings (higher aspect ratio) are thought to improve efficiency of prolonged flights and increase acceleration capacity or flight speed (Berwaerts et al. 2002; Marden 2000; Wootton 1992). Large body size reduces the mass-specific cost of flight and is thus associated with better dispersal ability (Roff 1991). Dispersal-associated morphological traits have been compared among (Gibb et al. 2006) as well as within (Bouget et al. 2015) species to differentiate between species or sexes with lower or higher dispersal abilities.

15.3.7 Indirect Measurement of Dispersal: Tethered Flight Experiments in Flight Mills

Tethered flight experiments are a suitable method to measure the physical dispersal capacity of individuals. As experiments are conducted under laboratory conditions with the surrounding “landscape” being similar for all individuals tested, it is assumed that motivational differences or differences due to environmental factors are reduced. Flight mills are the most common device used for tethered flight experiments, where an insect is attached to a flight arm that rotates due to the forces produced by the insect in flight. Flight time and speed are then used to calculate a maximum flight distance (Forsse and Solbreck 1985; Jactel and Gaillard 1991). Tethered flight experiments are suitable for the estimation of differences in dispersal abilities among species (Jonsson 2003) or within species (Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Taylor et al. 2010). When life-history traits associated with dispersal capacity are compared in parallel among the individuals used for the tethered flight experiments, the proximate mechanisms underlying differences in dispersal ability can be uncovered, e.g., by measuring sex-specific differences or the influence of body condition on flight capacity such as the presence and status of wings and wing muscles (wing load) or fat content

(Akbulut and Linit 1999; David et al. 2014; Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Jonsson 2003; Taylor et al. 2010).

A drawback of such experiments may be that flight behavior may be influenced by the insect being tethered. First insects must be handled and fixed to the device. Then, insects must accelerate the flight arm and have to overcome the friction of conventional bearings or the torsional resistance of magnetic mounds. This supposedly results in an underestimation of flight speed of the insects, which makes tethered flight experiments an excellent approach of measuring relative differences in dispersal capabilities but not absolute differences (Taylor et al. 2010).

15.3.8 Indirect Measurement of Dispersal: Inferring Dispersal Capabilities from Occurrence Patterns

The analyses of occurrence patterns (presence/absence) can be used to infer colonization abilities of saproxylic insects. Occurrence patterns of species result from their colonization abilities and local extinctions in respective habitat patches. In a number of studies, such occurrence patterns have been used as a proxy for colonization rates of specific habitat types and dispersal ability (Schiegg 2000a, b). However, as present occurrence patterns in habitat patches are confounded not only by current size and quality of the habitat patch itself but also by historical processes (Flensted et al. 2016; Gossner et al. 2008; Hanski and Ovaskainen 2002; Herrault et al. 2016; Janssen et al. 2016; Nordén et al. 2014), the estimation of dispersal abilities from such patterns is often difficult. Presence of a species within a habitat patch with low current connectivity to other habitat patches could either be due to a recent colonization event by a good disperser or the species has persisted locally if the habitat was formerly larger and/or less isolated and is therefore still found in spite of being a poor disperser (Herrault et al. 2016). This problem can be overcome when the same sites are sampled repeatedly, and thus colonization rate (and extinction rate in the metapopulation) can be inferred (Ranius et al. 2014). On the community level, colonization credit, i.e., lower than expected species richness in a habitat patch of a given area and quality, allows an estimation of the proportion of species that may be dispersal limited. After an increase in patch size, the number of species found would then be lower than expected in a habitat of a given size due to a time lag. For example, for hoverflies—a group that is thought to be highly mobile—Herrault et al. (2016) showed that they suffered a colonization credit in isolated woodlands, suggesting dispersal limitation.

In order to determine occurrence patterns, saproxylic insects need to be observed in a particular site or trapped. While direct observation in a particular site (e.g., by searching for individuals on the surface of potential host trees (Ranius et al. 2014) or opening deadwood structures) ensures that the particular insect really uses a site and is not only "passing through," using passive trapping is often preferred as it less labor intensive and captures a larger part of the saproxylic community. Emergence traps or flight interception traps are most often used to this end (Herrault et al. 2016; Irmler et al. 2010; Schiegg 2000a). By comparing the abundance of a particular species in flight interception traps within forest patches to that in traps in matrix habitat (open grassland), dispersal propensity and the potential of a species to cross matrix habitat can be tested, which helps to explain occurrence patterns.

Such an approach was used by Irmler et al. (2010), who showed that most of the 80 beetle species found in traps in the forest, as well as in grassland, were not very mobile, covering only distances of less than 30 m into the open grassland. Abundance of beetle species in forest patches was positively correlated with their mobility (Irmler et al. 2010).

15.3.9 Are Results of Different Methods Congruent?

Results obtained with the different methods described above yield different pictures of dispersal abilities of saproxylic insects (see Table 15.1 and overview of known dispersal distances below). Direct measurements of dispersal distances using telemetry or mark-release-recapture often suggest more limited dispersal abilities as distances measured are usually shorter than distances obtained in flight mill experiments or colonization experiments when conducted with the same species (e.g., several studies on *Bolitophagus reticulatus* Linnaeus, 1767, *Monochamus galloprovincialis* Olivier, 1795, or *Ips typographus* Linnaeus, 1758; for references see Table 15.1). This discrepancy may arise in capture mark-recapture-experiments due to the bias of individuals being recaptured. Recapture rate of those individuals dispersing over shorter distances only is higher than for those dispersing over longer distances. The potential for long-distance dispersal is captured more easily in tethered flight experiments. Likewise, the few population genetic analyses available to date often suggest that dispersal abilities are often better than hitherto thought. Here gene flow enabled by rare long-distance events is captured in absent or low genetic substructure or isolation by distance on larger spatial scales. As population genetic analyses also integrate over longer temporal scales, estimation of dispersal abilities is often not straightforward as genetic connectivity depends on the absolute number of dispersers among populations—and a few are enough to counteract population subdivision. For the persistence of a metapopulation of saproxylic insects, demographic connectivity is important though. Demographic connectivity means the relative contribution to population growth rates of dispersing individuals vs. survival and reproduction of residents (Lowe and Allendorf 2010). The use of a combination of different methods (direct and indirect measurement of dispersal) would therefore be important to gain a deeper understanding of the role of dispersal abilities in shaping community-level occurrence patterns of saproxylic insects locally and regionally.

Table 15.1 Studies addressing the dispersal abilities of saproxylic insects

	Dispersal strategy	Method	Distance	Author
Coleoptera				
Agrilus planipennis (Fairmaire 1888)	Flight	Flight mill	1.13 km	Fahrner et al. (2015)
Agrilus planipennis, (Fairmaire 1888)	Flight	Flight mill	>50% more than 750 m, 1% > 6 km	Taylor et al. (2010)
		Free flight experiment	>20 km	
Anaspis ruficollis (Fabricius 1792)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)
Anoplophora glabripennis (Motschulsky 1853)	Flight	Mark-recapture	2.6 km (98% of individuals recaptured within 920 m)	Smith et al. (2004)
Bolitotherus cornutus, (Panzer 1794)	Flight	Mark-recapture	50 m	Starzomski and Bondrup-Nielsen (2002)
Bolitotherus cornutus, (Panzer 1794)	Flight	Colonization experiment	365 m	Whitlock (1992)
Bolitophagus reticulatus (Linnaeus, 1767)	Flight	Field experiment	55 m	Sverdrup-Thygeson (2010)
Bolitophagus reticulatus (Linnaeus 1767)	Flight	Flight mill	29 h 36 min total flight time corresponding to 125 km	Jonsson (2003)
Bolitophagus reticulatus (Linnaeus 1767)	Flight	Genetic studies	200 km	Jonsson et al. (2003)
Cerambyx cerdo (Linnaeus 1758)	Flight	Mark-recapture	880 m for male, 1700 m for female	Torres-Vila et al. (2017)
Cerambyx welensii (Küster 1846)	Flight	Mark-recapture	1100 m for male, 580 m for female	Torres-Vila et al. (2017)
Dendroctonus frontalis (Zimmermann 1868)	Flight	Mark-recapture	500 m	Cronin et al. (1999)
Dendroctonus pseudotsugae (Hopkins 1905)	Flight	Flight mill	23 h continuous flight	Borden and Bennett (1969)
Diaperis boleti, (Linnaeus 1758)	Flight	Genetic studies	150 km	Oleksa (2014)
Elater ferrugineus, (Linnaeus 1758)	Flight	Mark-recapture	1.6 km, median 214 m	Zauli et al. (2014)
Elater ferrugineus (Linnaeus 1758)	Flight	Genetic studies	100 to ~650 m	Oleksa et al. (2015)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Hylobius abietis, (Linnaeus 1758)	Flight	Flight mill	10–80 km	Solbreck (1980)
Hylastes ater (Paykull 1800)	Flight	Colonization experiment	27.6 km	Chase et al. (2017)
Hylurgus ligniperda (Fabricius 1787)	Flight	Colonization experiment	26.3 km	Chase et al. (2017)
Hylurgus ligniperda (Fabricius 1787)	Flight	Mark-recapture	960 m, model based estimates 46% > 1 km, 1.6% > 5 km	Meurisse and Pawson (2017)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	1.1 km	Dolezal et al. (2016)
Ips typographus (Linnaeus, 1758)	Flight	Field experiment	8 km	Botterweg (1982)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	1.2–1.6 km	Forsse and Solbreck (1985)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	120 m (furthest trapping point)	Zolubas and Byers (1995)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	2 km	Rink and Sinsch (2007)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	200 m	Sprecher-Uebersax and Durrer (2001)
Lucanus cervus, (Linnaeus 1758)	Flight	Telemetry	2 km	Rink and Sinsch (2007)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	250 m for males, 144 m for females	Tini et al. (2017)
Monochamus alternatus (Hope 1843)	Flight	Mark-recapture	59 m	Shibata (1986b)
Monochamus carolinensis (Olivier 1792)	Flight	Flight mill	2200 m ± 1100 m	Akbulut and Linit (1999)
Monochamus galloprovincialis (Olivier, 1795)	Flight	Mark-recapture	>400 m	Torres-Vila et al. (2015)
Monochamus galloprovincialis (Olivier 1795)	Flight	Modeling of dispersal kernels in a mark-recapture study	> 4 km	Etxebeste et al. (2016)
Monochamus galloprovincialis (Olivier 1795)	Flight	Flight mill	63 km	David et al. (2014)
Monochamus sartor (Fabricius 1787)	Flight	Flight mill	3.14 km	Putz et al. (2016)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Monochamus sutor (Linnaeus 1758)	Flight	Flight mill	5.56 km	Putz et al. (2016)
Morimus asper (Sulzer 1776)	Walking	Mark-recapture	451 m	Rossi de Gasperis et al. (2016)
Odontotaenius disjunctus (Illiger 1800)	Flight, walking	Colonization experiment	Ø11.6 m	Jackson et al. (2009)
Oplocephala haemorrhoidalis (Fabricius 1787)	Flight	Flight mill	7 h 30 min total flight time corresponding to 29 km	Jonsson (2003)
Oplocephala haemorrhoidalis (Fabricius 1787)	Flight	Genetic studies	>12 km	Jonsson (2003)
Osmoderma barnabita (Motschulsky 1845)	Flight	Genetic studies	200 m	Oleksa et al. (2013)
Osmoderma eremita (Scopoli 1763)	Flight	Mark-recapture	190 m	Ranius and Hedin (2001)
Osmoderma eremita (Scopoli 1763)	Flight	Radio telemetry	1500 m	Chiari et al. (2013)
Osmoderma eremita (Scopoli 1763)	Flight	Radio telemetry	700 m	Dubois and Vignon (2008)
Osmoderma eremita (Scopoli 1763)	Flight	Flight mill	~2300 m	Dubois et al. (2010)
Protaetia marmorata (Herbst 1786)	Flight	Genetic studies	500 m	Oleksa et al. (2013)
Rhizophagus grandis (Gyllenhaal 1827)	Flight	Field experiment	4 km	Fielding et al. (1991)
Rosalia alpina (Linnaeus 1758)	Flight	Mark-recapture	1.6 km	Drag et al. (2011)
Rosalia alpina (Linnaeus 1758)	Flight	Genetic studies	600 km	Drag et al. (2015)
Spasalus crenatus, (MacLeay 1819)	Flight, walking	Colonization experiment	2–6 m	Galindo-Cardona et al. (2007)
Thanasimus dubius (Fabricius 1777)	Flight	Mark-recapture	1.25 km, 5% > 5 km, maximum one individual 8 km	Cronin et al. (2000)
Tomicus piniperda (Linnaeus 1758)	Flight	Field experiment	95.3% 400 m, 4.7% 780–2000 m	Barak et al. (2000)
Diptera				
Criorhina floccosa (Meigen 1822)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Hammerschmidtia ferruginea (Fallén 1817)	Flight	Mark-recapture	5 km	Rotheray et al. (2014)
Xylomya maculata (Meigen 1804)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)
Hymenoptera				
Tetrastichus planipennisi (Yang 2006) *(parasitoid of Agrilus planipennis)*	Flight	Flight mill	1.81 km	Fahrner et al. (2015)
Isoptera				
Coptotermes formosanus (Shiraki 1909)	Flight	Mark-recapture	890 m	Messenger and Mullins (2005)
Coptotermes formosanus (Shiraki 1909)	Flight	Mark-recapture	1.3 km	Mullins et al. (2015)
Coptotermes formosanus (Shiraki 1909)	Flight	Genetic studies	510 m	Simms and Husseneder (2009)
Pseudoscorpiones				
Allochernes wideri (C.L. Koch 1837)	Phoresy	Genetic studies	Small but significant genetic substructure at sites up to 900 km apart	Ranius and Douwes (2002)
Larca lata (Hansen 1884)	Phoresy	Genetic studies	Small but significant genetic substructure at sites up to 900 km apart	Ranius and Douwes (2002)

If no range or further information is presented in the column "distance" the maximum distance measured or estimated in the study is given

15.4 Dispersal Distances: What Is Known for Particular Taxa?

15.4.1 Beetles

The knowledge on dispersal seems to be best for saproxylic beetles compared to other taxa (see Table 15.1). Still there is only knowledge of few species in terms of their dispersal ability.

In the family of Scarabaeidae, *Osmoderma eremita* Scopoli, 1763 is the one species where most direct measurements of dispersal were conducted. Recorded maximum dispersal distances reported in different studies for *O. eremita* Scopoli, 1763 ranged from 190 m (Ranius and Hedin 2001) to 1500 m (Chiari et al. 2013). Physically *O. eremita* Scopoli, 1763 seems to be able to fly over larger distances, as in a tethered flight experiment a distance of ~2300 m was recorded (Dubois et al. 2010). This suggests that dispersal distances are influenced by local landscape and spatial distribution of suitable habitats. Shorter dispersal distances were recorded in the Swedish population with a high local density of suitable habitats surrounded by unsuitable matrix habitat, while in other study areas (Italy, France), larger dispersal distances were found where the beetles inhabit cork oaks in a large woodland area or chestnut trees that are patchily distributed in the landscape (Chiari et al. 2013; Dubois and Vignon 2008). Occurrence patterns on a larger geographic scale strongly suggest that *O. eremita* Scopoli, 1763 is dispersal limited as the presence of the beetle is positively correlated with spatial connectivity of habitat patches (Ranius et al. 2011). In the closely related species *Osmoderma barnabita* Motschulsky, 1845, Oleksa et al. (2013) estimated an average dispersal distance of 200 m and approximately 500 m in *Protaetia marmorata* Herbst, 1786 based on genetic data. Over a sampling range of 100 km, both species showed significant isolation by distance and thus limited gene flow due to the limited dispersal abilities (Oleksa et al. 2013).

In the family Tenebrionidae, the dispersal abilities of several beetle species with a very similar ecological niche have been studied. All species studied to date develop in and feed on the sporocarps of tinder or bracket fungi. Dispersal abilities of *Bolitophagus reticulatus* Linnaeus, 1767 have been measured with several different methods. An observed dispersal distances of 55 m in a field experiment (Sverdrup-Thygeson 2010) suggested that this beetle is likely to be dispersal limited. However, the dispersal abilities of *B. reticulatus* Linnaeus, 1767 should be much higher as the longest total flight time in flight mill-experiments for a single individual was 29 h 36 min which would correspond to an estimated dispersal distance of 125 km and median of ~7 km (Jonsson 2003). These results are corroborated by genetic analyses where no differentiation was found among populations as far apart as 200 km (Jonsson et al. 2003). Dispersal abilities of *B. reticulatus* Linnaeus, 1767 were compared to those of the rarer tenebrionid *Oplocephala haemorrhoidalis* Fabricius, 1787, which also feeds exclusively on tinder fungi. Both, flight mill experiments and genetic analyses suggested that the dispersal abilities were not as good as in *B. reticulatus* Linnaeus, 1767. While the median length of flight was estimated to be >12 km in *O. haemorrhoidalis* Fabricius, 1787, the maximum estimated flight time and distance was shorter (7 h 30 min and 29 km), and dispersal propensity was lower than in *B. reticulatus* (Jonsson 2003). Likewise genetic differentiation was moderate to strong in this species over the same geographic distance where no differentiation was found in *B. reticulatus* Linnaeus, 1767 (Jonsson et al. 2003). Studies on occurrence patterns on the one hand suggest that the beetle has excellent long-distance dispersal capabilities and is not dispersal limited as it occurs wherever the host fungus occurs (Jonsell et al. 2003). In contrast, another study shows habitat fragmentation may lead to a much higher differentiation in a fragmented landscape compared to a continuous area (Knutsen et al. 2000). A lack of spatial genetic substructure was similarly found for the fungus-associated *Diaperis boleti* Linnaeus, 1758 over a spatial scale of 150 km (Oleksa 2014). In the North American species *Bolitotherus cornutus* Panzer, 1794, mark-recapture data suggested a very limited movement radius of around 50 m (like in *B. reticulatus* Linnaeus, 1767, see above) (Starzomski and Bondrup-Nielsen 2002), while dispersal distances of 365 m were found in a colonization experiment (Whitlock 1992).

Dispersal in the family of Curculionidae has been studied for the subfamily Scolytinae, the bark beetles, as major forest pest species of economic interest. Measured dispersal distances in *Ips typographus* Linnaeus, 1758 ranged from 120 m (max. Distance at which traps with lure were placed in this mark-recapture study) (Zolubas and Byers 1995) to a range of 1.1 to 8 km in other studies and field experiments (Botterweg 1982; Dolezal et al. 2016; Weslien and Lindelöw 1990). The percentage of recaptured individuals was still around 2% of all marked individuals at the maximum distance sampled in these latter studies, suggesting that longer dispersal distances may occur under natural conditions. In addition, *I. typographus* Linnaeus, 1758 flies above the tree crowns which may allow the small beetles to be passively dispersed over larger distances by wind (Forsse and Solbreck 1985). Marked individuals of *Dendroctonus frontalis* Zimmermann, 1868 were found between 100 and 500 m from their releasing point (Cronin et al. 1999) and those of the common pine shoot beetle *Tomicus piniperda* Linnaeus, 1758 mostly within 400 m of the releasing point but a few up to 2 km away (Barak et al. 2000). For other Scolytinae, the estimated dispersal distances were much higher, with an estimated 10 to 80 km in a flight mill experiment for *Hylobius abietis* Linnaeus, 1758 (Solbreck 1980) or 23 h continuous flight in *Dendroctonus pseudotsugae* Hopkins, 1905, respectively (Borden and Bennett 1969). In mark-recapture experiment, many individuals were recaptured after a dispersal distance of 920 m, which was the furthest distance of traps from the site of release. Based on diffusion models, the authors estimate that nearly 50% of individuals of *Hylurgus ligniperda* Fabricius, 1787 disperse over at least 1 km and 1.6% further away than 5 km (Meurisse and Pawson 2017). The good dispersal abilities of this as well as another pine bark beetle species, *Hylastes ater* Paykull, 1800, were corroborated by colonization experiments using odor traps. Both species were caught in traps as far away as 26 km from the nearest pine resources (Chase et al. 2017). Based on mark-recapture studies, the dispersal distances of at least 50% of individuals of *Thanasimus dubius* Fabricius, 1777 (Cleridae), a predator of bark beetles in North America, were estimated to disperse at least 1.25 km, but around 5% should disperse over distances >5 km. The maximum dispersal distance of a marked individual was 8 km. Thus, the predator seems to have better or at least similar dispersal ability in comparison to its prey (Cronin et al. 2000).

Dispersal abilities of flightless Curculionidae were indirectly inferred by comparing occurrence patterns of woodlands in Northern Germany. The flightless weevils of the subfamily Cryptorhynchina *Acalles ptinoides* Marsham, 1802, *Trachodes hispidus* Linnaeus, 1758, and *Kyklioacalles navieresi* Boheman, 1837 (belonging to the subfamily Molytinae) were found only in ancient woodlands but not recent ones (Buse 2012), suggesting very strong dispersal limitation.

For Cerambycidae, longhorned beetles, dispersal distances vary considerably in the species that were studied to date, even in related species. The Japanese pine sawyer *Monochamus alternatus* Hope, 1843 seems to be a species with limited dispersal abilities as a dispersal distance of 59 m was observed (Shibata 1986b) using mark-recapture. Flight mill experiments on the congeneric *M. carolinensis* Olivier, 1792 suggest a better dispersal ability of this species, with mean flight distances being 2.2 km for both sexes (Akbulut and Linit 1999). In yet another congeneric, *M. galloprovincialis* Olivier, 1795, marked individuals were found at a distance of >400 m from the release site, while mean dispersal distance was app. 120 m (Torres-Vila et al. 2015). Based on modeling of dispersal kernels in a mark-recapture study, the estimated dispersal distance of *M. galloprovincialis* Olivier, 1795 is still larger though with >4 km (Etxebeste et al. 2016). Flight mill experiments again underscore the good dispersal abilities of *M. galloprovincialis* Olivier, 1795 with a mean estimated potential dispersal distance of 16 km and a maximum of up to 63 km (David et al. 2014). The good dispersal capacity of beetles of this genus was corroborated in a study on another two European species *M. sartor* Fabricius, 1787 and *M. sutor* Linnaeus, 1758 using a flight mill. The maximum distance flown in a single bout by *M. sartor* Fabricius, 1787 was 3.14 km, and the cumulative dispersal distance over the life span of a beetle was 7.5 km. The smaller *M. sutor* Linnaeus, 1758 flew even further, with a maximum flight distance of 5.56 km (Putz et al. 2016). The majority of marked and recaptured Asian longhorned beetles *Anoplophora glabripennis* Motschulsky, 1853 were found to disperse less than 1 km from the release site, while some individuals were caught at distances of 2.6 km from the release site (Smith et al. 2004). Earlier studies of *A. glabripennis* Motschulsky, 1853 showed slightly shorter dispersal distances (Smith et al. 2001).

Dispersal abilities of the threatened Rosalia longicorn *Rosalia alpina* Linnaeus, 1758 were studied using mark-recapture as well as genetic analyses. The maximum distance covered (which included flights over unsuitable matrix habitat) was 1600 m (Drag et al. 2011), suggesting good dispersal abilities. No genetic substructure was found among populations of *R. alpina* Linnaeus, 1758 as far apart as 600 km (Drag et al. 2015), suggesting that the observed dispersal distance translates into high levels of gene flow over large distances, in spite of habitat fragmentation. Dispersal abilities of *Cerambyx welensii* Küster, 1846 and *Cerambyx cerdo* Linnaeus, 1758 were estimated using mark-recapture methods in Spanish populations. Both species showed a pronounced dispersal polymorphism. While some individuals showed a high dispersal propensity and much larger dispersal distances than other individuals (*C. welensii* Küster, 1846, maximum recorded distance of 1100 m for a male and 580 m for a female; *C. cerdo* Linnaeus, 1758, 880 m for a male and 1700 m for a female), many individuals were sedentary and hardly moved away from the site of release (Torres-Vila et al. 2017). This subset of individuals should allow colonization of habitat patches that are further away. In contrast, in the flightless cerambycid *Morimus asper* Sulzer, 1776, only very few individuals left the point where they were released after marking, and the furthest dispersal distance measured was 451 m (Rossi de Gasperis et al. 2016).

Among elaterids, information on dispersal distance is available only for *Elater ferrugineus* Linnaeus, 1758, a facultative predator of *O. eremita* Scopoli, 1763. Here dispersal distances of more than 1.6 km were found using mark-recapture and a median dispersal distance of 214 m, suggesting again similar or better dispersal capacities of the predator in comparison to its prey (see above the clerid *T. dubius* Fabricius, 1777 and its bark beetle prey) (Zauli et al. 2014). Genetic analyses suggest a dispersal distance of 100 to ~650 m as isolation by distance was found at a scale of ~9 km, albeit in a fragmented agricultural landscape where this click beetle can mostly be found in old hollow trees along rural avenues (Oleksa et al. 2015).

In *Lucanus cervus* Linnaeus, 1758 (Lucanidae), telemetry studies revealed dispersal distances between 200 m in a Swiss population (Sprecher-Uebersax and Durrer 2001) and 2 km in a German population (Rink and Sinsch 2007). In another telemetry study conducted in a relict lowland forest in a nature reserve in Italy, the mean dispersal distance of *L. cervus* Linnaeus, 1758 males was 250 m compared to an average of 144 m for females (Tini et al. 2017).

The buprestid *Agrilus planipennis* Fairmaire, 1888 (emerald ash borer) has been shown to fly over distances of up to 1.13 km (Fahrner et al. 2015) to >6 km (Taylor et al. 2010) in flight mill experiments. As insects may show slower flight speed when tethered (see discussion of tethered flight experiments, Sect. 15.3.7), Taylor et al. (2010) measured the speed of flight in free-flying experiments in parallel. Flight distances obtained in the flight mill experiment were then calibrated with flying speed in free-flight and dispersal distances corrected. The median corrected flight distance of females was >3 km and 1% of females flew >20 km.

The passalid beetle *Spasalus crenatus* MacLeay, 1819 was shown to have very limited dispersal abilities. In a colonization experiment, beetles dispersed for 2 to 6 m only from a release point before initiating a colony. The beetles were functionally flightless as their wing muscles were not developed, strong enough to enable flight and thus most likely dispersed by walking (Galindo-Cardona et al. 2007). Similarly, the passalid *Odontotaenius disjunctus* Illiger, 1800 primarily disperses over short distances of on average 11.6 m by walking (Jackson et al. 2009) and has rarely be shown to fly over longer distances (Jackson et al. 2012).

The predator *Rhizophagus grandis* Gyllenhaal, 1827 (Rhizophagidae) was also shown to have good dispersal abilities as individuals were found at their prey 4 km from the release site (Fielding et al. 1991). In the scraptiid beetle *Anaspis ruficollis* Fabricius, 1792, inhabiting tree hollows but also lying deadwood, population genetic analyses did not uncover genetic differentiation in a ~10 × 10 km study area of large forest fragments. However, genetic differentiation was slightly stronger in this beetle species in comparison to the two dipteran species compared in the same study (Schauer et al. 2018b).

15.4.2 Other Saproxylic Taxa

For hoverflies and other dipteran species, not much is known about their dispersal abilities. In a mark-recapture study on the syrphid fly *Hammerschmidtia ferruginea*

Fallén, 1817, a dispersal distance of 5 km was shown (Rotheray et al. 2014). Schauer et al. (2018b) could show no genetic differentiation of the syrphid fly *Criorhina floccosa* Meigen, 1822 and the xylomid fly *Xylomya maculata* Meigen, 1804 in a ~10 x 10 km managed forest, suggesting good dispersal abilities of these two species.

The hymenopteran *Tetrastichus planipennisi* Yang, 2006, a parasitoid of the emerald ash borer *Agrilus planipennis* Fairmaire, 1888, has been shown to be able to disperse slightly further than its host. While *A. planipennis* Fairmaire, 1888 flew a maximum distance of 1.13 km, the parasitoid showed a maximum flight distance of 1.81 km under similar conditions in a flight mill experiment (Fahrner et al. 2015).

Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 have been shown to disperse over at least 500 m to 1300 m in an urban setting in New Orleans. Dispersing individuals could be assigned unambiguously to their parental colonies either based on multilocus genotypes (Simms and Husseneder 2009) or in mark-recapture experiments (Messenger and Mullins 2005; Mullins et al. 2015). Small flightless arthropods such as pseudoscorpions and mites often hitchhike on larger saproxylic insects for dispersal. Using population genetic analyses, Ranius and Douwes (2002) found very small genetic substructure among populations of *Allochernes wideri* C.L. Koch, 1837 and *Larca lata* Hansen, 1884 as far apart as 900 km, suggesting good passive dispersal through phoresy (Ranius and Douwes 2002). Nonetheless, *L. lata* Hansen, 1884 may still be dispersal limited as its occurrence was positively correlated with spatial connectance on larger spatial scales (Ranius et al. 2011).

15.5 Outlook and Conclusion

Researchers and naturalists alike often estimate dispersal abilities of particular taxa—or species—based on their morphology and notion of life-history traits as data on dispersal is often still scarce. To date dispersal distances have been measured mostly either for pest species or threatened species (often "flagship species"). Knowledge of dispersal behavior and its implications for gene flow, population persistence, and colonization of new habitats is still scarce. A better knowledge of dispersal abilities and behavioral aspects of dispersal are needed, especially with respect to the development of management strategies for saproxylic insects in managed forests or fragmented habitats.

Currently, there is ongoing debate in the field whether saproxylic insects are rather dispersal limited or habitat limited. Due to deforestation and ecological degradation of forests, connectivity and habitat availability are both low. Absence of a species in a seemingly suitable habitat patch is often interpreted as dispersal limitation. Local extinction may result from the absence of habitat, poor habitat quality, or unsuitable area around a habitat patch that is not crossed during dispersal (Fahrig 2013; Hanski et al. 1994). The relatively few population genetic analyses available to date suggest that saproxylic insects are often not dispersal limited on a local and regional scale—or at least not as much as assumed. However, this will depend strongly on the species studied as different taxa vary strongly in dispersal distances and dispersal abilities (e.g., passalids dispersing a few meters only in comparison to some flying cerambycids or scolytids that can disperse over several to dozens of kilometers). Studies on occurrence patterns over larger geographic scales have detected dispersal limitation for a broad range of different species. When forest fragments or other habitat structures are more isolated, fewer saproxylic insect species occur (Bergman et al. 2012; Ranius et al. 2011). Likewise, artificial deadwood structures mimicking tree hollows were less often colonized by saproxylic tree hollow specialists when placed further away from sources. As habitat quality was comparable, species have most likely been dispersal limited (Jansson et al. 2009).

Factors influencing different aspects of dispersal behavior, such as the decision to leave a patch, the movement pattern (e.g., what kind of matrix habitats are crossed during dispersal?), and the decision to settle at a particular site are often still unknown. These factors include the sex of an individual, body condition, feeding strategy, breadth of ecological niche, or competition. Even less is known about the interplay of several of these factors. However, such data is needed to assess whether structural connectivity among habitat patches also results in functional connectivity.

The use of a combination of methods that integrate several temporal and spatial scales would be desirable to characterize dispersal abilities of species. By combining mark-recapture techniques and population genetic analyses, the dispersal ability of a large proportion of individuals can be tested directly using the former, and the influence of the often small percentage of individuals dispersing over much larger distances on the population structure would be captured with the latter. And how strongly do dispersal distances vary with landscape and are they consistent over time? If such data was available for more species, this would allow for comparative analysis to be conducted, allowing more general conclusions of the dispersal abilities of species with similar ecological niches. For example, the suite of species of tenebrionid beetles feeding on fungal sporocarps seems to have relatively similar dispersal abilities, in spite of belonging to different genera and living on different continents. Does this hold for more groups of species with a similar ecological niche? How strongly is dispersal behavior influenced by spatial and temporal heterogeneity? In the light of climate change and anthropogenic habitat destruction, it is important to assess the plasticity or evolutionary potential of dispersal strategies for different species.

A better knowledge of dispersal of saproxylic insects is required for an understanding of ecological processes but also to inform management decisions for the conservation of threatened species. However, as dispersal is a highly complex phenomenon, more integrative studies would be vital that on the one hand examine physiological and behavioral aspects of dispersal and on the other hand measure dispersal distances using different methods. An increase in availability of data on dispersal collected with different methods will allow drawing more general conclusions and potentially also relatively well-informed predictions of the dispersal abilities of species.

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Chapter 16
Seasonality and Stratification: Neotropical Saproxylic Beetles Respond to a Heat and Moisture Continuum with Conservatism and Plasticity

Amy Berkov

Abstract Insect niche breadth informs community assembly and impacts the resilience of populations, species, and ecosystems. Niches are poorly known for most tropical insects, especially concealed feeders associated with tall trees. This chapter synthesizes data regarding seasonality and stratification in the early colonists of moribund wood, Cerambycidae and saproxylic Curculionidae. These data, from five rearing experiments conducted at four Neotropical moist forest sites over two decades, are of particular value because they can be used to generate predictions in an unpredictable time. Beetle species currently associated with warmer, drier, microhabitats (in the subfamily Cerambycinae and some Curculionidae) might withstand drier conditions, but not necessarily higher temperatures. Those currently associated with relatively cool, moist microhabitats (most Curculionidae) may be more vulnerable to changes in the length and severity of the dry season. Rather than characterizing tropical saproxylic insects by their periods of adult activity or flight height, which can be variable, it would be useful to conceptualize them with preferences along a continuum, from warm and dry to cool and moist.

16.1 Introduction

16.1.1 Seasonality and Stratification in Tropical Forests

For almost all species in temperate and boreal regions, the annual rhythms of life are dictated by climatic oscillations that determine the availability of food and water. The phenologies of dormancy, germination, mating, reproduction, dispersal, and

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duration of life cycles are all fundamentally influenced by the tilt of the Earth's axis. At latitudes approaching the equator, tilts toward or away from the sun diminish. Divisions into day and night become progressively more egalitarian—leading to short summer days—and seasonal shifts in temperature become less dramatic. In the tropics, mean temperatures throughout the year typically vary less than daily temperatures and often vary less than temperatures between canopy and ground stratum (Denlinger 1986; Lee et al. 2014). Even at tree line in montane tropical forests, where warm days are often followed by freezing nights, annual fluctuations are minor (Rehm and Feeley 2015). The amazing profusion of life in tropical rain forests attests to their thermal suitability. There is still no consensus on the main mechanisms leading to the latitudinal diversity gradient, but these patterns—while not universal—are conspicuous and consistent and have persisted over many millions of years (Hillebrand 2004; Mittelbach et al. 2007; Schemske and Mittelbach 2017). Some potential explanations for the generation and maintenance of tropical species richness are related to increased exposure to solar energy: relatively short generation times and high mutation rates might lead to higher rates of speciation, and increased productivity might allow narrower niches and increased coexistence. In addition, because the tropics are less affected by cycles of glaciation, climatic stability over time could enable species to accumulate and/or reduce the likelihood of extinction.

Cyclical changes in temperature, one of the major drivers of seasonality at higher latitudes, would be less likely to lead to seasonality in tropical arthropods. Does this mean that tropical forest arthropods are active and reproduce throughout the year? Not necessarily; even in evergreen Neotropical forests, annual precipitation varies more than threefold (from <2000 mm to >6000 mm). Dry season(s), months receiving <100 mm precipitation, range from 0 to 6 months (Christoffersen et al. 2014; Taylor et al. 2015; Tuomisto et al. 2014). Rainfall potential is determined by the amount of moisture carried by the prevailing winds, and precipitation gradients are especially steep across the narrow, but topographically complex, land masses of Central America. In Panama, annual precipitation in the Atlantic coast is 3140 mm (supporting evergreen wet forest), while in Pacific coast, annual precipitation is only 1740 mm (supporting tropical, dry, deciduous forest); only 40 km separates the coasts (Ødegaard 2006).

Some kind of dormancy is fairly common among tropical agricultural pests, and collection records of other adult tropical insects are also used to infer seasonal activity. It's not always possible to distinguish quiescence (stimulated by adverse conditions) from diapause (a programmed hiatus that, depending on the species, can occur during any stage of the life cycle) (Denlinger 1986). Diapause can last as long as 10 months, and while it frequently enables insects to avoid the dry season, some species bypass the rainy season, and other species avoid parts of both. Because precipitation cycles are linked to biotic components of the environment (leaf flush, flower and fruit production, litter accumulation, tree falls, abundance of competitors or predators), it is seldom clear exactly where the selective advantage lies.

Seasonal activity is defined by its predictable nature: it may not actually occur every year, but when it does, it occurs at the same time. There can be one or more seasonal peaks in activity, the peaks can be sharp or broad, and activity outside of the peak(s) can be entirely absent or continue at low levels (Wolda 1988; Kishimoto-Yamata and Itioka 2015). In temperate regions, insect activity is usually brought to a halt when temperatures drop, and dormancy is synchronized with winter. In the tropics, seasonality is generally inferred by changes in adult abundance (Kishimoto-Yamata and Itioka 2015). Only a handful of studies include data from more than 1 year. These are needed to determine if the timing of abundance peaks has predictive value and can therefore be considered seasonal. In Kishimoto-Yamata and Itioka's (2015) review, most insects in drier tropical forests (in which the driest month received no more than 60 mm of rainfall) demonstrated seasonal behavior: they entered diapause in either the dry or rainy season. Some insects were seasonal even in wetter forests (in which the driest month received more than 60 mm of rainfall), but more were aseasonal. In some cases, abundance maxima fluctuated in timing, from year to year.

While annual temperatures—and sometimes precipitation—are more uniform in tropical forests, vertical gradients are generally more pronounced (Basset et al. 2003). Vertical stratification, like seasonality, can involve both biotic (resource availability, species interactions) and abiotic (microclimate) variables (Wardhaugh 2014). Insects that feed on new leaves, flowers, seeds, fruits, or epiphytes may have increased access in the forest canopy, but they must contend with greater fluctuations in light, temperature, humidity, and wind. Insects that depend on resources that are more abundant at ground stratum, like leaf litter, dung, carrion, fungi, or low-growing plants, might be subject to inundation or excessive humidity or vulnerable to terrestrial predators. In most forests, the soil fauna is generally distinct from the aboveground fauna, but there may be vertical migration associated with different seasons, stages of the life cycle, or even the time of day. In tropical forests, stratification within the canopy often represents changes in relative abundance, although the upper canopy may be distinct in species richness and community composition (Basset et al. 2003; Stork et al. 2016). Perhaps this is not surprising, given that most feeding substrates can be found at more than one stratum. Dragonflies lay eggs in pools of water that accumulate in epiphytic tank bromeliads, soil arthropods colonize pockets of litter and soil that accumulate high in the trees, and individual tree species are found at multiple strata as seedlings, saplings, and mature trees.

16.1.2 Seasonality and Stratification in Saproxylic Beetles

Because saproxylic insects belong to various feeding guilds and are associated with wood in different stages of decay (Grove 2002; Stokland 2012; Stokland and Siitonen 2012), their phenologies may track those of their preferred resources. Primary saproxylic species colonize and create galleries in trunks and branches that still have their bark attached, in which wood is not yet decayed. These early colonists tend to be bark beetles, accompanied or followed by other saproxylic weevils and cerambycids. They are often limited to a single generation within a particular tree, because they rapidly consume the most nutritious tissues. Primary saproxylic species set the stage for insects at higher trophic levels or those associated with wood in a more advanced stage of decay.

The availability of moribund wood is determined by tree mortality; the causes affect the quantity and quality of the nutrient pulse and its periodicity. Some trees are lucky enough to live out their life spans and then senesce. Others succumb to competition, attack by insects or pathogens, or wind damage. In more extreme cases, the entire stands can be transformed by large-scale disturbances. Trees that die as part of background mortality may already be declining in vigor, and the process is often gradual (Stokland and Siitonen 2012). In temperate forests, there is seldom a single cause. Insects colonize stressed trees, and even trees that succumb to mechanical damage appear to have suffered biotic challenges prior to death (Das et al. 2016; Gonzalez-Akre et al. 2016).

Background mortality rates in tropical moist and wet forests range from approximately 1.1–2.2% per year (Lugo and Scatena 1996). Wind damage appears to be particularly prevalent, with uprooted trees especially common at forest edges (D'Angelo et al. 2004). Catastrophic events can leave behind a high-nutrient banquet, but such events can completely transform the light and moisture regimes, leading to altered successional trajectories. On the island of Dominica, a single hurricane in 1979 was estimated to kill 5 million trees in 10 hours (Lugo and Scatena 1996), and in the Amazon basin, a squall line (storm cluster) in 2005 may have resulted in the loss of more than 500 million trees (Negrón-Juárez et al. 2010). When mortality is episodic—with regular peaks due to either natural enemy attack or cyclical disturbance—it could certainly impact the seasonality of primary saproxylic insects.

Seasonal behavior in saproxylic beetles, like other insects, is also impacted by local climate and body mass, which affect the ability to avoid desiccation (Addo-Bediako et al. 2001). Species inhabiting higher latitudes have their active periods constrained by low temperatures, but at lower latitudes, they are more likely to be constrained by excessive heat or prolonged dry periods. In southern Norway, 13 years of trapping data indicated that saproxylic beetle species were active for periods ranging from approximately 29 through 96 days (Gillespie et al. 2017). Smaller species (including curculionids) were active for longer periods than large species (including cerambycids), and cerambycid flight periods decreased with increasing body size. In a 4-year study in Illinois, USA, cerambycid flight seasons began in March, peaked in July, and declined in August through September (Hanks et al. 2014). Cerambycines flew early spring through late fall, while lepturines were limited to summer, and lamiines were active from summer to fall. Most sympatric species had somewhat short, staggered, and predictable adult flight periods, probably facilitating mate encounter, but also showed year-to-year variation. In Louisiana, USA, scolytine activity patterns were fairly consistent at three sites (Schoeller and Allison 2013). Species in the genus *Ips*, secondary pests of weakened pines, were trapped throughout the year with abundance peaks during the early spring and early fall. Depressed abundance in the summer might be explained by the extremely warm temperatures, which often exceed 37 °C.

The most notable findings in a study of bark and ambrosia beetles in a Brazilian tropical dry forest were the overall low abundances, especially of bark beetles (Macedo-Reis et al. 2016). Ambrosia beetle adults were more abundant when precipitation was increasing or decreasing, perhaps avoiding desiccation during the driest months and also avoiding flight during heavier rains. Most cerambycids in a Mexican tropical dry forest showed little tendency to avoid the rainier times of the year: 85% of the species were captured only during the (relatively short) rainy season, and both species richness and abundance peaked during the wettest months (Noguera et al. 2002). In Panama, a multi-site light-trapping study of curculionids (including saproxylic weevils but excluding bark and ambrosia beetles) showed that sites with greater seasonality in rainfall were associated with greater seasonality in weevil abundance (Wolda et al. 1998). There were sharp peaks in trap yields at the onset of the rainy season and, sometimes, smaller peaks within the rainy season. Adult flight activity during the initial peaks seemed to correspond with the timing of the initial rains, which shifted from year to year. At the more seasonal sites, >80% of the weevil species were considered seasonal; only 60% of the species were seasonal in the less seasonal sites. Despite the overall increased abundance during the rainy season, different species reached their peak abundances throughout the entire year.

Just as resource availability impacts seasonality, it affects microhabitat association and vertical stratification (Wardhaugh et al. 2012). While dead trees and branches are certainly more conspicuous on the ground, there can be a surprising amount of dead wood available high in the air. In a study of managed coniferous forests in Sweden, the surface area of dead branches attached to living trees was about the same as the surface area of snags, stumps, logs, and branches on the ground (Svensson et al. 2014). In a tropical dry forest in Mexico (with a low, dense canopy), >70% of the coarse dead woody biomass was standing, hanging, or attached to live trees (Maass et al. 2002). This does not imply that saproxylic beetles will always have equivalent access to a preferred host plant in a suitable stage of decay at both canopy and ground stratum. If, however, an appropriate resource is available at both strata, preference is likely to be determined by abiotic variables. In tropical moist forests, light intensities can be 500× higher in the canopy than in the understory (Kelber et al. 2006). In closed canopy forests, temperature and wind decrease, and humidity increases, along a gradient from the upper canopy to the forest floor (Ulyshen 2011).

Assessments of vertical stratification in saproxylic insects are heterogeneous, making it difficult to generalize. Both abundance and species richness in forest canopies can be higher than, similar to, or lower than ground stratum (Bouget et al. 2011). Species turnover is often high, even at different levels within the understory, but this can be due to the number of uncommon species (species represented by relatively few individuals are more likely to be collected at a single stratum) (Weiss et al. 2016; Wolda et al. 1998). Several studies in temperate forests found that about 30% of the saproxylic beetle species were recorded only at canopy stratum (Bouget et al. 2011), although rearing studies have detected higher species richness in logs than in standing snags (Ulyshen and Hanula 2009). In temperate deciduous forests near Montreal, Canada, curculionids (excluding bark and ambrosia beetles) were significantly more abundant at ground stratum, and cerambycids were more abundant at canopy stratum. Scolytines were much more abundant than other curculionids and tended to be more numerous in the canopy (Maguire et al. 2014). In the southeastern USA, saproxylic species that fed on bark or wood (buprestids, cerambycids, and some curculionids) tended to be more abundant and rich in higher traps, while scolytines that fed on ambrosia fungi were preferentially captured at ground stratum (Ulyshen and Sheehan 2017).

Some apparently inconsistent results may reflect differences in forest composition, structure, and/or management. The remaining ancient European woodlands are thought to provide appropriate microclimate conditions (moist, shaded) for relict forest species, including saproxylic weevils (Buse 2012). A Czech Republic trapping study, in the closed canopy forest that succeeded a coppice woodland, documented a saproxylic assemblage that was rich in sun-loving species (Vodka and Cizek 2013). Species richness was highest on forest edges, and within the forest interior, many species preferred canopy stratum, perhaps representing a legacy of past management.

A couple of intriguing studies suggest that there may be less stratification in moist tropical forests—which seems surprising, given their height and structural complexity. In Panama, no more than 20% of curculionids (excluding bark and ambrosia beetles) were restricted to either canopy or ground stratum (Wolda et al. 1998). In an Australian lowland rain forest, when singletons and doubletons were excluded, just 28% of all beetles were restricted to a particular stratum (Stork and Grimbacher 2006). Scolytines tended to be slightly more abundant at ground stratum, while other curculionids and cerambycids tended to be captured more frequently at canopy stratum. Stratification might be minimized in tropical forests due to their thermal heterogeneity, which is more extreme than would be predicted by ambient conditions: sunflecks warm, and microhabitats thermally buffer, the available substrates (Scheffers et al. 2017).

16.1.3 Objectives and Significance

Trapping studies provide much of the data for seasonality and stratification; these document flight height, but not the stratum of the larval substrate. The microhabitat of the larval substrate is particularly important for subcortical insects, because larvae cannot escape adverse conditions. Although rearing may be less effective than long-term trapping to detect seasonality, it does provide information about periods of adult activity. The objective of this chapter is to compare results from five rearing projects conducted at four Neotropical sites to make inferences about, and assess the stability of, patterns of seasonality and stratification within the beetle families Cerambycidae and Curculionidae. Interpretations of these studies, conducted over two decades in forests with different precipitation and disturbance regimes, with different objectives and methodologies, should be interpreted as testable hypotheses, to help guide future efforts.

Over the twenty-first century, Amazonian forests are expected to experience warming temperatures and longer, more severe dry seasons (Betts et al. 2008). Tropical ectotherms appear to have relatively narrow thermal tolerances and may already experience temperatures close to their maxima, with little safety margin (Deutsch et al. 2008; Kaspari et al. 2015). Due to phylogenetic conservatism, related species may share seasonal activity patterns and microhabitat associations that affect their exposure to hot or dry conditions; members of entire lineages might therefore be similarly impacted by climate change. Beetles consistently associated with the warmest, driest microhabitats might require behavioral changes to avoid even small upward shifts in temperature. Beetles associated with cool, moist microhabitats might be more vulnerable to increasingly severe dry seasons.

16.2 Methods

16.2.1 Overview of Rearing Projects

Five rearing projects were conducted at four lowland moist Neotropical forests: central French Guiana (1995–1996, FG95, and 2007–2008, FG07), southeastern Peru (2003–2005, Peru03), Panama Canal Zone (2010–2011, Pan10), and the Osa Peninsula, Costa Rica (2013–2014, CR13) (Table 16.1). The South American studies aimed to describe the host, stratum, and seasonal specificity of cerambycids associated with trees in the Brazil nut family, Lecythidaceae. The second French Guiana study assessed the stability of specialist classifications over time and captured more precise data for curculionids (previously considered "bycatch," with just host plant species and season recorded). The Central American studies included more host plants, focusing on families that had been well-sampled in French Guiana (Tavakilian et al. 1997): legume (Fabaceae), Brazil nut (Lecythidaceae), *Hibiscus* (Malvaceae), fig (Moraceae), and chicle (Sapotaceae). Both cerambycids and curculionids were preserved for analysis. Pan10 was a salvage project on a headland destined to be clear-cut prior to the widening of the Panama Canal; CR13 compared specialization within forest successional stages.

The forest in French Guiana was the least disturbed, those in Peru and Costa Rica were mosaics of old growth and secondary forests, and the Panama site supported more mature secondary forest. All sites have considerable interannual variation in precipitation. The Costa Rica site receives, by far, the most rain, approximately 4000 mm (Taylor et al. 2015), while other sites receive annual means of roughly 2450–2650 mm (Panama data are from Barro Colorado Island and may be an overestimate) (Comita and Engelbrecht 2009; Paine et al. 2009; Ringard et al. 2015). Mean daily temperatures recorded in the understory for 29 days following the dry season cuts, when primary saproxylic beetles should be active, show that Panama and Costa Rica were warmer—presumably due to the close proximity of large water bodies (mean temperature ± SD: 27.3 °C ± 0.58 and 26.4 °C ± 0.61, respectively). French Guiana, closest to the equator but surrounded by minimally

Table 16.1 Saproxylic beetles (Cerambycidae, Curculionidae) reared in four lowland moist Neotropical forests

Project	Locality, coordinates	Plant sample	Baits cut/caged	Species	Abundance	References
French Guiana (1995–1996)	Les Eaux Claires	Lecythidaceae (25 ind., 5 spp.)	Dry: Sept 1995/Dec–Jan 1996	38[a]	1813[a]	Berkov and Tavakilian (1999) and Berkov (2002)
	3°37–39′N		Rainy: Jan/Apr 1996	64[b,c]	982[b]	
	53°12–13′W					
Peru (2003–2005)	CICRA, Madre de Dios	Lecythidaceae (30 ind., 6 spp.)	Dry: Aug/Nov 2003	82[a]	7638[a]	CICRA (2004), Fassbender (2013) and Berkov (unpubl. data)
	12°32–34′S		Rainy: Jan/Apr 2004	72[b,d]	2929[b,d]	
	70°05–06′W					
French Guiana (2007–2008)	Les Eaux Claires	Lecythidaceae (9 ind., 3 spp.)	Dry: Aug/Nov 2007[e]	25[a]	1809[a]	Lee et al. (2014) and Fassbender et al. (2014)
	3°37–39′N		Rainy: Jan/Apr 2008[e]	51[b,c]	1262[b]	
	53°12–13′W					
Panama (2010–2011)	ACP site 7	25 families (67 ind., 36 spp.)	Dry: Mar/May 2010[e]	63[a]	1984[a]	Torres in prep.; Berkov, Barrios, Pinzon, Eng unpubl. data
	9°07′N			34[b]	367[b]	
	79°45′W					
Costa Rica (2013–2014)	Osa Conservation	6 families (41 ind., 9 spp.)	Dry, transition: Mar–Apr/June–July 2013[e]	49[a]	3549[a]	Li et al. (2017) and Morillo (2017)
	8°24′N			91[b]	8761[b]	
	83°20′W					

[a] Cerambycidae

[b] Curculionidae

[c] Platypodinae are underestimated because females cannot be placed in genera

[d] Platypodinae and Scolytinae are not included

[e] Microclimate data (temperature, relative humidity, wind speed) were collected with Kestrel Pocket Weather Meters (models 4000 or 4100, Nielsen-Kellerman, Boothwyn, PA)

disturbed forest, was intermediate (24.1 °C ± 0.68). Peru was the most heterogeneous (20.7 °C ± 3.60, with means estimated at CICRA, the research station, as averages of daily maximum and minimum); it experiences periodic winter *friajes*, in which masses of cold air move northward and temperatures drop as low as 8 °C (Pitman 2008).

Stratification is likely because abiotic conditions vary by season and stratum: in French Guiana, maximum temperature at canopy stratum during the dry season is approximately 7 °C higher than at ground stratum during the rainy season (Lee et al. 2014). In Panama, where the site was a headland surrounded by the Panama Canal, dry season temperatures were similar at ground and canopy stratum (Berkov, unpubl. data), but the canopy baits still lost moisture more rapidly than the ground baits—and on the ground, thin branches lost moisture more rapidly than thick branches (Torres in prep.).

16.2.2 Rearing Protocol

Our preferred protocol is to use single-line climbing techniques to remove a single branch (diameter 8–9 cm) from each tree. In the South American projects, branches were cut during both the dry and rainy seasons (Table 16.1). In the Panama project, branches were cut in the middle of the dry season, and in the Costa Rica project, they were cut shortly before the transition from the dry to rainy season. We removed the basal section of each branch (65–70 cm) and suspended it in the tree from which it was cut and left the remainder of the branch on the ground. These baits were exposed to insects for 2–3 months (Table 16.1). We then collected the canopy bait, three sections of ground bait of equivalent diameter and six sections of thinner secondary branch (diameter 2–3 cm), and placed them into individual cages constructed from no-see-um insect netting (625 holes/in^2; Barre Army Navy Store, Barre, VT). We estimate that branch biomass, for canopy thick to ground thick to ground thin, is 1:3:1. All branches cut during the dry season were exposed to some rain; in FG95, Peru03, and CR13, dry season baits were still exposed at the beginning of the rainy season and received substantial precipitation. Notable deviations from protocol were in FG95, when we attempted a more symmetric experimental design (see Berkov and Tavakilian (1999) for a detailed discussion of what not to do!) and in the salvage project, Pan10. Because the Panama site was destined to be clear-cut and we had limited site access, we cut down trees and suspended canopy baits for many of them in three large trees. Rearing cages were monitored (optimally, each day) until adult emergences tapered off, and adults were preserved in 95% EtOH. Beetles were first sorted to morphospecies, and synoptic collections were provided to specialists (see Acknowledgments) for identification.

16.2.3 Analyses

For the South American studies in which baits were exposed in both the dry and rainy seasons (Table 16.1: FG95, Peru03, FG07), I calculated, for each species represented by at least five individuals, the proportion of individuals that emerged from branches cut during the dry or rainy season. These data suggest that adults are (1) exclusively active during either the dry or rainy season; (2) preferentially active during either the dry or rainy season ($\geq$75% individuals), with depressed abundance during the alternate season; or (3) active during both seasons. For each saproxylic subfamily, I calculated the proportion of individuals that emerged from branches cut during the dry and rainy season.

Our experiments exposed approximately four times as much wood at ground stratum as at canopy stratum. Therefore, I used goodness-of-fit (G) tests to determine if abundances of selected saproxylic subfamilies were proportional to the amount of wood available in the four partitions: dry canopy, dry ground, rainy canopy, and rainy ground. I analyzed both cerambycid subfamilies and the curculionid subfamily Conoderinae (both localities), along with Platypodinae and Scolytinae (FG07 only). Conoderinae accounted for over 90% of the curculionids reared in Peru, but because we initially considered them "bycatch," we did not record stratum for almost half of the individuals reared during the dry season and extrapolated stratum for those.

Seasonality requires activity occurring at the same time each year. I therefore compared season classifications for beetle species reared, and represented by at least five individuals, in both FG95 and FG07. I also calculated the number of individuals that emerged from canopy and ground stratum branches (N ground divided by 4 to compensate for uneven resource abundance). Species were considered stratum specialists if $\geq$90% of the corrected total was from a particular stratum. In FG95, stratum was not recorded for curculionids.

Although the two Central America projects took place at roughly the same time of the year (Table 16.1), in Panama this represented mid-dry season (in a region with some deciduous trees), and in Costa Rica this represented the transition to the rainy season (in a wetter region with evergreen forest). In Panama, we expected higher species richness and abundance of Cerambycinae, the group most routinely associated with dry conditions in South America. The transition season was expected to be optimal, especially for curculionids (Wolda et al. 1998), and in Costa Rica we expected higher species richness and abundance of curculionids, especially species-rich Scolytinae. I used EstimateS 9.1.0 (Colwell 2013) to construct rarified species accumulation curves for cerambycid and curculionid subfamilies at each locality, with each tree considered as a sample. I then compared, for each subfamily, relative species richness and relative abundance.

To better interpret patterns of adult activity for subfamilies in Costa Rica (the more productive project), I analyzed the mean emergence week with ANOVA, followed by post-hoc Tukey HSD pairwise comparisons (JMP-SAS 9.0). Mean emergence week was calculated as the mean number of weeks after branches were cut. Tukey HSD comparisons were considered significantly different at an overall

$\alpha = 0.05$. In conjunction with rainfall data collected by the Instituto Meteorológico Nacional at the Greg Gund Center at Osa Conservation, I constructed emergence curves by subfamilies, in cohorts interpreted as having a preference for moist conditions, dry conditions, or intermediate conditions.

16.3 Results

Cumulatively, the five rearing studies yielded 16,793 cerambycids in 206 species and >14,300 curculionids in at least 267 species. The cerambycid species belonged to the subfamilies Cerambycinae and Lamiinae; most curculionid species belonged to the subfamilies Conoderinae, Cryptorhynchinae, Molytinae, Platypodinae, and Scolytinae.

16.3.1 Seasonality and Stratification in South America

Seasonal associations for saproxylic beetles reared from the Brazil nut family in South America are shown, by subfamily, in Fig. 16.1. In French Guiana, 42–46% of the species emerged from branches cut during both the dry and rainy season, but over half of these (25–29% of the total) had season preferences (2a, 2c). In Peru, 75% of the species emerged from branches cut during both the dry and rainy season, and again over half of these (39% of the total) had season preferences (2b). The cerambycid subfamily Cerambycinae was most consistently associated with the dry season, in terms of species and, more dramatically, abundance. The cerambycid subfamily Lamiinae and the curculionid subfamily Conoderinae were both species-rich. They included considerable variety in the species classifications, with the majority of species reared from branches cut during both the dry and the rainy seasons. In French Guiana, more lamiine individuals were reared during the dry season and more conoderine individuals during the rainy season (2d, 2f); Peru showed the opposite trend (2e). Other curculionid subfamilies were even more heterogenous. In French Guiana, Molytinae were reared exclusively from rainy season baits, while in Peru more individuals were reared from dry season baits. In general, FG07 produced higher proportions of species and individuals from rainy season branches (2c, 2f). This was largely due to the curculionid subfamilies Cryptorhynchinae, Platypodinae, and Scolytinae, which in FG95 were commonly reared from dry season baits (2d) but in FG07 were reared almost exclusively from rainy season baits (2f).

In both FG07 and Peru03, with approximately 80% of the wood exposed at ground stratum, cerambycines were disproportionately abundant in baits exposed at canopy stratum (Fig. 16.2): in French Guiana, during the dry season (3a, $G = 289.9$, $\mathrm{df} = 3$, $P < 0.0001$), and in Peru, in both seasons (3e, $G = 1314$, $\mathrm{df} = 3$, $P < 0.0001$). In FG07, lamiines made a seasonal change in stratum preference: when branches were

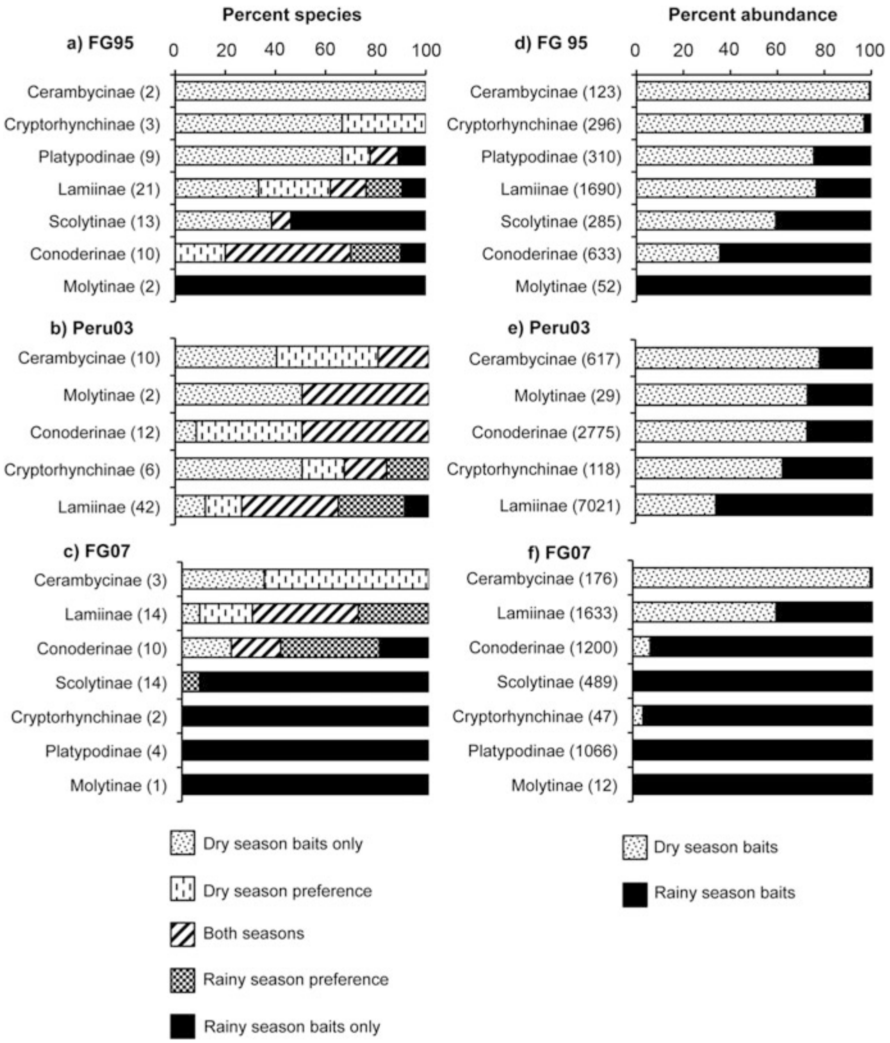

Fig. 16.1 Saproxylic subfamilies showing seasonal classifications for species and relative abundance by season: FG95 (**a**, **d**), Peru03 (**b**, **e**), FG07 (**c**, **f**) subfamily names are followed by *N* species (**a**, **b**, **c**) or *N* individuals (**d**, **e**, **f**)

exposed during the dry season, they emerged in greater abundance from ground stratum baits, and when branches were exposed during the rainy season, they emerged disproportionately from canopy stratum baits (3b, $G = 1265.9$, df = 3, $P < 0.0001$). In Peru03, lamiines were disproportionately abundant during the rainy season, at both strata (3f, $G = 702.1$, df = 3, $P < 0.0001$). In FG07, conoderines were disproportionately abundant at both strata during the rainy season (3c, $G = 1059.2$, df = 3, $P < 0.0001$), while in Peru they were disproportionately abundant at canopy

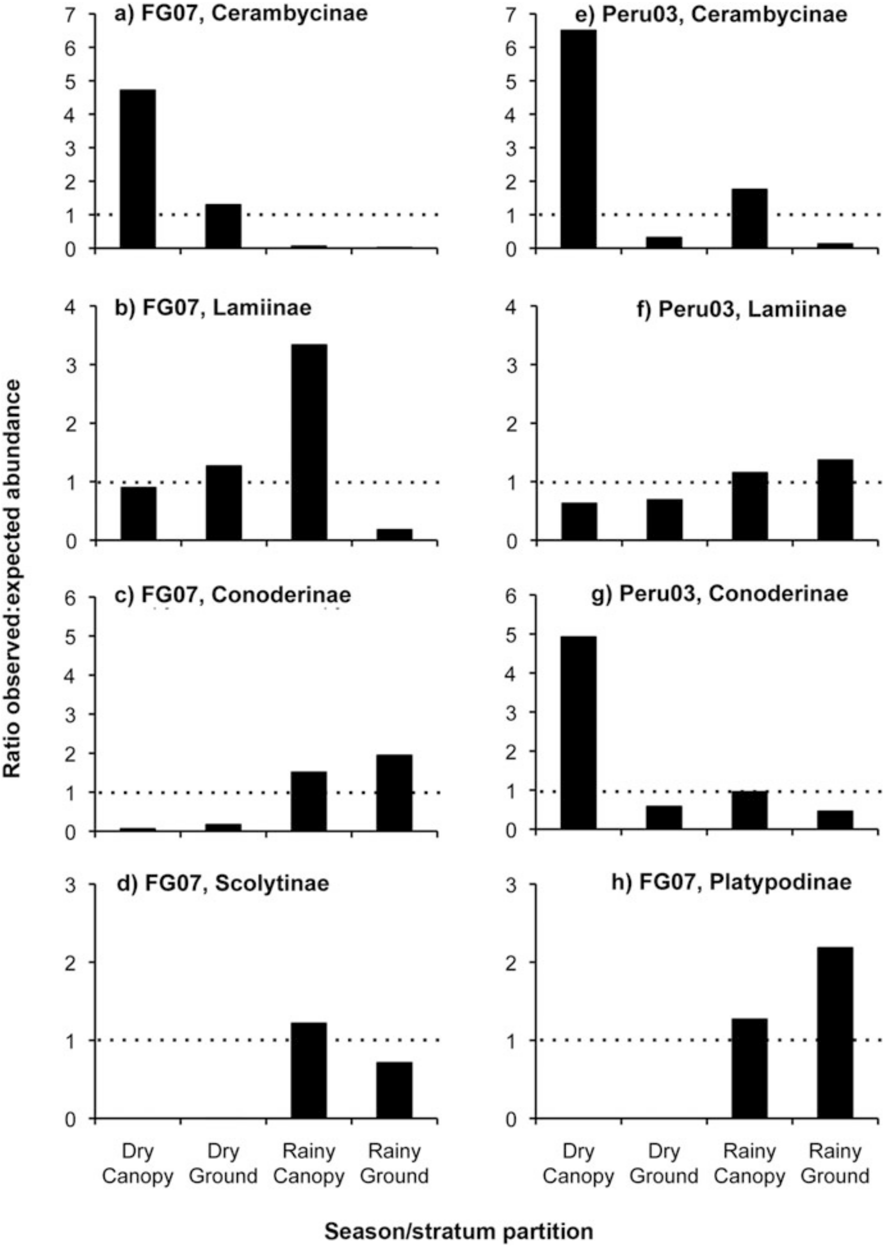

Fig. 16.2 Preferential associations of saproxylic subfamilies with season/stratum partitions in FG07 and Peru03: dry canopy, dry ground, rainy canopy, and rainy ground; dotted lines indicate the expected number of individuals, if emergences were proportional to the amount of wood available

stratum during the dry season (3g, $G = 2819.7$, $df = 3$, $P < 0.0001$; ratios remained similar without extrapolated data, 4.0 for dry canopy, 0.5 for dry ground, 1.4 for rainy canopy, and 0.7 for rainy ground). Scolytinae and Platypodinae, only recorded for FG07, were disproportionately abundant in rainy season: at canopy stratum for scolytines (3d, $G = 691$, $df = 3$, $P < 0.0001$) and more conspicuously at ground stratum for platypodines (3 h, $G = 1146.2$, $df = 3$, $P < 0.0001$).

When season classifications were compared for 27 species represented by ≥ 5 individuals in both FG95 and FG07, 9 (33%) were stable, and 7 (26%) shifted between a preference category and "both" (Table 16.2). These were mostly lamiines and conoderines. The two cerambycines shifted from exclusive to the dry season to dry preference, but very few individuals were reared from rainy season baits (Fig. 16.1d, f). One cryptorhynchine, three platypodines, and two scolytines were reared, at least in part, from dry season baits in FG95 but exclusively from rainy season baits in FG07 (Table 16.2). When stratum classifications were compared for the 13 cerambycid species, they were stable for 9 (69%). Many of the lamiine species present at both strata emerged preferentially from ground stratum during the dry season and canopy stratum during the rainy season (Fig. 16.2b, Lee et al. 2014). Although we lack stratum data for curculionids reared in FG95, it is notable that in 2007, nine curculionid species (64%) were ground specialists, compared with only one cerambycid (8%).

16.3.2 *Species Richness, Relative Abundance, and Emergence Sequence in Central America*

In Panama, we reared 2351 cerambycid and curculionid specimens in a total of 97 species (Berkov and Eng, unpubl. data); in Costa Rica, we reared 12,310 cerambycid and curculionid specimens in a total of 140 species (Li et al. 2017; Morillo 2017). Of the 67 plants sampled in Panama, 54 yielded cerambycids, and 41 yielded curculionids. Cerambycinae emerged from 40 plants (60%), Lamiinae from 34 (51%), Conoderinae from 24 (36%), Cryptorhynchinae from 18 (27%), and Scolytinae from 10 (15%). Sporadic subfamilies included Platypodinae (six samples), Cossoninae (three samples), Molytinae (two samples), and Dryophthorinae (one sample). Of the 41 plants sampled in Costa Rica, 39 yielded cerambycids, and all 41 yielded curculionids. Lamiinae and Scolytinae each emerged from 39 plants (95%), Conoderinae and Cryptorhynchinae from 32 (78%), Molytinae from 20 (49%), and Cerambycinae and Cossoninae from 12 (29%). Sporadic subfamilies included Platypodinae (four samples), Curculioninae (two samples), and Baridinae (one sample).

Figure 16.3 shows species accumulation curves for Cerambycidae (Pan10, 4a, and CR13, 4c) and the three most consistently sampled subfamilies of Curculionidae (Pan10, 4b, and CR13, 4d). In Panama, observed species richness was marginally higher for Lamiinae than for Cerambycinae (4a). In Costa Rica, Cerambycinae had very low species richness, rapidly approaching an asymptote (4c). In Panama, all

Table 16.2 Seasonality and stratum preferences of saproxylic beetles associated with the Brazil nut family in French Guiana (FG95 and FG07)

Subfamily	Tribe	Species[a]	Season[b]	Stratum[c]
Cerambycinae	Elaphidiini	*Periboeum pubescens* (Olivier)	**D**/D	both/both
Cerambycinae	Clytini	*Pirangoclytus triangularis* (Castelnau and Gory)	**D**/D	**Grd/Grd**
Lamiinae	Acanthocinini	*Neobaryssinus altissimus* (Berkov and Monné)	both/both	**Can/Can**
Lamiinae	Acanthocinini	*Neoeutrypanus mutilatus* (Germar)	D/D	both/**Can**
Lamiinae	Acanthocinini	*Neoeutrypanus nobilus* (Bates)	**R/D**	**Can/Can**
Lamiinae	Acanthocinini	*Oedopeza leucostigma* (Bates)	D/both	both/both
Lamiinae	Acanthocinini	*Ozineus* sp.	R/both	both/both
Lamiinae	Acanthocinini	*Palame anceps* (Bates)	both/D	**Can**/both
Lamiinae	Acanthocinini	*Palame crassimana* (Bates "bicolor" form)	**D**/both	both/both
Lamiinae	Acanthocinini	*Palame crassimana* (Bates "unicolor" form)	R/R	**Can/Can**
Lamiinae	Acanthocinini	*Palame mimetica* (Monné "runt" form)	D/both	both/**Can**
Lamiinae	Acanthocinini	*Xylergates elaineae* (Gilmour)	both/both	both/both
Lamiinae	Acanthoderini	*Oreodera simplex* (Bates)	D/D	**Grd/both**
Conoderinae	Lechriopini	*Copturomorpha* sp. (1)	D/R	—/**Grd**
Conoderinae	Piazurini	*Piazurus alternans* (Kirsch)	**R/R**	—/both
Conoderinae	Piazurini	*Piazurus incommodus* (Boheman)	both/R	—/**Grd**
Conoderinae	Piazurini	*Piazurus psuedoalternans* (Hustache)	both/R	—/**Grd**
Conoderinae	Piazurini	*Piazurus* sp. (3)	R/R	—/**Can**
Conoderinae	Piazurini	*Pseudopinarus cerastes* (Fabricius)	D/both	—/both
Conoderinae	Zygopini	*Zygops histrio* (Boheman)	both/both	—/both
Cryptorhynchinae	Cryptorhynchini	*Pisaeus* sp. (1)	D/**R**	—/**Grd**
Molytinae	Conotrachelini	*Microhyus* sp. (1)	**R/R**	—/**Grd**
Platypodinae	Platypodini	Cf *Teloplatypus brasiliensis* (Nunberg)	both**/R**	—/both
Platypodinae	Platypodini	*Euplatypus segnis* (Chapuis)	**D/R**	—/**Can**
Platypodinae	Platypodini	*Megaplatypus* sp. (053)	D/**R**	—/**Grd**
Scolytinae	Xyleborini	*Xyleborus* sp. (19)	both/**R**	—/both
Scolytinae	Xyleborini	*Xyleborus spathipennis* (Eichhoff)	**D/R**	—/**Grd**

[a] Species are included if ≥5 individuals were reared in both projects

[b] Season, FG95/FG07: D = dry season baits, R = rainy season baits, bold = reared exclusively from baits cut in one season, regular face = ≥75% of the individuals from the season indicated

[c] Stratum, FG07 only: Can = canopy specialist, Grd = ground specialist, bold = ≥ 90% of the individuals from the stratum indicated

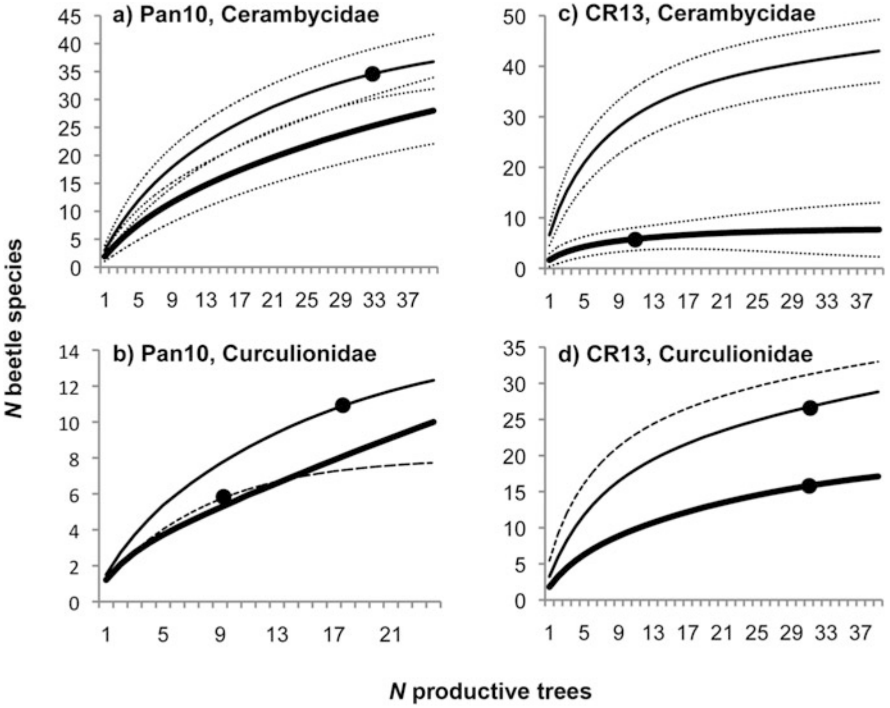

Fig. 16.3 Species accumulation curves for cerambycid and curculionid subfamilies in Panama and Costa Rica; for Cerambycidae (**a**, Pan10, and **c**, CR13) thick lines show Cerambycinae, thin lines Lamiinae, and dotted lines 95% confidence intervals; for Curculionidae (**b**, Pan10, and **d**, CR13), thick lines show Conoderinae, thin lines Cryptorhynchinae, and dashed lines Scolytinae; confidence intervals are not shown, for clarity, but Conoderinae (CR13) is the only subfamily in which they did not overlap; when samples were extrapolated, a circle shows the number of actual samples

curculionids had low species richness, particularly Scolytinae, which appeared to be approaching an asymptote (4b). Conoderinae was represented by fewer observed species than Cryptorhynchinae, although the accumulation curve was rising more steeply. In Costa Rica, observed curculionid species richness was highest for Scolytinae (4d), although the 95% confidence intervals (not shown) overlapped with Cryptorhynchinae. Of the three most consistently sampled subfamilies, Conoderinae had the lowest species richness (Morillo 2017).

In both localities, subfamily relative species richness and relative abundance have roughly corresponded (Fig. 16.4), with two obvious exceptions. In Panama (5a), Cerambycinae accounted for 29% of the species—but 55% of the abundance—while in Costa Rica (5b), Scolytinae accounted for 24% of the species, but 53% of the abundance. Lamiinae was consistently species-rich and abundant (31–36% of all species and 24–30% of the abundance). Cryptorhynchinae and Conoderinae

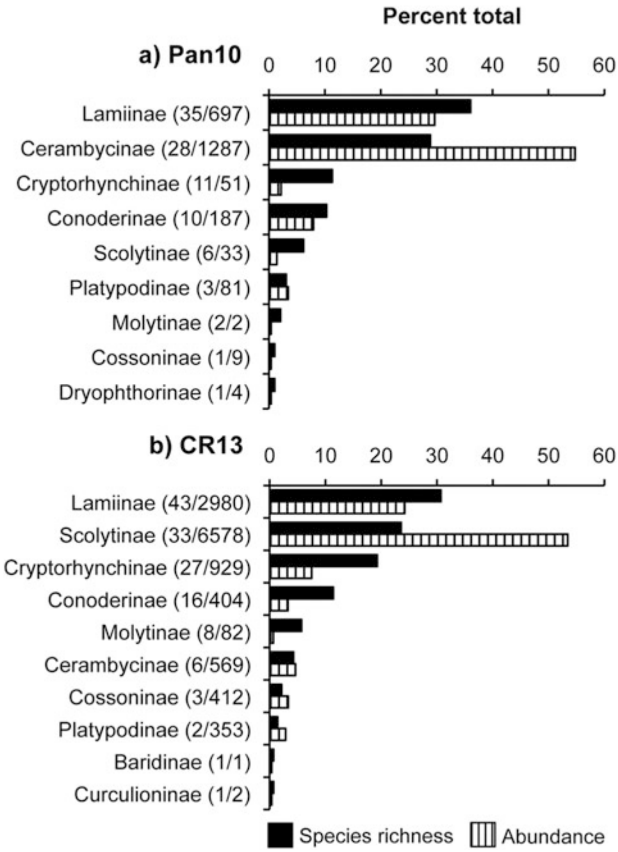

Fig. 16.4 Relative species richness and abundance for saproxylic subfamilies in (**a**) Panama and (**b**) Costa Rica; subfamilies are followed by *N* species/*N* individuals

consistently accounted for 10–20% of the species and 2–8% of the abundance. Other curculionid subfamilies each contributed ≤6% of the species richness and no more than 3% of the total abundance.

In Costa Rica, mean emergence week differed among subfamilies (mean ± SD; Fig. 16.5a, $P < 0.0001$). Platypodines (16.2 ± 1.4) emerged significantly earlier than scolytines (21 ± 6.4) and conoderines (22.8 ± 6.1), which emerged significantly earlier than lamiines and cossonines (28.9 ± 10.2 and 29.4 ± 9.9, respectively). Molytines (36.6 ± 10.8), cryptorhynchines (36.8 ± 11.3), and cerambycines (39.4 ± 7.6) all emerged significantly later. Among these, Cerambycinae emerged significantly later than Cryptorhynchinae. In Fig. 16.5b, Platypodinae, Scolytinae, and Conoderinae were considered moisture-dependent. Adult emergences peaked in late July through late August, when rainfall was still heavy (Berkov, pers. obs.), and

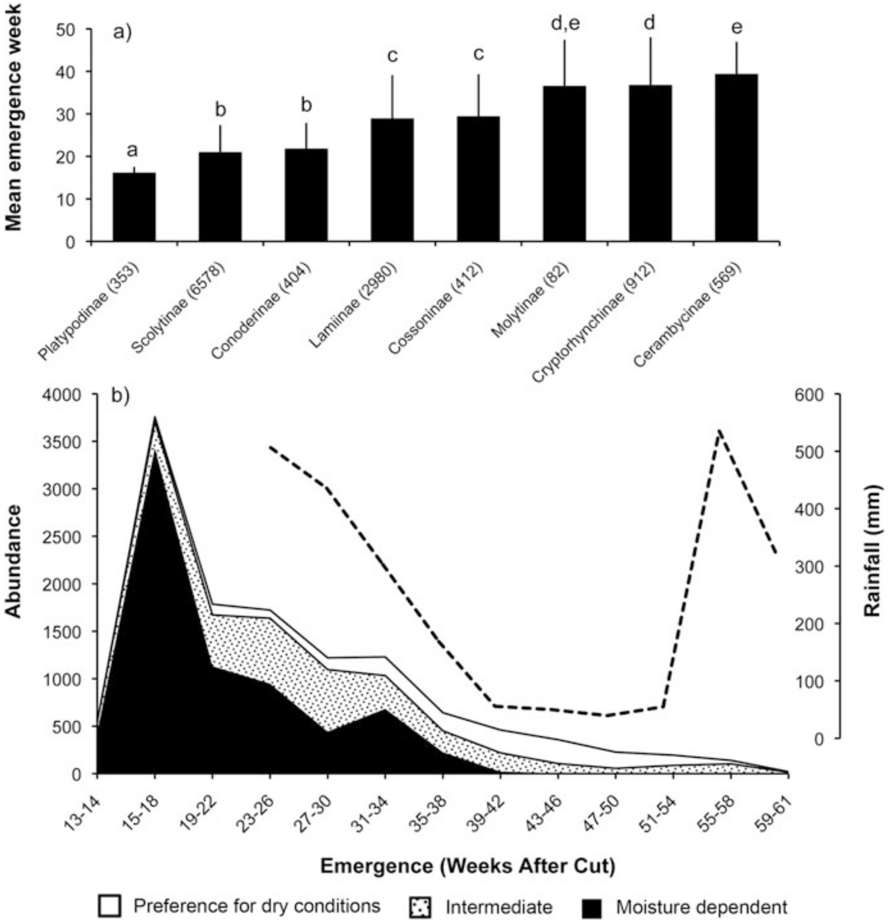

Fig. 16.5 Emergence sequence for saproxylic subfamilies in the Osa Peninsula, Costa Rica; (**a**) for mean emergence weeks, subfamilies are followed by *N* individuals; lines above bars show standard deviation, with different letters above lines showing significant differences in mean emergence week; (**b**) emergence sequences for three putative cohorts, moisture-dependent, intermediate, and preference for dry conditions, are plotted against rainfall, shown by the dashed line (with scale to the right)

ceased by the dry season. Lamiinae and Cossoninae were considered intermediate; emergences peaked in late October, when rainfall was progressively declining, and continued into the dry period. Molytinae, Cryptorhynchinae, and Cerambycinae appeared to have preferences for dry conditions; emergences peaked in December, toward the beginning of the dry period, and continued until the rains returned.

16.4 Discussion

16.4.1 Cerambycidae

While temperate cerambycids usually require at least a year to complete their life cycles, almost all Neotropical cerambycids emerged from baits in considerably less than a year, with cerambycines typically emerging later than lamiines. In Costa Rica, cerambycine emergences peaked early in the dry season, 39 weeks after the branches were cut (10 weeks after lamiine emergences peaked, Fig. 16.5). Cerambycines also emerged later than lamiines in French Guiana (Berkov, unpubl. data). Adults emerged from dry season baits during the rainy season, but cerambycine emergences peaked during the drier periods. Many cerambycines visit flowers (Noguera et al. 2002) and are colorful, diurnal, and active during the warmest parts of the day. Although some of our reared cerambycines belong to genera with nocturnal eye phenotypes (Zhu 2016), in the South American projects, they also emerged preferentially from the warmer, drier, microhabitats: canopy stratum, especially in the dry season (Fig. 16.2, Lee et al. 2014). Cerambycines also reached their highest species richness and abundance in Panama (Fig. 16.3), from baits exposed at relatively high temperatures, in the middle of the dry season.

There are several potential explanations for longer subcortical periods for cerambycines. Some—but not all—cerambycines are larger than our most abundant lamiines and might take longer to mature. They might be feeding on less nutritious tissues that support slower growth, tunneling into the heartwood (Berkov, pers. obs.), and/or selecting host plants with relatively dense, dry wood (Torres, in prep.). Cerambycines might also undergo periods of dormancy and emerge when conditions improve. Whatever is responsible for the duration of the subcortical period, there may be a selective advantage in avoiding the wettest part of the rainy season. If, like some temperate cerambycines, Neotropical cerambycines meet and mate on flowers, that could explain both canopy preference and potential synchrony with plant phenology. In a wet forest in Australia, xylophagous beetle species had their mean peak of adult flight activity in the middle of the dry season, followed by a second peak that appeared to correspond with peak flowering period (Grimbacher and Stork 2009). In a tropical dry forest in Mexico, cerambycids also had two activity peaks; the richness and diversity of one group of species seemed to be synchronized with the appearance of flowers (Noguera et al. 2017).

While Cerambycinae is the most species-rich cerambycid subfamily in Australia, southern South America, and North America, Lamiinae is more species-rich in the Neotropics (Monné et al. 2009, 2012; Švácha and Lawrence 2014). In our studies, 76–97% of the lamiines belonged to relatively small, cryptic species in the tribe Acanthocinini—presumably active at dusk (Noguera et al. 2002)—when temperatures drop and humidity increases (Lee et al. 2014). In Costa Rica, lamiines had shorter subcortical periods than cerambycines and emerged into an environment that was still fairly rainy (Fig. 16.5). In South America, many lamiine species colonized bait branches exposed during both the dry and rainy seasons (Fig. 16.1), but in both

FG95 and FG07, lamiines made a seasonal change in stratum. When baits were exposed during the dry season, lamiines emerged in greater abundance from ground stratum baits, but when baits were exposed during the rainy season, they emerged disproportionately from canopy stratum baits (Fig. 16.2, Berkov and Tavakilian 1999; Lee et al. 2014). Dry/ground and rainy/canopy represent intermediate microclimates, with moderate temperatures and fairly high humidity levels. Lamiine species richness was fairly low in Panama, given the number and diversity of host plants sampled (Figs. 16.3 and 16.4). Still, given the hot, dry environment at the time of the study, it was surprising that species richness in Panama approached that documented in Costa Rica. Lamiines may have withstood harsh conditions by colonizing host plants with less dense wood and high moisture content (Torres, in prep.).

16.4.2 Curculionidae

Many curculionids seem to be moderately to strongly moisture-dependent. In Costa Rica, branches from 41 host plants yielded >8700 individuals in 91 species (Morillo 2017), while in Panama, branches from 67 host plants yielded <400 individuals in 35 species (Eng, unpubl. data). Yields in Panama may have been low in part because we felled, but did not cage, the entire trees, but certain lineages do appear to tolerate warm, dry conditions better than others. The most abundant curculionid in Panama was an apparently diurnal species in the tribe Zygopini (Conoderinae; Fig. 16.6d). In Costa Rica, the adults of one species in the tribe Gasterocercini (Cryptorhynchinae) and four species in the tribe Anchonini (Molytinae) emerged during the dry season along with the cerambycines. Members of related tribes Cryptorhynchini (Crytochynchinae) and Conotrachelini (Molytinae) emerged 4 or 5 months earlier, along with the majority of the scolytines (Fig. 16.5, tribes not shown). Among the Scolytinae, the most abundant tribes, Corthylini and Xyleborini, emerged very early when the rains were still heavy, while other tribes emerged with the cossonines, as the rains declined. Most Conoderinae also emerged early, but the tribes Zygopini and Lechriopini peaked about a month after the tribe Piazurini. Emergence peaks may have been influenced by host plant traits including wood density, but these were not analyzed in Costa Rica.

In South America, most of the curculionids consistently associated with the Brazil nut family were in the subfamily Conoderinae. Species in the conoderine tribe Zygopini (the showy counterparts of showy Cerambycinae?; Fig. 16.6b, d) appear to prefer dry conditions: they emerged from dry season branches and, in Peru, made up the bulk of the curculionids reared at canopy stratum (Fig. 16.2). In French Guiana, most species in the conoderine tribe Piazurini (the cryptic counterparts of cryptic Lamiinae?; Fig. 16.6a, c) were reared primarily from ground stratum baits exposed during the rainy season (a relatively cool, very moist microhabitat, Lee et al. 2014); in Costa Rica, they were also preferentially reared from ground stratum branches (Morillo 2017).

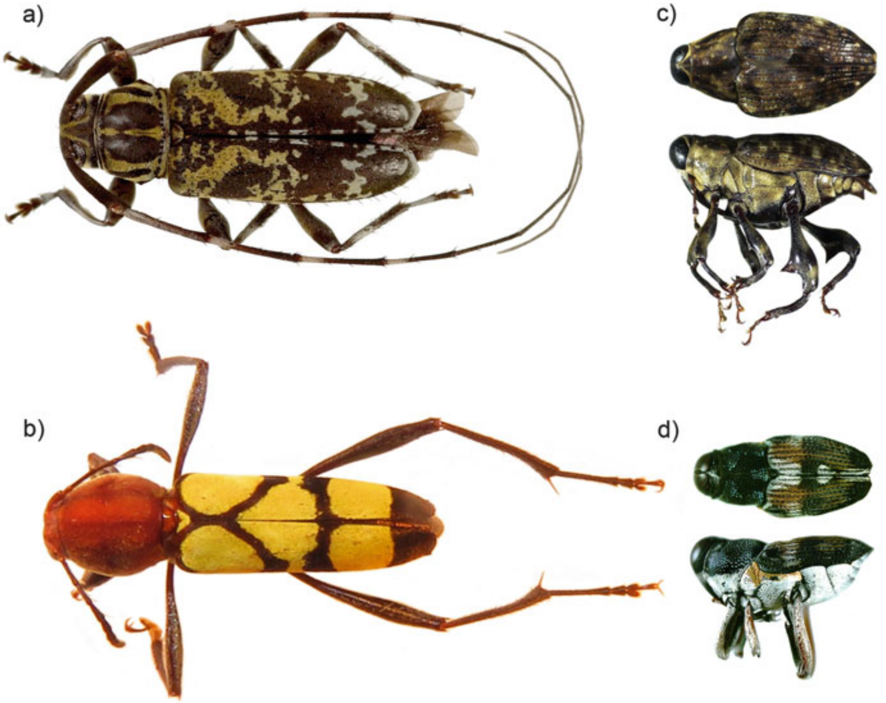

Fig. 16.6 Putative crepuscular/nocturnal (**a**, **c**) and diurnal (**b**, **d**) saproxylic species. (**a**) *Palame crassimana* Bates (Lamiinae: Acanthocinini), a cryptic cerambycid reared in French Guiana; (**b**) *Pirangoclytus amaryllis* (Chevrolat) (Cerambycinae/Clytini), a showy cerambycid (with a red pronotum) reared in Panama; (**c**) *Piazurus incommodus* (Boheman) (Conoderinae/Piazurini), a cryptic curculionid reared in French Guiana; (**d**) *Archocopturus* sp. (Conoderinae/Zygopini), a showy curculionid (with iridescent green on the pronotum) reared in Panama

This synthesis supports the importance of sampling during the transition to the rainy season (Wolda et al. 1998) or excluding the transitional period if the objective is to document adults active during the dry season. Sampling period probably affected the very different yields at the two Central American sites and may have contributed to the interannual seasonal discrepancies noted for curculionids in South America. Some taxa that emerged, at least in part, from dry season branches in FG95 were restricted to rainy season branches in FG07; this was especially notable for Cryptorhynchinae, Molytinae, Platypodinae, and Scolytinae (Fig. 16.1). In FG95 and Peru, the dry season baits were exposed until we prepared the rainy season baits, and they may have been colonized by curculionid adults active during the transitional period. In FG07, the dry season baits were recovered about 6 weeks earlier (Fassbender et al. 2014); they probably provide a more realistic record of dry season activity and will be referenced in the following section of the discussion. The Peru site also appeared to have precipitation more evenly distributed throughout the year (Eng, in prep.); this would be expected to decrease seasonality, as demonstrated by the high proportion of species active in both seasons (Fig. 16.1).

16.4.3 Conservation Implications

Although boreal and temperate forest area is expanding, and the rate of tropical deforestation has declined, tropical countries including Brazil and Peru continue with large net losses. Costa Rica is one of several tropical countries in which forest cover now appears to be increasing (Keenan et al. 2015). In the forest mosaic of the Osa Peninsula, specialized cerambycids and saproxylic curculionids appear to tolerate fragmentation. Secondary forest may pose a dispersal barrier to some species, but specialists persist, and sometimes reach high densities, within small patches of old growth forest (Li et al. 2017; Morillo 2017). Forest conversion not only reduces habitat; it potentially alters patterns of evapotranspiration, delaying the onset of the rainy season and increasing the duration of the dry season (Wright et al. 2017). The greatest challenges to residents of tropical moist forests may come with large-scale landscape change or with the advent of novel climates. By mid-century, most tropical regions are expected to experience climates outside of their historic ranges of variability (Mora et al. 2013). In the face of persistent climate stress, insects might seek suitable microhabitats, alter activity periods, adapt (via selection), migrate (if possible), or decline. Some temperate insects rapidly adapt to novel conditions, but adaptation seems to be less of an option for tropical insects (Chown et al. 2011). In Australia, a rain forest species of *Drosophila* demonstrated little potential to adapt to desiccation, relative to more widely distributed species that experience more variation in environmental conditions (Hoffman et al. 2003). In Costa Rica, rolled-leaf beetle species (Chrysomelidae) restricted to high elevations were less tolerant of high temperatures than those restricted to low elevations, and those with northern distributions were less tolerant of high temperatures than those with southern distributions. In most cases, there was little of the plasticity that would favor adaptation (García-Robledo et al. 2016).

In European temperate forests, saproxylic insects and the threats to their persistence are fairly well-characterized (Grove 2002; Nieto and Alexander 2010). Climate change is expected to affect range, phenology, voltinism, and activity periods; it may actually enhance performance and population growth, at least in opportunistic species (Jaworski and Hilszczanski 2013). In Neotropical forests, saproxylic insects are diverse, seldom seen, and often unknown; their study typically calls for some kind of data reduction. Niche breadth is an important predictor of extinction risk (Kotiaho et al. 2005); it may be possible to generalize about common risk in species-rich environments, if phylogenetic conservatism dictates shared preferences or physiological constraints. For instance, in Addo-Bediako et al.'s (2001) review of water loss in insects, 68% of the interspecific variation was at or above the genus level. We started with a taxonomic focus on cerambycids associated with trees in the Brazil nut family but have progressively shifted focus to the community structure of saproxylic beetles associated with a broader group of host plants. This synthesis explored patterns within cerambycid and curculionid subfamilies, although there are exceptions to these generalizations. Particularly within Curculionidae, it might be more informative to analyze by tribe.

Lineages that are preferentially associated with canopy stratum during the dry season (Cerambycinae and, perhaps, the conoderine tribe Zygopini) are already exposed to high temperatures and relatively low relative humidity (Lee et al. 2014). In lab settings, potential responses to changes in humidity include changes in the duration of larval development, adult longevity, and fecundity (Tochen et al. 2016). Even without invoking the more severe dry seasons predicted for tropical forests, insects might be challenged by increased respiratory water loss, due to warming temperatures and ensuing increases in insect metabolism (Chown et al. 2011). But insects are able to detect even minor (2–5%) shifts in relative humidity, and adults can simply avoid unfavorable microhabitats (Spicer et al. 2017). Insects also protect themselves against desiccation by modifying cuticular hydrocarbons, producing glycerol or other sugars that protect against desiccation or reducing fecal water content; acclimation can decrease water loss (Chown et al. 2011). Thus far, temperate wood borers appear to have positive responses to moderate decreases in humidity (Jaworski and Hilszczanski 2013). During the dry season in French Guiana, relative humidity in the canopy can drop to <50% in the afternoon, but there are also approximately 12 hours when it is >90% (Lee et al. 2014). These conditions are not likely to be represented in lab experiments, and it is not known how they might impact the larval substrate.

Daily ranges in both humidity and temperature are both greatest at canopy stratum during the dry season (Lee et al. 2014); this would be expected to select for relatively broad tolerances in canopy residents. Unfortunately, a growing body of research suggests that ectotherms inhabiting low latitudes, particularly those in warm microhabitats, may already be exposed to temperatures close to their critical thermal maxima (CT_{max}, the point at which they lose muscular control) (Deutsch et al. 2008; Somero 2010; Kaspari et al. 2015). In Costa Rica, the CT_{max} of rolled-leaf beetles in lowland forests ranges from 37 to 46 °C; in Panama the CT_{max} of most understory ants ranges from 40 to 53 °C and the CT_{max} of canopy ants from 46 to 57 °C (Kaspari et al. 2015; García-Robledo et al. 2016). Relative to French Guiana, the Panama Canal Zone appears to have minor differences in temperature at canopy and ground stratum (Berkov, unpubl. data, Kaspari et al. 2015). Nevertheless, branches exposed to the sun at canopy stratum retain considerable heat; Kaspari et al. (2015) found that exposed branch surfaces were about 10 °C warmer than ambient temperatures and the adjacent boundary layers of air approached 55 °C. Although canopy-dwelling ants tolerated higher temperatures than understory ants, at canopy stratum there was considerable overlap between ant CT_{max} and measured surface temperatures. Thermal tolerance was inversely correlated with desiccation resistance for canopy-dwelling, but not understory, ants. Canopy ants might maintain suitable internal temperatures via evaporative cooling, which would limit their ability to tolerate low humidity levels (Kaspari et al. 2015; Bujan et al. 2016).

What are the prospects for saproxylic beetles in the warmest microhabitats? Thus far, it appears that many Cerambycinae have conserved preferences for branches in warm, relatively dry, windy conditions and preferentially colonize host plants with dense, dry wood (Torres, in prep.). They have longer subcortical periods and might be constrained to a univoltine habit. In our studies, these taxa were seldom species-rich. They may represent outliers in lineages that are better represented in drier forests and persist in moist forests by occupying less saturated niches—the warmer, drier microhabitats. Ovipositing adults of diurnal species might circumvent thermal stress due to color or large body size; in particular their long hind legs (Fig. 16.6) could elevate them above the hot boundary layer of air (Kaspari et al. 2015). Should temperatures increase, adults might restrict their activity to branch surfaces that are not directly exposed to the sun. They might avoid thermal extremes by shifting from canopy to ground stratum—which could increase the potential for competitive interactions. Adults with superposition visual systems, optimized for light capture over resolution (Warrant 1999; Zhu 2016), are presumably active under low-light conditions and thereby avoid the warmest times of the day. Because vision systems are optimized to light conditions, it might not be possible for diurnal cerambycines, with apposition eyes, to avoid adverse conditions by shifting activity periods.

In a planthopper pest of rice, nymphs had CT_{max} that were ≥ 2 °C lower than those of adults (Piyaphongkul et al. 2012). Saproxylic beetles that are active at canopy stratum during the dry season probably oviposit in senescing branches that lose leaves and become progressively more exposed. Their progeny may be the first to experience deleterious impacts of warming temperatures; subcortical larvae have restricted mobility and few options for escape.

During the rainy season, canopy stratum seems to be much more hospitable to saproxylic beetles. In French Guiana, mean maximum temperatures are >4 °C lower than at canopy stratum during the dry season, with a corresponding reduction in daily range (Lee et al. 2014), and clouds should minimize excessive heating of exposed branch surfaces and the boundary layer (Kaspari et al. 2015). Relative humidity generally remains above 90% (Lee et al. 2014). Maximum species richness was close to twice as high as in dry season canopy baits (21 vs. 11 species) and maximum abundance over three times greater (223 vs. 50 individuals; Berkov, unpubl. data). Increased species richness was due to an influx of curculionids; Lamiinae, Conoderinae, Scolytinae, and Platypodinae were all more abundant than would be expected based on branch biomass available (Fig. 16.2). Canopy baits in Costa Rica, cut during the transition to the rainy season, were also rich in both cerambycids and curculionids; the most densely colonized bait yielded 444 individuals in 17 species (Li et al. 2017; Morillo 2017; Heath, unpubl. data).

Beetles that colonize rainy season canopy baits are in a cooler, moister, more stable microhabitat. A few species were also reared at canopy stratum during the dry season and appear to be true canopy specialists (Lee et al. 2014). Most species were also reared at ground stratum—from baits cut in the dry season (mostly lamiines), the rainy season (mostly scolytines and platypodines), or both (some conoderines). Many lamiines belong to crepuscular/nocturnal lineages, preferentially colonize host plants with less dense, moist wood (Torres, in prep.), and appear to have shorter life cycles than cerambycines. Although seasonality should be more pronounced among insects that are susceptible to desiccation (Wardhaugh 2014), this does not seem to apply to lamiines nor to species in the curculionid subfamily Conoderinae (especially the tribe Piazurini). These groups were species-rich and, in South

America, included numerous species that were reared from baits cut in both the dry and the rainy season. They tended to have consistent peaks in abundance (Fassbender et al. 2014; Lee et al. 2014) and may represent a seasonal pattern in which adults peak during one period but occur at low levels throughout the year (Wolda 1988). Most conoderines in the tribe Piazurini were preferentially reared at ground stratum, and based on the low richness and abundance of Conoderinae in Panama, they may be more moisture-dependent than lamiines (Fassbender et al. 2014; Morillo 2017).

Both lamiines and conoderines appear to use behavioral plasticity to colonize branches in microhabitats that remain relatively cool and moist. Because they currently experience a narrower range of conditions than the taxa that colonize dry season canopy baits, they may have narrower tolerances. Nevertheless, if their thermal tolerances are similar to those of understory ants (Kaspari et al. 2015), they might have more of a thermal safety margin than species associated with warmer microhabitats. This seems particularly likely with lamiines, which often occur at ground stratum during the dry season and which were the highest in richness in Panama. If, in coming decades, rainy seasons are shorter and dry seasons more severe, it might lead to decreased opportunities to occupy this currently suitable microhabitat—and again increase competitive interactions on the ground. Should the behavioral strategy of shifting strata be disrupted (for instance, if ground stratum branches in the rainy season are still not suitable for colonization by lamiines, Fig. 16.2), it could ultimately lead to decreases in voltinism and population declines.

Lineages that were reared primarily from branches cut during rainy season include the scolytine tribes Xyleborini and Corthylini and the subfamily Platypodinae (Fassbender 2013). Like the cerambycines, they appear to be strongly seasonal, and they experience the narrowest range of climatic conditions (Lee et al. 2014). These are ambrosia beetles that feed on the fungi they introduce into the host plant; high substrate moisture content may be required to support fungal growth. Short subcortical stages (of ambrosia beetles relative to bark beetles, data not shown) may be an outcome of nutritional benefits provided by the cultivated fungi (Kirkendall et al. 2015). In Costa Rica, several common species had early initial peaks, followed about 20 weeks later by smaller secondary peaks (Fig. 16.5) that probably represented second generations within the bait branches. Nevertheless, almost all scolytines emerged and would presumably have dispersed, while the external environment was still moist.

Ambrosia beetles, and members of the subfamily Cossoninae, were sometimes abundant but only sporadically present in our rearing experiments, consistent with the idea that these small beetles require rather specific environmental conditions. Conoderines were almost six times as abundant as scolytines in Panama and more than 20 times as abundant as scolytines in Peru (Eng, in prep.). Platypodines were moderately species-rich and abundant from the Brazil nut family in French Guiana, but sparse in Peru, and had relatively low species richness and abundance in Central America. Cossonines were not reared from the Brazil nut family in South America and were reared almost exclusively from the fig family in Costa Rica (Eng, in prep., Fassbender 2013; Morillo 2017). The erratic presence of these curculionid groups may be due in part to the particular species or diameters of host plants sampled, biogeography, dispersal limitations, or competitive interactions, but our intermittent rearing is consistent with the idea that they will be vulnerable to environmental change. Like understory ants, they might have more of a thermal safety margin but would be less likely to thrive in a drier world. It seems counterintuitive to propose that small curculionids—including bark and ambrosia beetles—might be at risk, because these groups are best known due to the occurrence of voracious pests and the efforts made to exclude them. Pests represent a very small portion of scolytine species richness (Kirkendall et al. 2015), and the paucity of bark and ambrosia beetles recorded in a Brazilian tropical dry forest provides some indirect support for the notion that they decline when environmental conditions are warm and dry (Macedo-Reis et al. 2016). Among small curculionids, bark and ambrosia beetles benefit from their diverse feeding strategies and social systems (Kirkendall et al. 2015); these should enable populations to rebound rapidly if conditions are suitable.

16.4.4 Conclusions

Neotropical moist forests are heterogeneous, and saproxylic beetles are impacted by precipitation magnitude and periodicity. When topography results in steep environmental gradients, precipitation changes over short distances. In addition, interannual variation in precipitation should favor species with behavioral plasticity. There is, however, considerable conservatism in seasonality, stratification, and, apparently, thermal tolerances. This would be expected if these are correlated with diel behavior, which is often conserved at high taxonomic levels (i.e., subfamily or tribe), or if the associations facilitate mate encounter. Beetle lineages that appear to be adapted to more extreme conditions are more seasonal. They are less species-rich, less abundant, or absent when conditions are not suitable. Those occupying the warmest, driest microhabitats may already be experiencing temperatures close to their thermal limits. Those occupying the coolest, moistest microhabitats may have a greater thermal safety margin but might not tolerate increased moisture deficits. If selection for enhanced tolerance is possible, it would presumably be accompanied by steep population declines. These declines could be particularly problematic for insects associated with resources that are patchily distributed in space and time. The lineages that have been most consistently species-rich and abundant in our projects occupy intermediate microhabitats; they are cryptic and probably active in low-light conditions, and they evade adverse conditions through behavioral plasticity. If conditions should change in a way that disrupts current behavioral strategies, it could potentially impact forest nutrient cycling.

Ultimately, the future of Neotropical saproxylic beetles will depend on the fates of their preferred host plants. Assuming a 1% compound annual increase in CO_2 emissions, by the end of the century, an estimated 43% of Amazonian tree species may be represented by nonviable relict populations (Miles et al. 2004). However, Neotropical forests are still vast; responses to recent climate anomalies (Bonal et al. 2016; Jiménez-Muñoz et al. 2016) and projections of future moisture deficits (Miles et al. 2004) differ by region. The less seasonal forests of western Amazonia, adjacent to the Andes, are anticipated to serve as a potential refugia for rain forest trees. Widely distributed tree species should be the most resilient (Miles et al. 2004). Our project in this region (Peru03) yielded high species richness and abundance of both cerambycids and curculionids (other than scolytines and platypodines) (Fassbender 2013, Eng, unpubl. data). Most of the saproxylic taxa consistently associated with the Brazil nut family were reared in both French Guiana and Peru, so they are widely distributed in South America (although only a few species extend into Central America). These species (like many other Neotropical cerambycids) are host specialists, but they don't have excessively narrow host ranges that would be expected to restrict their distributions (Tavakilian et al. 1997). Their favored host tree species is abundant throughout all regions of Amazonia (ter Steege et al. 2013). If this is the case with preferred hosts in other plant families then, should other strategies for avoiding or adapting to environmental stresses fail, migration would still be an option.

16.4.5 Practical Tips for Rearing Beetles

Tropical rain forests make infinitely rewarding, but often exasperating, field sites. Scheduling is constrained by the vagaries of permits and academic calendars, and seasons defined by changes in precipitation are moving targets. Some, but not all, climate extremes are due to El Niño/La Niña events (Marengo and Espinoza 2016). Drought can bring punishing heat and fire risk; when the rains arrive, they can bring flooded routes and equipment failure. Electricity and running water are available at some but not all field sites, and access to supplies can be lacking. Furthermore, most biological classifications are imperfect: families and subfamilies are re-circumscribed, species are transferred to new genera, species limits are revised and new species described, and concepts of specialization change over time (Berkov and Tavakilian 1999; Berkov 2002; Wardhaugh 2014). Rearing may be old school, but it's an excellent way to learn about niches of diverse insects that are seldom collected, the only reliable way to investigate community structure and track changes over time, and every time you open a rearing cage, it's like opening a present!

- Should you not want to experience this pleasure yourself, excellent assistants are now available at some field stations (including second-generation conservation workers). Master's student Lin Li supervised her field assistant in Costa Rica for more than a year, using Google Translate and Facebook.
- Future studies should attempt to integrate body size, diel activity, seasonality, microhabitat, and wood traits. If correlations can be generalized, it might actually permit beetle phenotype [coloration and/or vision system (Zhu 2016)] to predict vulnerability to global change.

- In studies including cerambycids, leaves should be left attached to—or in the proximity of—the bait branches; small cerambycids often hide among leaves or cling tenaciously to small twigs.
- In moist forests, we never waxed the ends of our canopy baits; this might be important in drier environments. Make sure that canopy lines do not rub against each other; friction leads to breakage.
- Even in studies restricted to the early colonists of moribund wood, dozens of species can co-occur within a single branch. Assume that all "bycatch" and associated data will be of value, if only to the next generation of students.
- Collaboration is the best strategy for coping with taxonomic diversity, but it's also helpful to generate DNA barcodes for rapid identification. These are invaluable for morphospecies spot-checks and identifying larvae, as well as matching genders and ruling out sexual dimorphism.

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Part III
Conservation

Chapter 17
Importance of Primary Forests for the Conservation of Saproxylic Insects

Thibault Lachat and Joerg Müller

Abstract Primary forests represent the ultimate intact habitat for saproxylic insects. However, their extent has been considerably reduced over the past centuries, and those remaining are very heterogeneously distributed. Primary forests are still locally abundant in tropical and boreal zones but are rare in temperate zones. Consequently, many saproxylic insects that were adapted to typical characteristics of primary forests, such as large amounts of dead wood or overmature and senescent trees, might have become extinct regionally due to habitat loss. The remaining primary forests therefore function as refuges for those saproxylic species that cannot survive in managed forests because of their high ecological requirements. Here we identify six characteristics of primary forests important for saproxylic insects that differentiate these forests greatly from managed forests, namely, absence of habitat fragmentation, continuity, natural disturbance regimes, dead-wood amount and quality, tree species composition and habitat trees. These six characteristics highlight the importance of primary forests for the conservation of saproxylic insects in all three main climatic domains (tropical, boreal and temperate). As primary forests are rare in northern temperate zones and are being dramatically lost in boreal and tropical zones, we propose that they should be strictly conserved independently of their climatic zone. Furthermore, we recommend that studies in primary forests intensify to provide reference data for integrating primary forest characteristics into managed forests to improve the conservation of saproxylic species.

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17.1 Introduction

As one of the last remnants of intact nature in terrestrial ecosystems, primary forests have been a focus of conservation efforts for decades. They are an irreplaceable habitat for thousands of species, including saproxylic insects (Bengtsson et al. 2000). Such forests serve as a refuge and reservoir for species that cannot survive in managed forests. Those saproxylic species that can survive in managed forests even under very unnatural conditions, e.g. in Douglas-fir plantations in Europe (Goßner and Ammer 2006) or teak plantations in tropical Africa (Lachat et al. 2007), deliver important ecosystem services, such as biomass decomposition. By contrast, specialized species cannot cope with forest degradation, especially when it impacts their livelihood as they have higher ecological requirements (Grove 2002b), namely, large amounts of dead wood, dead or old trees of large dimension, habitat continuity or natural dynamics such as wildfires or windthrows.

As the anthropogenic pressure on natural forest ecosystems increases, the importance of forests with negligible human influence becomes more apparent. These irreplaceable primary forests (also known as primaeval or virgin forests or even called ancient or old-growth forests if human impact cannot be excluded) worldwide have unique qualities that significantly contribute to biodiversity conservation, climate change mitigation and sustainable livelihoods (Foley et al. 2007; Luyssaert et al. 2008; Körner 2017). Yet most of the world's forests have been influenced in the last centuries by logging, clearing or land-use change. For example, approximately half of the tropical forest that was present at the beginning of the twentieth century has already disappeared, with peak deforestation in the 1980s and 1990s (Wright 2005). In Central Europe, where the main deforestation occurred in the eighteenth century or earlier, primary forests are now scarce (Williams 2002).

Depending on the definition, the status of natural primary forests can be very exclusive. The irrevocable loss of their status is reflected in their definition by the Food and Agriculture Organization of the United Nations (FAO 2016), i.e. a "naturally regenerated forest of native species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed". This definition does not completely exclude human intervention in the distant past, which cannot always be known. However, the FAO definition specifies that significant human intervention has not been known to occur or was long ago enough to have allowed the natural species composition and processes to become re-established (FAO 2016). Such recovery processes can last centuries depending on the intensity of the disturbance and on the surrounding landscape (Chazdon 2003).

A key factor of primary forests is the absence of human activities that could disturb ecological processes. However, some forests that experienced human activities more than 500 years ago qualify as primary forests. For example, recent archaeological research in the Amazon basin revealed pre-Columbian earthworks and settlements throughout the area (Piperno et al. 2015). Lasting legacies of these past human disturbances include earthworks, soil modification and introduction of species. However, given the spatial and temporal pattern of the data, the human impact on the Amazonian forest is not evident (Bush et al. 2015). It is therefore conceivable that large forest areas recovering from forest management and set aside as forest reserves during the past decades could be considered as primary forests in few hundreds of years, as long as the protection status is maintained.

Another definition of primary forest is based on the intactness of the ecosystem as a forest landscape of conservation value. Intactness is related to ecosystem integrity and resilience to natural disturbances and to other forest ecosystem functions, such as biodiversity (Potapov et al. 2017). A seamless mosaic of forests and associated natural treeless ecosystems with a minimum area of 500 km^2 that exhibits no remotely detected signs of human activity or habitat fragmentation and is large enough to maintain all native biological diversity is classified as an intact forest landscape (Potapov et al. 2017). Considering this concept, the size and the location of a primary forest also influence its status.

In the following, we will first provide an overview of the state of primary forests in three main climatic domains: tropical, temperate and boreal. We will then focus on important characteristics of primary forests that might influence saproxylic insects as compared to managed forests. Finally, we will provide implications for conservation and make recommendations for the role of primary forest in the conservation of saproxylic insects.

17.2 What Remains of Primary Forests and Consequences for Conservation

Globally, the history of primary forest loss mirrors the development of human settlements and population density. For example, the Roman Empire exploited forests early on in a way that left only degraded shrub vegetation cover around the Mediterranean Sea (Hughes 2011). Particularly the high demand for wood for war vessels thousands of years ago caused the loss of primary forests around the sea (Ehrlich et al. 1977). By contrast, other forest areas, e.g. in the tropics and boreal zones, were only little affected up to a few hundred years ago due to limited access and unfavourable conditions for human life, such as tropical diseases and short vegetation periods. Under the favourable conditions in Central Europe, forest degradation occurred in a cascade of pressure, starting with a clearance period up to 800 AD. After this, humans started to convert remaining forest fragments through silvicultural practices of coppicing, pasture establishment and the like. A shift to modern forestry starting in the late 1700s followed agricultural concepts of enhancing wood production, mainly through even-aged forestry and a focus on fast-growing conifers (Bürgi and Schuler 2003; Kirby and Watkins 2015; McGrath et al. 2015). In eastern North America, most of temperate deciduous forests were cleared for agriculture during the settlement from the 1600s to the mid-1800s. Consequently, in Europe and North America, less than 1% of all temperate deciduous forests remain free of deforestation or other intensive use (Reich and Frelich 2002).

Boreal forests were managed later. Studies on fire regimes highlighted the predominance of climate-driven fire regimes in Fennoscandia up to 1600s, followed by an increased fire frequency due to anthropogenic influence up to 1800s (slash-and-burn cultivation and forest pasture burning) (Niklasson and Drakenberg 2001; Storaunet et al. 2013). Later, fires were suppressed due to increased value of timber resources (Rolstad et al. 2017). Similar patterns have been indicated for North American and Russian boreal forests (Drobyshev et al. 2004; Wallenius et al. 2011).

In the tropics, with exception of pre-Columbian farming in the Amazon, a number of forests experienced such shifts even later, from primary forest to forest fragmentation, followed by logging and plantations, e.g. of oil palms (Hughes 2017). This latter process lasted less than a century but led to a dramatic and rapid loss of the most diverse forest ecosystems (Williams 2002). In line with this history, primary forests are scarce or absent in landscapes intensively and extensively impacted by humans.

The cumulative loss of forest worldwide over the last 5000 years is estimated at 1.8 billion hectares. This represents an average net loss of 360,000 hectares per year (Williams 2002) or in other words equivalent to nearly 50% of the total forest area today. In 2015, primary forests accounted for about one-third of the world's forests (Table 17.1). These data are the most comprehensive statistics available today, but many of the countries rely on forest proxies (e.g. in national parks or protected areas) to estimate the extent of primary forest (FAO 2016). Half of the world's primary forests are found only in Brazil, Canada and the Russian Federation. The forests in these three countries well represent the distribution of the remaining primary forest and highlight the role of tropical and boreal regions for the conservation of primary forests, as shown by Mackey et al. (2015), who found that 50% of the intact forest landscape (primary forest in contiguous blocks >500 km^2) occurs in boreal zone, 46% occurs in equatorial areas and 3% occurs in warm temperate climatic zones.

The global trend for primary forests is still negative, with an annual change of −0.1%. This decline is mainly due to the decreasing area of primary forests in the tropical climatic domain (South America, −0.32%; Africa, −0.45%). Primary forests in the boreal and temperate domains are slightly increasing. This is not a

Table 17.1 Surface area of natural forests and primary forests remaining today and the proportion of natural forests that is regarded as primary forest (FAO 2016)

	Natural forest (10^6 ha)	Primary forest (10^6 ha)	Proportion (%)
Africa	624	135	0.22
Asia	593	117	0.20
Europe	1015	277	0.27
North and central America	751	320	0.43
Oceania	174	27	0.16
South America	827	400	0.48
Worldwide	3999	1277	0.32

real increase in surface area, but this increase is mostly due to the reclassification of old-growth forest into primary forests following the definition of the FAO which does not exclude human impact in the past (FAO 2016). Between 1990 and 2015, primary forest area actually declined by 2.5% globally and by 10% in the tropics (Morales-Hidalgo et al. 2015).

17.3 Differences Between Primary and Managed Forests for Saproxylic Insects

Several studies could highlight differences regarding species richness, abundance or species composition between primary and managed forests. Grove (2002a) provided an overview of studies published on the relationship between saproxylic insects and forest management. Additional studies, published since 2000, are listed in Table 17.2. Generally, saproxylic insects show a positive relationship with respect to "old-growthness" of the forest stands, independently of the climate zone and forest type (Table 17.2). In this chapter, we further discuss how characteristics of primary forests that change through forest management and land-use changes could affect saproxylic insects. The topics are organized based on the spatial or temporal scale at which a characteristic affects the insects.

17.3.1 Absence of Habitat Fragmentation

One major effect of the exclusion of human activities in forest ecosystems is the absence of fragmentation driven by anthropogenic disturbances. According to the Convention on Biodiversity (CBD), forest fragmentation refers to any processes that result in the conversion of formerly continuous forest into patches of forest separated by non-forested lands (Fig. 17.1). It can be argued that for saproxylic species dependent on primary forests, even the conversion of continuous primary forest into secondary forest rather than non-forest can qualify as habitat fragmentation. The process of forest fragmentation generally starts with forest degradation driven by land-use changes and results in habitat loss, increased edge effects and isolation of populations of forest species (Laurance and Bierregaard 1997). Habitat fragmentation therefore has two consequences, namely, reduction of forest habitat and reduction of connectivity. Because these two consequences of fragmentation are often interdependent, very few studies have been able to fully disentangle the importance of habitat area and connectivity for saproxylic species (Komonen and Müller 2018). It is important to note that an improvement in connectivity usually leads to an increase in the amount of habitat. However, an increase in the habitat amount does not necessarily lead to improved connectivity (Komonen and Müller 2018).

Table 17.2 Chronology of studies comparing saproxylic insects between reference (primary, old-growth forests) and managed forests published since 2000

Country	Taxa	Forest type	Reference forests	Managed forests	Method	Abundance	Species richness	Assemblages composition	Source
Finland	Coleoptera	Boreal forests	Old-growth forests	Mature managed forests	Flight-intercept traps	+	+	+	Martikainen et al. (2000)
Australia	Coleoptera	Lowland tropical forests	Old-growth forests	Selectively logged, regrowth rainforests	Flight-intercept traps	+	+	+	Grove (2002b)
Japan	Coleoptera: Disteniidae, Cerambycidae	Humid warm-temperate forests	Old-growth forests	Secondary forests + conifer plantations	Yellow/white collision traps (baited)	0	+	+	Maeto et al. (2002)
Brazil	Wood-feeding termites	Highland evergreen forests	*Primary forests*	Plantation + *secondary forests*	Active searching along transect	–	0	+	Bandeira et al. (2003)
Mexico	Coleoptera: Passalidae	Tropical evergreen forests	*Primary forests*	Secondary forests	Manual extraction from logs	0	+	0	Castillo and Lobo (2004)
Benin	Wood-feeding termites	Semi-deciduous tropical forests	Natural forests	Teak plantations	Active searching along transect	+	+	+	Attignon et al. (2005)
Benin	Coleoptera	Semi-deciduous tropical forests	Natural forests	Teak and fuelwood plantations	Emergence traps	0	+	+	Lachat et al. (2006)
Canada	Coleoptera: Nitidulidae	Hemlock-hardwood forests	Old-growth forests	Mature managed forests	Flight-intercept traps + trunk-window traps	–	0	+	Zeran et al. (2006)

Colombia	Coleoptera: Passalidae	Andean tropical forests	Old growth forests	Andean alder plantations	Manual extraction from logs	+	+	NR	Kattan et al. (2010)
Italy	Coleoptera	Deciduous forests (oak-beech)	Old-growth forests	Conservation-oriented managed forests	Rearing + vinegar pitfall traps + flight-intercept traps	NR	+	+	Persiani et al. (2010)
Brazil	Wood-feeding termites	Semi-arid forests	Primary forests	Disturbed woodlands	Active searching along transect	+	+	+	Vasconcellos et al. (2010)
USA	Coleoptera	Eastern deciduous forests	Old-growth forests	Secondary forests	Emergence chambers	+	0	+	Ferro et al. (2012)
Singapore	Wood-feeding termites	Hill dipterocarp forests	Old-growth forests	Selectively logged forests + secondary forests	Active searching along transect	NR	0	+	Bourguignon et al. (2017)

Symbols indicate reported relationships with respect to reference forests (primary, old-growth forests): +, positive relationship; 0, no relationship; −, negative relationship; NR, not reported

Fig. 17.1 Habitat fragmentation and degradation of primary forests generally leads to habitat loss (schematic view) (Picture: J. Müller)

Not all saproxylic species react similarly to forest fragmentation, regardless of whether the consequence is the loss of habitat area or the loss of connectivity. Many saproxylic insect species are able to track dead wood, which is a spatio-temporally dynamic habitat (Seibold et al. 2017).Their dispersal ability might have been underestimated; many species are able to disperse over long distances as they are naturally adapted to search for their ephemeral resources (Komonen and Müller 2018). Even flightless species can disperse farther than expected, such as *Morimus asper* (Sulzer), which colonizes fresh dead wood and disperses over 400 m (de Gasperis et al. 2016). Furthermore, secondary users of dead wood are not affected by isolation caused by salvage logging (Saint-Germain et al. 2013), and common saproxylic beetle species are not affected by fragmentation in a forest-dominated landscape (Ranius et al. 2015). However, it is important to recognize that common saproxylic species in modified landscapes may be the ones best able to cope with such landscapes, and they may be a subset of species from common species in primary forests. Bouget et al. (2015) did not find any consistent differences in the flight ability of saproxylic beetles in woodlots of different sizes or isolation. These observations were confirmed in experimental approaches controlling the amount of dead wood in areas of differing isolation, which indicates that the amount of dead wood is independent of the spatial arrangement (Seibold et al. 2017). On the other hand, Schiegg (2000) found a correlation between species richness and composition of saproxylic *Diptera* and *Coleoptera* and found connectivity between logs at a small scale (150 m). Brunet and Isacsson (2009) detected a lower dispersal capacity of red-listed saproxylic beetles, which underlines the higher sensitivity of such species to fragmentation. The effects of fragmentation on saproxylic insects with different ecological traits, such as mobility, body size and habitat requirements, are therefore contrasting, and no general conclusions can be drawn. Furthermore, extinction of very sensitive species in the past owing to habitat fragmentation and loss might have selected species communities that react less sensitively to changes in their habitat compared to the original species assemblages.

The main effect of fragmentation on saproxylic insects in primary forest might be more indirect. Fragmentation influences forest dynamics, which in turn has an impact on the amount and quality of dead wood. Natural disturbances that affect forests at the landscape scale, such as fire and windthrow, are driven by the size, shape and position of the surrounding landscape (Saunders et al. 1991). Larger areas of intact primary forest should therefore be maintained to enable natural dynamics such as the minimum size of 500 km^2 set by the concept of intact forest landscape (Potapov et al. 2017). According to Carbiener (1996), only surface areas of several thousand hectares can harbour all forest development phases, including the variability of natural disturbances and the associated fauna and flora.

17.3.2 Habitat Continuity

Another characteristic of primary forests is the continuous supply of high amounts of dead wood and senescent trees over several centuries or longer (Whitehead 1997). This habitat continuity focuses on the need for species to breed continuously in a stand (Eckelt et al. 2018; Müller et al. 2005). Habitat continuity can be an important driver that influences the presence of saproxylic insects in forests (Buse 2012; Herrault et al. 2016). Many so-called old-growth forests harbour amounts of dead wood and habitat structures similar to those of primary forests but have encountered in the past an interruption in the supply of dead wood because of management and wood harvesting (Brunet and Isacsson 2009). As a consequence, some saproxylic insect species have disappeared and are still absent today, even though the present structure would be favourable for them (Müller et al. 2005; Gossner et al. 2013). Particularly specialized insect species with low mobility, such as some associated with tree hollows, might be sensitive to an interruption of habitat continuity because they are not able to find an alternative habitat within the reach in their distribution range at the right time (Ranius and Hedin 2001). Consequently, not only spatial continuity but also temporal continuity of dead wood and senescent structures available in primary forests represent key factors for the conservation of saproxylic species with high habitat requirements and low mobility.

17.3.3 Natural Disturbance Regimes

The intensity, frequency and severity of natural disturbances in primary forests have a major effect on the quantity and quality of dead wood available for saproxylic insects. The combination of small gap dynamics associated with the breakdown of a single tree (Yamamoto 2000) and the disturbance of several square kilometres of forest over millennia has shaped forest biomes that differ in composition and structure throughout the world, which in turn has shaped the communities of species (Gauthier et al. 2015) (Fig. 17.2). Through co-evolution and selection, forest species are preadapted to the natural prevailing disturbance regime typical for their respective forests biome (McPeek and Holt 1992). Consequently, saproxylic insects are prone to react sensitively to natural disturbances that produce dead wood in primary forests (Grove and Stork 1999). For example, in natural boreal forests, where natural

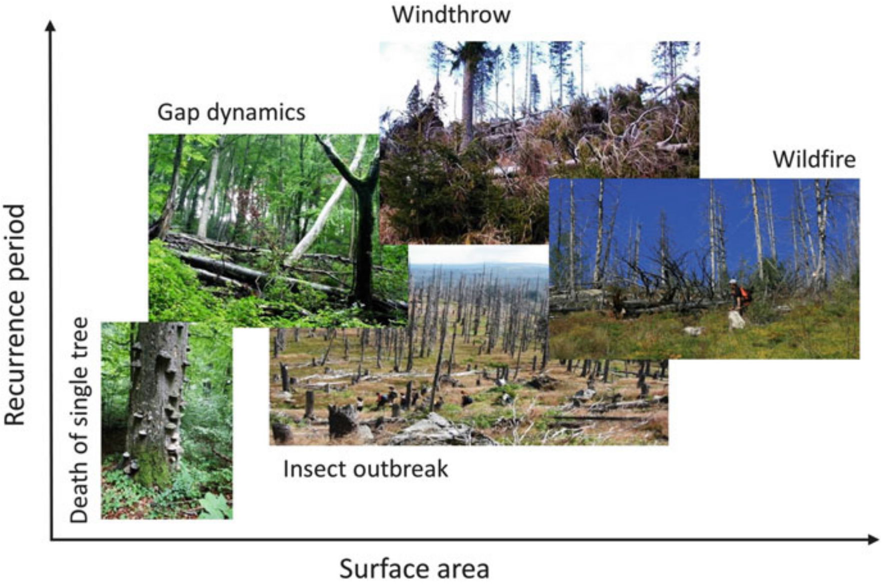

Fig. 17.2 Schematic view of the surface area affected by natural disturbances in relation to their recurrence periods [after Spies and Turner (1999)] (Pictures: T. Lachat, J. Müller)

disturbances such as fire or storms can extend over several thousands of hectares (Boulanger et al. 2010) and can recur, saproxylic insects are adapted to the resulting mosaic structure and are therefore less sensitive to fragmentation than species in tropical ecosystems (Langor et al. 2008). Because of the distribution of their ephemeral habitat at the landscape scale, these species are therefore generally good dispersers and are able to colonize newly formed habitats (Grove 2002b; Messier et al. 2003). It is important to note that secondary users of dead wood also benefit from the large quantities of dead wood created by natural disturbances on large areas (Nappi et al. 2010). In temperate forests, such as primary beech forests dominated by gap dynamics, most species will be adapted to single-tree replacement dynamics, which lower the importance of heliophilous species because of the lack of large open disturbed areas (Lachat et al. 2016).

The major dynamics of forests strongly depends on the climate zone and on the soil in which they grow. On steep mountain slopes, avalanches and rockslides create bare soil and open patches in forests, which regularly open the avenue for establishment of pioneer tree species, e.g. species of the genera *Pinus* and *Betula*. In floodplains, the rearrangement of rivers creates a diverse composition of tree species mainly triggered by their inundation tolerance. In temperate broad-leaved forests, major dynamics are gaps caused by fallen veteran trees and summer storms. In boreal forests, insects and fires with stand-replacing dynamics dominate the natural forest landscape. In the tropics, forests are naturally affected by hurricanes, gap dynamics and fires (Chazdon 2003). In wet Australian eucalypt forests, for example, infrequent fires lead to stand-replacing or partial stand-replacing dynamics sometimes across tens of thousands of hectares, leading to long-lasting pulses of very high volumes of standing dead trees and dead wood. In drier eucalypt woodlands, by contrast, more frequent but lower-intensity fires maintain a semiopen structure with lower, but more constant, amounts of dead wood (Fox and Fox 2003).

Currently, most of these inherent dynamics of primary forests are interrupted by channelling rivers, suppression of fires, pest species management and forest management measures aimed at lowering the sensitivity of stands to natural disturbances (Kurz et al. 2008; Seidl et al. 2014). The mitigation or suppression of the effect of natural disturbance might have dramatic effects on saproxylic species and can compromise a large proportion of the regional species pool. This is especially the case for those adapted to habitats created by disturbances such as the large inputs of dead wood created by windthrows or regeneration of broad-leaved trees in boreal forests after fire (Martikainen 2001).

17.3.4 Dead Wood

The main resource for saproxylic insects—dead wood—might be very heterogeneously distributed in space and time in all forests regardless of disturbance of management history (Christensen et al. 2005; Ylisirniö et al. 2009; Amanzadeh et al. 2013). Because of the natural dynamics in primary forests (from competitive thinning in younger forests to tree death in older forests), the average amount of dead wood is generally higher than in managed forests (Siitonen et al. 2000; Grove 2002b; Christensen et al. 2005; Lachat et al. 2007). However, in contrast to the most intensively managed forests, where fallen woody biomass is generally and mostly exported out of the harvested forest stands, the quantity of fallen coarse wood might temporarily increase in many forests after logging, especially when legacy debris and logging slash are left on the site (Keller et al. 2004). As Spies et al.(1988) showed in northwestern North America, this results in a fairly typical "U-shaped" distribution of log volume among different stand ages, with lower wood volume reported from forests of intermediate age than in recently harvested stands. Consequently, a large amount of dead wood is not always an indicator of naturalness, as it has been shown for European temperate forests (MCPFE 2007). Gerwing (2002) found that in the Brazilian Amazon, the amount of dead wood increased in relation to the intensity of logging. A study in Malaysian Borneo has shown that up to 64% of the above-ground biomass in selectively logged forests could consist of dead wood (Pfeifer et al. 2015). Such observations might be reinforced in tropical forests without major natural disturbances leading to low amount of natural coarse woody debris because of the rapid decay of the woody biomass. Saproxylic species might therefore benefit from this artificial high amount of coarse woody debris. However, especially in the tropics, the continuity over time is not guaranteed, because dead wood will decompose before a new coarse woody debris will be created.

Grove and Stork (1999) designed a framework for future research on the effect of logging on saproxylic species in tropical forests that considers the peculiarities of the logging practices. Short-term results highlighted the changes in the species richness and composition of saproxylic beetles, but long-term studies are needed to reveal the effect of repeated logging on saproxylic species (Grove 2002b), especially for species that depend on large old trees or dead wood of large dimensions (Seibold and Thorn 2018) (Fig. 17.3). Another peculiarity of tropical forests is the presence of wood-feeding termites. Several studies have revealed changes in termite species richness and abundance along a gradient of logging intensity from primary forests to forest cleared for agricultural production (Bandeira and Vasconcellos 2002; Jones et al. 2003; Ewers et al. 2015). However, soil-feeding termites seem to be more sensitive to logging than wood-feeding termites (Eggleton et al. 1997). Therefore, it has been recommended to let dead wood decay in situ after a forest disturbance to mitigate the loss of termite species (Jones et al. 2003).

Natural dynamics at a small scale, e.g. death or breakdown of a single large senescent tree, and at a large scale, e.g. windthrow, fire or bark-beetle infestation, are the main drivers that determine the amount of dead wood in primary forests. Nevertheless, dead wood production in the absence of a major disturbance is not limited to the senescent phase, e.g. breakdown of single old trees. Already during regeneration phases, significant amounts of dead wood can be created through exclusion of young trees by competition (Peet and Christensen 1987). This gives rise to a continuous production of dead wood of different types and quality throughout the forest and during the entire forest development phase (Saniga and Schütz 2002; Larrieu et al. 2014). Under natural condition in forests dominated by gap dynamics, regeneration is characterized by remnants of large old trees that slowly die and continuously produce coarse woody debris (Larrieu et al. 2014). In forests dominated by stand-replacing disturbance such as fire, dead wood from competitive thinning during regeneration is of small diameter and short-lived which might limit its value for most saproxylic species. However, in boreal forests, pioneer deciduous trees typically available after fire might harbour rare and threatened saproxylic insect species (Siitonen and Martikainen 1994).

The continuous production of dead wood in the various forest development phases enables the accumulation of dead wood with a high diversity of positions, decay stages, diameters, tree species and sun exposure (Stokland et al. 2012). As the diversity of dead wood also has an important effect on saproxylic beetles (Brin et al. 2009), not only the dead-wood amount but particularly the dead-wood diversity should be promoted for the conservation of saproxylic beetles (Seibold and Thorn 2018).

Different inventory methods can influence the amount of dead wood recorded (Vidal et al. 2016). Furthermore, both the scale and the number of sampling plots considerably influence the results of the dead-wood inventory in the field, especially because dead wood is generally heterogeneously distributed. Therefore, caution should be used when comparing dead-wood amounts of different studies. In a non-exhaustive literature search for minimal and maximal amounts of dead wood in different primary or natural forests, we established the ratio of dead wood to living

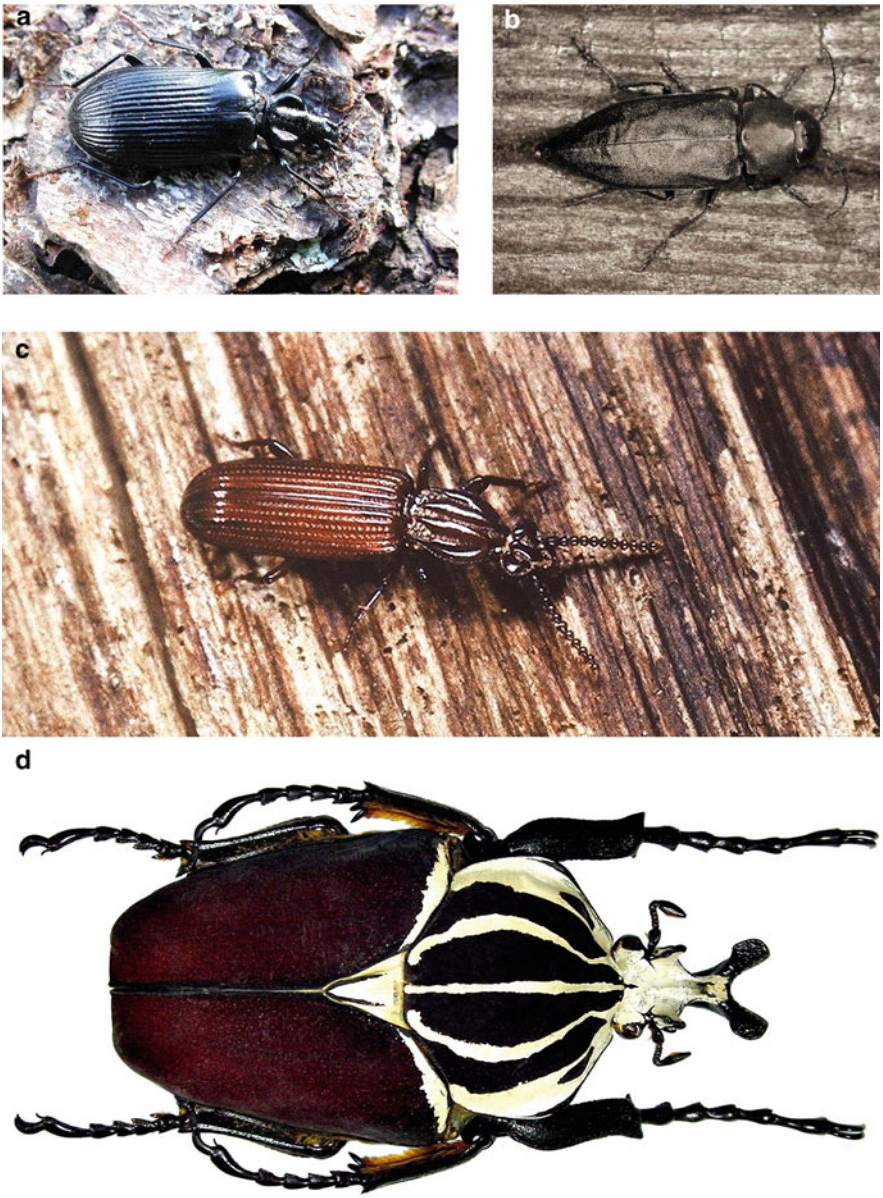

Fig. 17.3 Saproxylic beetle species associated with primary forest and their natural dynamics: (**a**) *Pytho kolwensis* Sahlberg lives in boreal virgin spruce forests and needs high volumes of dead wood (73–111 m^3/ha) and a long habitat continuity (Siitonen and Saaristo 2000) (Picture: J. Müller). (**b**) *Melanophila acuminata* DeGeer is a pyrophilous species that detects infrared radiation emitted by forest fires. This species requires burned trees to reproduce (Picture: H. Bussler). (**c**) *Rhysodes sulcatus* (F.) has disappeared from most European countries because of the suppression of primary beech forests since the Neolithic (Speight 1989) (Picture: J. Müller). (**d**) *Goliathus goliatus* Drury is one of the heaviest beetles worldwide. This species from West and Central Africa lives in savanna and woodland and needs large logs at the end of the decay process for its development (Picture: G. Goergen)

Table 17.3 Overview of the amount of dead wood in natural forests in different climatic domains (not always primary)

Climatic domain	Deadwood lower range (m^3/ha)	Deadwood upper range (m^3/ha)	Proportion dead wood/ living trees (%)	Source
Boreal or coniferous forests	56	389	13–89	Korpel (1997) and Herrmann et al. (2012)
Temperate forests	32	345 1600[a]	4–70	Tabaku (1999), Kucbel et al. (2012) and Woldendorp et al. (2004)
Tropical forests	30	126	6–18	Lachat et al. (2007), Harmon et al. (1995), Chambers et al. (2000) and Gerwing (2002)

[a] Extreme value from tall open *Eucalyptus* forests in Tasmania

trees for three main climatic domains (Table 17.3). The lower range was relatively consistent over the three climatic domains (30 to 56 m^3/ha). The upper range in temperate and boreal/coniferous forests reached about 350 m^3/ha. Extreme values were registered in tall open forests dominated by *Eucalyptus* in Tasmania where the volume of coarse woody debris can reach 750 to 1600 m^3/ha for a basal area reaching 150 m^2/ha (!) (Woldendorp et al. 2004). In tropical forests, the upper range was about 150 m^3/ha. These relatively low quantities in the tropics might be due to the absence of studies of dead wood in large-scale disturbed primary forests and to the high rate of decomposition owing to high temperature and humidity.

17.3.5 Tree Species Composition

In all climatic domains, tree species composition of primary forests is expected to represent the natural tree species community and to harbour typical saproxylic insect communities associated with native tree species. Forest management and tree selection affect the composition of tree species, which in turn can influence saproxylic insect communities. Changes in tree species composition at a high taxonomic level, such as the transition from broad-leaved or mixed forest to coniferous forest, are mostly caused by human activities (Nilsson 1992). In boreal forests, logging and forest fire suppression leads to impoverished forests by actively or indirectly (fire suppression) eliminating deciduous trees such as aspen (*Populus tremula* L.) (Vanha-Majamaa et al. 2007). In Central Europe, forest ecosystems have dramatically changed during the conversion of broad-leaved forests to coniferous forests for wood production (Kirby and Watkins 2015). The simplification of tree species composition at this level (broad-leaved/mixed forest to coniferous forest) has dramatic consequences for saproxylic species associated with deciduous trees because few species are able to develop on both of these tree types and because the proportion of monophagous saproxylic species on a specific tree genus can comprise up to 40% of the community (Jonsell et al. 1998). This is especially true for species associated with early decomposition stages of wood (Jonsell et al. 1998).

In tropical forests, logging and especially reduced-impact logging might have a positive effect on the tree species community (Imai et al. 2012). Indeed, Hall et al. (2003) reported little difference in tree species composition and diversity between highly selectively logged and unlogged plots in Central Africa. On the other hand, more intensive logging in tropical forests might dramatically affect tree diversity, leading to about 25% of tree species loss (Saiful and Latiff 2014). The consequences of such loss in tropical forests are poorly understood because of the high diversity of tree species. However, even though alpha diversity might increase in tropical forests managed by reduced-impact logging, beta-diversity of trees would decrease as well as the prevalence of old trees and all the microhabitats that they offer (see 3.5 Habitat Trees).

17.3.6 Habitat Trees

Habitat trees are characterized by the tree-related microhabitats (TreMs) they carry (Larrieu et al. 2018). A TreM is defined as a distinct, well-delineated structure that occurs on living or standing dead trees and that constitutes a particular and essential substrate or life site for species or communities during at least a part of their life cycle to develop, feed, shelter or breed (Larrieu et al. 2018). The majority of TreMs can be considered saproxylic structures caused by biotic or abiotic impacts, such as bark lesion, cavities and breakage, which expose sapwood and heartwood. Because such structures have mostly disappeared from managed forests, many of the species associated with TreMs have become rare and threatened and require special conservation efforts for their survival (Ranius 2002b). The lack of TreMs is especially critical for highly specialized saproxylic insects, which cannot find an alternative habitat in the vicinity if needed (Gouix and Brustel 2012).

Tree cavities are one of the best-studied tree-related microhabitats (Fig. 17.4). Tree cavities can be created by primary excavators such as woodpeckers. Worldwide, more than 350 bird species are considered as primary excavators, whereas about 1900 bird species nest in tree cavities (van der Hoek et al. 2017). In absence of primary cavity excavator such as in Australia, cavity-dependent species rely on decay processes following bark or wood injury (e.g. fire, rock fall or branch breakage) and induced by fungi and insects. Species involved in excavation of cavities can be considered as ecosystem engineers.

Hollow trees are considered keystone structures in managed forest (Müller et al. 2014) because they can harbour the full range of dead-wood decomposition stages. While rare in managed forests, they are a common character in many primary forests, e.g. in *Fagus orientalis* L. forests in Iran, one-third of all mature trees have a cavity (Müller et al. 2016). The effect of reduction of these trees on wildlife has been shown by various studies focusing on cavity-nesting birds, such as parrots in Amazonia

Fig. 17.4 Habitat trees with cavities offer very valuable, long-lasting and complex microhabitats for saproxylic insects, with mould (dry, humid), fungi, heartwood and sapwood, and different decay stages (Photograph: T. Lachat)

(de Labra-Hernández and Renton 2016), and on bird and mammal cavity users in New Guinea (Warakai et al. 2013), where at least three times more cavities were detected in primary forests than in secondary forests. Tree cavities can remain for decades to centuries and evolve towards larger cavities with mould (Gibbons and Lindenmayer 2002; Lindenmayer et al. 2012; Stokland et al. 2012). Such cavities can then harbour saproxylic insects of high conservation value, whose larval development requires constant conditions for several years (Dajoz 2000; Gouix and Brustel 2012). A loss of such structures is expected to threaten specialized saproxylic insect species even though the mechanism of colonization and extinction of such species are still poorly understood (Ranius 2002a).

At the scale of a single tree, the older or larger a tree is, the higher is the probability that it carries TreMs (Koch et al. 2008; Ranius et al. 2009). Even though no evidence has been found for a higher number of TreMs in late development stages in natural temperate forests compared with early phases of the silvicultural cycle (Larrieu et al. 2014), ecologically more valuable TreMs, such as large mould cavities which are slow to develop, will be more abundant in overmature and senescent phases dominated by very old trees.

For all forest types, logging considerably reduces the lifespan of trees. Independent of the diameter or age at which a tree is harvested (e.g. at small diameters in boreal forests and at large diameters in tropical forests), logging prevents trees from a natural death and from ageing—the major process characteristic of primary forest ecosystems. Consequently, managed forests lack the natural number of old trees and associated TreMs. One way to mitigate this negative effect of logging on species dependent on specific structures is to retain single habitat trees with evidence of TreMs (Whitford and Williams 2001). Beyond their role as a habitat, habitat trees are also important producers of dead wood. During the senescence process, they ensure a slow input of dead wood in the form of, e.g. dead branches in the canopy and a dead part of the trunk, until they completely die and remain as a snag or fallen dead tree.

17.4 Implications for Conservation

Saproxylic species represent a significant proportion of the biodiversity in primary forest in all climatic domains. For some species groups, this proportion can reach up to 60%. For example, 56% of all forest beetles are associated with dead wood in Central Europe (Köhler 2000), 35% in boreal forests in Finland, 33% in lowland tropical forests of Sulawesi (Hanski and Hammond 1995) and 60% in *Eucalyptus* forests of Tasmania (Grove, personal communication). Overall, about 25% of all forest species are considered saproxylic. Many studies have shown the role of old-growth forests for the conservation of saproxylic species (Martikainen et al. 2000), and even more have revealed the impact of forest management on this sensitive species group (Paillet et al. 2010). However, few studies have focused on saproxylic insects in primary forests (Grove 2001; Lachat et al. 2006; Lachat et al. 2016; Müller et al. 2016) because (1) most research is conducted in areas with few remnants of primary forests; (2) studies of primary forests are logistically demanding, mostly because of the remoteness of the remaining primary forests; (3) the uniqueness of remnants of primary forest considerably limits the possibility of researching beyond case studies; and (4) the taxonomic knowledge on saproxylic insects from primary forest is insufficient (especially in the tropics).

Saproxylic insects are a highly threatened taxonomic group (Davies et al. 2008). The threat goes back to the Neolithic clearances and concomitant woodland management practices and has been intensified in the past centuries. In Europe and Northern America, two centuries of intensive commercial forestry and agricultural management practices have strongly impacted natural forest ecosystems and their associated species (Speight 1989). In tropical forests, the status of many saproxylic species remains undocumented (Grove 2002b), but the situation for saproxylic fauna is likely to be similar to that in Europe (Ghazoul and Hill 1999). In all climatic domains, the loss of intact forests contributes directly to the biodiversity extinction crisis (Mackey et al. 2015).

Nowadays, different conservation measures for saproxylic species such as the retention of key structural habitat elements (habitat trees, snags or lying dead wood) can be integrated in commercially used forests (Kraus and Krumm 2013). Conservation-oriented forest management can therefore play a very important function for the conservation of saproxylic insects. Unfortunately, many of the resources required both quantitatively and qualitatively by saproxylic species cannot be integrated completely into forest management schemes because the ecological requirements of highly demanding species cannot be fulfilled in managed forests. In landscapes where primary forests have mostly disappeared like in Europe or North America, segregative conservation instruments such as protected forest areas are needed for the conservation of saproxylics. Such approach often leads to tiny relict forest reserves in a matrix dominated by intensive forestry or agriculture. Such reserves, however, represent the backbone of the saproxylics conservation. For regions with large areas of primary forest coverage or where there is a shorter history of forest loss or intensive use, applying conservation principles at the landscape scale is probably more likely to succeed. In this scenario, large reserves are important. Because such large reserves are mostly isolated, smaller reserves help to fill the gaps and to improve the migration of individuals from population sources.

17.5 Conclusions

For the conservation of saproxylic insect species, all types of primary forest should be strictly protected as these forests represent the last intact biome on Earth where these species can develop under natural conditions. The conservation priority might be higher in regions with high endemism and high annual rates of primary forest destruction, such as in the tropics, even though the rate of decline appears to be slowing (Morales-Hidalgo et al. 2015). Strict protection is also needed in regions with very low remaining proportions of primary forest, such as Central Europe, where only 0.2% of the deciduous forests are considered to be in a natural state (Hannah et al. 1995). Species associated with primary forest in Central Europe are therefore also highly threatened, and their destruction would be fatal for the species that have been maintained to date. Besides their role as refuges for saproxylic species (Bengtsson et al. 2000), primary forests also represent references for managed forests. Dead-wood amount, density of habitat trees, proportion and area of canopy gaps and species assemblages in primary forests should be considered when setting goals for the management of near-natural forests (Lachat et al. 2016). For this, more research in primary forests worldwide is urgently needed to better understand their complex ecology to stimulate sustainable forest management.

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Chapter 18
The Importance of Dead-Wood Amount for Saproxylic Insects and How It Interacts with Dead-Wood Diversity and Other Habitat Factors

Sebastian Seibold and Simon Thorn

Abstract Natural amounts of dead wood in a forest vary considerably, depending on living tree biomass, decomposition rates, and rates of dead-wood development. In natural forests, dead wood is created by the senescence of trees and natural disturbances. However, dead-wood amounts in many forest ecosystems worldwide nowadays are largely influenced by human activities, such as timber and fuel wood production and post-disturbance salvage logging. The biodiversity of saproxylic insects is usually positively correlated with the amount of dead wood, and dead-wood amount affects species composition and functional characteristics of saproxylic assemblages. Dead-wood amount is in turn correlated with dead-wood diversity, and several studies highlight the importance of dead-wood diversity for saproxylic biodiversity, which suggests that habitat heterogeneity is a major driver behind the positive relationship between dead-wood amount and biodiversity. The strength of this relationship is mediated by temperature. Effects of both temporal forest continuity and spatial connectivity are often linked to differences in dead-wood amount. Frequent interactions and correlations between dead-wood amount and other habitat factors indicate that future studies should aim more precisely at unraveling the importance of individual factors for saproxylic biodiversity, which will help to improve conservation strategies to counteract negative effects of anthropogenically altered dead-wood amount and diversity. Such conservation strategies, particularly in Europe and North America, include passive and active measures to retain dead wood in managed forests and to restore amounts and diversity of dead wood similar to levels in natural forests. More research is needed in the subtropics and tropics where conservation

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strategies rarely consider dead wood, although the few existing studies suggest that dead wood is an important factor for biodiversity in these regions.

> When one walks through the rather dull and tidy woodlands [...] that result from modern forestry practices, it is difficult to believe that dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna. (Elton 1966)

As Charles Elton noted, human activities, such as timber production and fuelwood harvesting, have changed stocks of dead wood in most forest ecosystems worldwide and caused serious declines and extinctions of many species associated with dead wood (Speight 1989; Grove 2002b; Seibold et al. 2015b). Numerous studies over the last decades have thus studied natural and anthropogenic drivers of dead-wood dynamics and the role of dead-wood characteristics in biodiversity, particularly the amount and diversity of dead wood (see Box 18.1). Earlier studies, mainly from the American Pacific Northwest, focused on forest structure and especially on the dynamics of dead-wood amounts in response to natural and anthropogenic drivers (Maser and Trappe 1984; Harmon et al. 1986; Speight 1989; Siitonen 2001). In these studies, the importance of dead wood in general for biodiversity was often discussed qualitatively, e.g., by listing species associated with dead wood and discussing their habitat preferences. The switch to a focus on biodiversity or conservation started in Fennoscandia and increasingly spread to other parts of Europe and North America as concerns about the negative effects of anthropogenically decreased dead-wood amounts on biodiversity increased. These studies helped to elucidate how dead-wood amount, dead-wood diversity, or other dead-wood measures affect population dynamics of individual species, species richness, and composition of saproxylic communities to provide a scientific basis for conservation strategies (Müller and Bütler 2010; Lassauce et al. 2011).

Based on general ecological theory, dead-wood amount can affect saproxylic communities via two major mechanisms (Müller and Bütler 2010; Seibold et al. 2016). One potential mechanism follows the *more-individuals hypothesis* (a variant of the *species-energy hypothesis*), which states that more available energy leads to more individuals and more individuals enable more species to attain viable populations (Wright 1983; Srivastava and Lawton 1998; Clarke and Gaston 2006). As the amount of dead wood represents the amount of chemical energy available to species able to utilize it, the abundance of saproxylic species and thereby the number of saproxylic species will increase with increasing amounts of dead wood. The second potential mechanism follows the *habitat-heterogeneity hypothesis*, which predicts that the number of different habitat types increases with area and that, if species differ in their habitat requirements, species richness will increase with increasing area (MacArthur and MacArthur 1961; Tews et al. 2004). The habitat niche of most saproxylic species comprises only some types of dead wood, and the types can vary greatly with regard to tree species, decay stage, diameter, position, and sun exposure (Stokland et al. 2012; Bouget et al. 2013). Therefore, habitat heterogeneity can increase with increasing size of a single dead-wood object since microclimate, decay stage, and fungal communities can vary strongly within the object (Graham 1924; Leather et al. 2014). Moreover, habitat heterogeneity can also increase with increasing numbers of dead-wood objects (Hottola et al. 2009; Müller and Bütler 2010) because a higher number of dead-wood objects will usually comprise more types of dead wood. Thus, dead-wood amount and dead-wood diversity are usually correlated (Similä et al. 2003; Brin et al. 2009; Müller and Bütler 2010; Bouget et al. 2013).

The relationships between biodiversity, dead-wood amount, and other dead-wood factors have been mostly studied in field surveys. Such surveys have been particularly applied for management- and conservation-oriented studies that evaluate effects of natural or anthropogenic gradients of dead-wood amount or other dead-wood factors on saproxylic biodiversity (Müller and Bütler 2010; Riffell et al. 2011; Lassauce et al. 2011; Bouget et al. 2012). These field surveys have been complemented by an increasing number of experimental studies (Seibold et al. 2015a). Such experimental manipulations are needed when differences between dead-wood objects (e.g., decay stage or cause of death) or differences in management history and/or abiotic conditions (e.g., sun exposure or altitude) between studied stands would otherwise hamper the interpretability of biodiversity patterns. Moreover, manipulations allow correlated drivers of biodiversity, such as dead-wood amount and dead-wood diversity, to be disentangled. Experimental studies thus provide additional information on general ecological patterns and driving mechanisms and allow evidence-based conservation strategies to be formed and refined.

In this chapter, we will discuss natural and anthropogenic drivers of dead-wood amount and other dead-wood factors, most importantly dead-wood diversity, and will review the literature linking dead-wood amount and saproxylic insect communities. The effects of dead-wood amount on saproxylic communities might be attributed to resource availability, habitat heterogeneity, or both because dead-wood amount and dead-wood diversity are correlated, and most studies did not disentangle these factors. Finally, we will discuss interacting effects between dead-wood amount and other factors, such as dead-wood diversity, microclimate, and connectivity.

Box 18.1 Definitions

Dead-wood amount refers to the available dead wood in a certain area. Measurements of the amount include volume, biomass, or surface area of dead wood, the number of dead-wood objects (e.g., logs, snags, tree hollows), or the area of forest floor covered by dead wood. Due to the heterogeneity in size and shape of dead-wood objects, the potentially high number of fine dead-wood objects, and the patchy distribution of dead wood on larger spatial scales, measurements of dead-wood amount can only provide estimates. Since these depend strongly on the applied protocol, e.g., minimum diameter and length of dead-wood objects considered, a detailed description of the protocol should be provided when estimates of dead-wood amount are published to allow comparison between studies.

(continued)

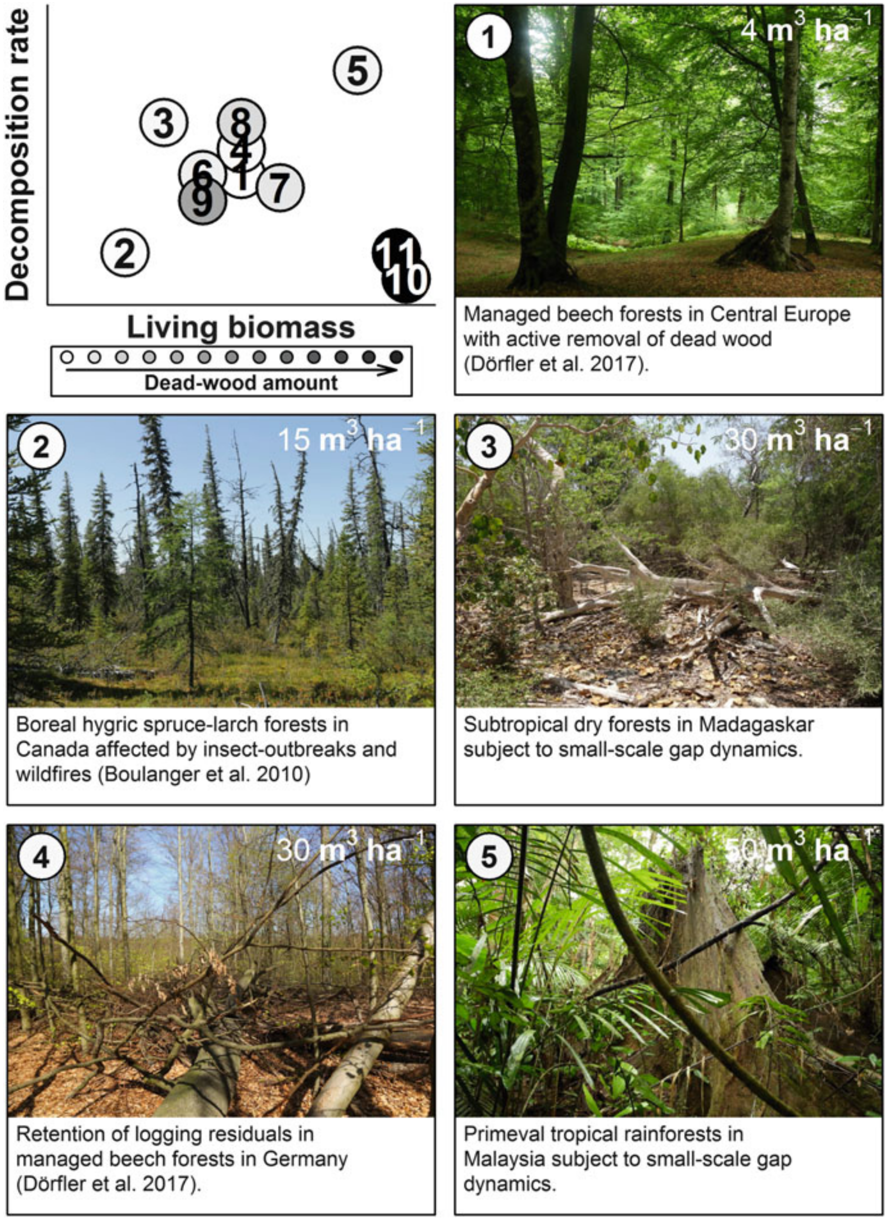
Box 18.1 (continued)

Dead-wood diversity refers to the number of different dead-wood qualities or types, such as tree species, diameter, and decay stage. Differences in dead-wood type can also occur within single dead-wood objects since, e.g., moisture, temperature, decay stage, and biotic communities are not distributed homogenously. However, estimates of dead-wood diversity usually consider only differences between objects. Measures of dead-wood diversity can be calculated as the number of dead-wood types (Siitonen et al. 2000), as Shannon's diversity index considering the number of objects per dead-wood type, or as a combined measure of number, volume, and diversity of dead-wood objects (Hottola et al. 2009).

Natural disturbance refers to any event of natural origin that causes the mortality of old and young trees in the main canopy and/or any other forest layers. Natural disturbances typically result in an increased amount and diversity of dead wood and include windstorms, insect outbreaks, wildfires, and ice storms.

18.1 Natural Drivers of Dead-Wood Amount and Diversity

In natural forest ecosystems, dead wood is frequently created by the complete or partial die-off of senescent trees (Lindenmayer et al. 2012; Müller et al. 2014) and by natural disturbances, which can affect single or multiple trees or complete stands (White and Pickett 1985). The amounts of dead wood in natural forests vary considerably between forest types and between biomes (Lachat and Müller 2018, see Chap. 17). This variation is caused by the high variability in the volume of living trees, dead-wood input rates, and wood-decomposition rates (Fig. 18.1). All these variables depend on climate, site productivity, tree species, tree/stand age, the biotic community inhabiting dead wood, and the dominant disturbance regime. The highest amounts of dead wood, i.e., several hundreds to $>1000\ \mathrm{m}^3\ \mathrm{ha}^{-1}$, occur where high productivity meets low decomposition rates owing to high rot resistance, as in temperate rainforests (Harmon et al. 1986; Richter and Frangi 1992; Stewart and Burrows 1994; Lindenmayer et al. 1999), or when forests of intermediate productivity experience high input rates of dead wood from stand-replacing disturbances, as in boreal conifer-dominated forests (Lindenmayer et al. 1999; Müller et al. 2010). These two examples, however, could differ in dead-wood diversity. A continuous supply of dead wood could lead to a higher variability in decay stages in temperate rain forests than in forests where most dead wood originates from a single disturbance event. Despite high volumes of living trees, tropical rain forests have comparatively low amounts of dead wood because of high decomposition rates (Delaney et al. 1998; Grove 2001), but the high number of tree species constitutes high dead-wood diversity.



(1) Managed beech forests in Central Europe with active removal of dead wood (Dörfler et al. 2017).

(2) Boreal hygric spruce-larch forests in Canada affected by insect-outbreaks and wildfires (Boulanger et al. 2010)

(3) Subtropical dry forests in Madagaskar subject to small-scale gap dynamics.

(4) Retention of logging residuals in managed beech forests in Germany (Dörfler et al. 2017).

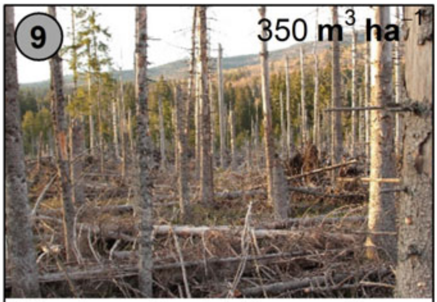
(5) Primeval tropical rainforests in Malaysia subject to small-scale gap dynamics.

Fig. 18.1 The amount of dead wood (indicated by shading of the numbered circles) depends on site productivity, i.e., living biomass, decomposition rates, and other factors. The highest amounts of dead wood can be found where high productivity meets low decomposition rates. (1–11) Examples of amounts of dead wood that differ because of site productivity and the history of anthropogenic and natural disturbances. Unless a reference is provided, values represent rough estimates of the photographer (SS or ST) for the depicted site

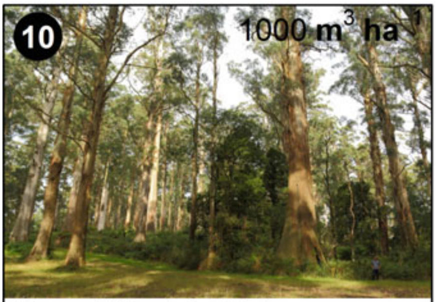
Salvage-logged spruce stands in central Europe with comparably high amounts of dead wood (Priewasser et al. 2013).

Gaps with high amounts of dead wood in primeval beech forests in northern Iran (Müller et al. 2015).

Hurricane disturbance in subtropical forests in Florida with high local amounts of dead wood.



Natural spruce forests in Germany after outbreaks of European spruce bark beetle (Müller et al. 2010).



Old-growth forests in Victoria, Australia dominated by mountain ash (Lindenmayer et al. 1999).

Old-growth forests in the Pacific Northwest dominated by Douglas fir (Harmon et al. 1986).

Fig. 18.1 (continued)

Not only the amount but also the quality and diversity of dead wood differ depending on the origin (Stokland et al. 2012). Natural senescence creates a high diversity of dead wood, including the full diameter range from branches to large trunks, standing and downed dead wood, different levels of sun exposure, and a variety of microhabitats, such as rot holes and canopy dead wood (Stokland et al. 2012; Larrieu et al. 2014; Kraus et al. 2016). However, natural disturbances often create or leave behind disturbance-specific dead-wood structures (some are often called biological legacies; Franklin et al. 2000). For instance, wildfires create large numbers of standing dead trees and snags, whereas severe windstorms create uprooted trees that lie on the forest floor with sun-exposed dry branches (Swanson et al. 2011). Biological legacies, such as remnant living trees that survived a wildfire, can enhance the recovery of total ecosystem carbon stocks after a disturbance, facilitate the recolonization of late-seral species (Seidl et al. 2014), and enable the colonization of early-seral species (Swanson et al. 2011; Kortmann et al. 2017). Thus, conservation strategies in forests naturally prone to large-scale natural disturbances typically try to mimic the creation of biological legacies (Burton et al. 2006; Foster and Orwig 2006). Nevertheless, the amount and diversity of dead wood depends on the type of natural disturbance (Hammond et al. 2017). For instance, in an extremely short time, windstorms can create dead wood in large amounts but of low diversity as the fresh dead wood is only of susceptible tree species. By contrast, bark beetle populations commonly increase over months and years and result in a higher diversity of dead wood on a landscape scale (Thorn et al. 2016b). In addition, dead-wood diversity can change over time as abiotic and biotic conditions change because of the saproxylic community involved in wood decomposition (Graham 1924; Fukami et al. 2010). Fungal communities, for example, can vary within a single log and can thus cause differences in microhabitats that contribute to dead-wood diversity (Saint-Germain et al. 2010; Leather et al. 2014).

18.2 Anthropogenic Decrease of Dead-Wood Amount and Diversity

Anthropogenic loss of dead-wood habitat for saproxylic species can be separated into two steps (Stokland et al. 2012). The first, rather obvious, step is the loss of forest area when forests are cleared for other land use forms; existing dead wood is removed, and its future development is stopped. The second step is the change in amounts of dead wood in the remaining forested area and in forests arising after afforestation. Both steps of dead-wood habitat loss can have interacting effects on saproxylic communities because habitat amount on the landscape scale and forest continuity could affect both local communities and local habitat amount (see below). In anthropogenically altered forests, dead-wood amounts can differ from those in natural forests owing to differences in the rate of dead-wood input or output or both (Fig. 18.1).

The most important decline in dead-wood input rates is the decrease in mean stand age due to timber harvesting. When trees are harvested before they can reach an age of natural senescence, i.e., their partial or complete die-off, an important mechanism of dead-wood creation is lost (Stokland et al. 2012; Burrascano et al. 2013). Dead-wood development is then restricted to self-thinning, i.e., the die-off of typically small diameter trees due to competition with larger trees. Self-thinning produces not only lower amounts of dead wood compared to the die-off of overmature trees but also less diverse dead wood, dominated by dead wood of small diameter under shady conditions. Green-tree retention in clear-cut forestry is increasingly applied to maintain at least some older trees (Gustafsson et al. 2010). If trees are retained at low densities, high mortality rates can occur within the first years after the harvest because of, e.g., windthrow; in this way, dead wood is supplied short-term instead of the long-term supply from trees allowed to become senescent (Heikkala et al. 2014). By contrast, the retention of "habitat trees," i.e., trees with hollows or other structures that serve as microhabitats for different taxa (Kraus et al. 2016), in selection-cut forestry could be a strategy for allowing the development of senescent trees (Müller et al. 2014; Dörfler et al. 2017).

Rates of dead-wood output increase with the removal of dying and dead trees for energetic or material use. This includes harvesting of such trees while retaining healthy trees (Müller et al. 2016) and slash or stump removal after a regular harvest (Riffell et al. 2011; Uri et al. 2015), which might also remove dead wood that was present before the harvest. Dead wood is also removed for reasons linked to "forest hygiene." The principle of forest hygiene has its origin in Europe in the nineteenth century (Day 1950) and was followed in other regions of the world, such as the North American Pacific Northwest (Harmon 2001). This principle considers a forest that contains dying or dead trees as "untidy" and that such trees are a source of pathogens and pest species that threaten healthy trees. For example, German foresters in the eighteenth and nineteenth centuries were advised to remove all dead, wounded, or insect-infested trees, particularly of large diameter (Gmelin 1787; Hartig 1808; Cotta 1865).

Among other arguments, the concept of forest hygiene is still used to justify the suppression of natural disturbance dynamics in various forest ecosystems through salvage logging (i.e., the removal of dead wood) following disturbances, insecticides to avoid insect outbreaks, and fuel reduction burning to prevent intense wildfires. Besides a priori attempts to eradicate natural disturbances from forested landscapes, logging to "salvage" economic return has become the most common management intervention of naturally disturbed forests, particularly in the Northern Hemisphere (Lindenmayer et al. 2008). The main arguments used to justify salvage logging include capturing some of the economic value of disturbance-affected trees (Prestemon et al. 2006), reducing fuel loads for fires (Sessions et al. 2004), and avoiding population increases of insect pests that might affect vital forests nearby (Wermelinger 2004; Kausrud et al. 2011). Particularly storm-affected trees, such as Norway spruce (*Picea abies*), are rapidly and rigorously salvage logged to limit increasing populations of bark beetles (Eriksson et al. 2005, 2008; Stadelmann et al. 2013, 2014). Salvage logging can be more intense (e.g., removing more trees) on the stand and landscape level than green logging (Schmiegelow et al. 2006). Even large and old trees that are otherwise not allowed to be harvested might be removed (Thrower 2005), such as large Siberian larch (*Larix sibirica*) trees in burned forests of Mongolia (Müller et al. 2013). Salvage logging typically focuses on removing the main trunks. This intervention reduces dead-wood amounts in disturbed forests to a small fraction of the amount initially generated by the natural disturbances, but due to the large amount of logging residuals, dead-wood amounts in salvage logged areas can exceed those of conventionally managed forests nearby (Priewasser et al. 2013; Thorn et al. 2014). Nevertheless, salvage logging—as well as conventional harvesting—often results in a reduction in the diversity of dead wood by altering diameter and decay distributions (Waldron et al. 2013). For instance, in salvage logging, logging operations and machinery can fragment individual dead-wood pieces from the pre-harvest period, particularly so in regions with highly mechanized harvesting (Bouget et al. 2012). This can ultimately result in an overall reduction in snag abundance and mean snag diameter (Russell et al. 2006).

18.3 The Loss of Dead-Wood Habitats: A Global Perspective

Globally, the history and current state of forest use differ strongly between regions, countries, and continents, and both determine how much forest remains and how dead-wood dynamics have been altered. We will highlight three examples of regions that differ in the history of dead-wood habitat loss, degree of biodiversity loss owing to reduced dead-wood availability, and extent of the focus on dead wood in current conservation strategies.

Example 1 European forests in temperate and boreal zones have experienced an extreme large-scale reduction in dead-wood amount. The history of forest use and clearance, particularly in temperate regions, is older than 5000 years (Grove 2002b); since the last glacial maximum, forest cover reached its smallest extent between 1750 and 1850 (Whitehouse 2006). The use of dead wood and leaf litter as source of fuel by local populations and the systematic removal of dying and dead trees by foresters as part of forest hygiene since the eighteenth century have dramatically reduced the amount and diversity of dead wood (Speight 1989; Siitonen 2001; Grove 2002b). Furthermore, the prevention of natural disturbances, e.g., fires, and salvage logging after disturbance, e.g., by the European spruce bark beetle *Ips typographus*, are common practices (Lindenmayer et al. 2004). Today, amounts of dead wood in boreal and temperate forests have been reduced to an average of ~13 m^3 ha^{-1} across all forest types (European Environment Agency 2015) and may even be lower (2–10 m^3 ha^{-1}) in managed forests (Siitonen 2001). Considering natural amounts of dead wood of 60–90 m^3 ha^{-1} in boreal European forests (Siitonen 2001) and a median of 157 m^3 ha^{-1} in temperate European old-growth forests (Burrascano et al. 2013), the remaining dead wood accounts for 10–20% of natural amounts. Moreover, since the late eighteenth century, indigenous broad-leaved tree species in temperate forests have been replaced by fast-growing conifers to increase timber yields (Grove 2002b), and thus, dead wood today is often dominated by non-indigenous tree species (Ulyshen et al. 2018, see Chap. 23). Current concepts of dead-wood management range from intentional creation of dead wood to promote biodiversity (Davies et al. 2007; Seibold et al. 2015a) to whole-tree harvest and stump removal as a source of fuel wood (Bouget et al. 2012).

Example 2 The history of stocks of dead wood has also been well studied in the rainforests of the North American Pacific Northwest (Harmon 2001). Forest exploitation in the region started during the late nineteenth century. Initially, only high-quality wood was harvested, and more than 65% of the living woody biomass was left as logging residues, including logs of up to 50 cm in diameter and stumps of 3–6 m in height (Gibbons 1918; Convey 1982). The amount of dead wood comprised by these logging residues equaled roughly that created by natural disturbances. Around 1930, the amount of logging residuals was reduced to about 10% of that previously left (Harmon 2001). Moreover, even pre-harvest dead wood was removed to avoid the spread of pest species and pathogens, decrease fuel loads for fires, and increase safety of forest workers; this practice led to <15% of the amounts of dead wood in natural forests (Harmon 2001). The negative effects that these practices had on biodiversity and ecosystem functions spurred a series of studies on dead-wood dynamics and the role of dead wood in the ecosystem (Maser and Trappe 1984; Harmon et al. 1986) and eventually led to the introduction of minimum standards for dead-wood amounts in managed forests. More recently, also active measures to provide dead wood, particularly snags, are increasingly applied (e.g., Arnett et al. 2010).

Example 3 The Hyrcanian Forest in Iran and Azerbaijan is one of the last extensive temperate primeval forest relicts. To protect this ancient forest, logging is prohibited by law, but the harvesting of dead or injured trees is allowed to provide resources for local markets, even though the mostly hollow and partly decayed trees harvested are of low economic value (Müller et al. 2016). This strategy has the consequence that large and old veteran trees, i.e., one of the ecologically most valuable structures and consequently the source of many other types of dead wood, are removed. Therefore, although these forests are considered protected, they face severe ecological degradation. Such management practices occur in similar forms in many regions, particularly in the tropics and subtropics (e.g., Ribot 1999; ASFMT 2002), where local communities are not allowed to harvest vital trees to maintain the forest but are allowed to collect dead wood and branches for domestic use or to produce charcoal. Such a form of exploitation in a program allegedly aiming at forest protection reduces the amount and diversity of dead wood and leads to ecological degradation.

18.4 The Importance of Dead-Wood Amounts for Biodiversity

In the following, we will discuss the relationship between dead-wood amount and biodiversity of saproxylic taxa. We will focus on information published in review articles to cope with the large body of literature originating from Europe and North America but will also include information from the few publications dealing with subtropical and tropical regions.

Grove (2002b) provided the first qualitative review of effects of "availability of mature timber habitat" on saproxylic insect diversity. The 15 publications considered—13 from Europe, 1 from Australia, and 1 from North America—reported a positive relationship between the amount of dead-wood habitat and saproxylic insect biodiversity, both of which were determined using various measures. Measures of habitat amount included the number of fungal fruit bodies, degree of habitat fragmentation, and distance to suitable habitat, which serves as a proxy for habitat amount on the landscape scale.

Müller and Bütler (2010) published the first quantitative review summarizing 37 minimum thresholds of dead-wood amount that are required to host a broad range of taxa in temperate and boreal European forests. Biodiversity data included occurrence of single species, species numbers, and species density. Thresholds peaked at 20–30 m^3 ha^{-1} (range: 10–70 m^3 ha^{-1}) in boreal coniferous forests, 30–40 m^3 ha^{-1} (range: 10–150 m^3 ha^{-1}) in temperate mixed-montane forests, and 30–50 m^3 ha^{-1} (range: 10–150 m^3 ha^{-1}) in temperate lowland forests. The authors suggested that these values can be used as target values for minimum dead-wood amounts in European forests, but they added two cautionary notes: (1) these amounts are unlikely sufficient for some species that require particularly high amounts, such as *Pytho kolwensis* Sahlberg and *Antrodiella citrinella* Niemelä and Ryvarden, and (2) reference forests in Europe might already be depleted of the most demanding species, and thus, these thresholds should be viewed as an underestimation. They further pointed out that due to the correlation between dead-wood amount and dead-wood diversity, it is impossible to identify the underlying mechanism without experimental manipulation.

Lassauce et al. (2011) conducted the first meta-analysis of 29 datasets reporting 46 independent correlations between dead-wood amount and species richness of saproxylic beetles and fungi in temperate and boreal European forests. Overall, species richness of beetles and fungi was significantly positively correlated with dead-wood amount, but the correlation was rather weak ($r = 0.31$). Correlations were significantly stronger in boreal forests than in temperate forests. When different types of dead wood were analyzed separately, the amount of logs and snags but not the amount of stumps was significantly correlated with species richness, and correlations with log volume were stronger than with snag volume. One possible explanation for the weak correlation strength given was the importance of other drivers, such as dead-wood diversity and the presence of certain microhabitats.

In a qualitative review, Bouget et al. (2012) focused on effects of fuel-wood harvesting on biodiversity in temperate and boreal European forests. They discussed how demands for forest-based bioenergy can reduce dead-wood amounts owing to increased logging pressure on natural-like forests and legacy trees; increased removal of logging residues, particularly of small diameter (slash); and increased stump harvesting. The majority of cited publications that evaluated the effects of these practices on biodiversity reported negative effects on saproxylic and non-saproxylic taxa.

A meta-analysis of Riffell et al. (2011) included 26 North American studies that experimentally added or removed dead wood and recorded the response of invertebrates, birds, mammals, amphibians, and reptiles (745 effect sizes). The authors found significant negative response ratios when they compared the effect of low and high amounts of dead wood on invertebrate biomass and bird abundance and diversity, i.e., the abundance, diversity, and biomass were higher on plots with higher amounts of dead wood. However, invertebrates were rarely identified at the species level, and thus, more refined analyses of saproxylic and non-saproxylic groups were not possible.

In the global meta-analysis of Seibold et al. (2015a), the effects of added dead wood on the biodiversity of a broad range of saproxylic and non-saproxylic taxa were evaluated. The analysis considered 39 datasets from North America, Europe, Australia, and the Caribbean that reported species numbers from control plots and plots to which dead wood was added experimentally (Fig. 18.2). The effects of added dead wood were consistently positive for saproxylic taxa (dominated by saproxylic beetles) and overall significantly positive for non-saproxylic taxa, although some negative effects were found, e.g., for epigeal arthropods and litter microbes.

The most recent global meta-analysis on this topic (Thorn et al. 2018) evaluated how salvage logging after natural disturbances affects species numbers and community composition of various saproxylic and non-saproxylic groups. The removal of dead wood led to a decreasing number of species of eight, mostly saproxylic species groups, including saproxylic beetles, and an increasing number of species of carabids, epigeal spiders, and land snails. Moreover, salvage logging altered the community composition of 7 of 17 species groups.

Given the global distribution of resources available to science, it might not be surprising that most of our knowledge about how the amount of dead wood affects biodiversity originates from Europe and North America and that studies of subtropical and tropical forests are rare. Moreover, scientists might have considered that forest loss in subtropical and tropical regions is a more important driver of biodiversity loss than the loss of dead-wood habitat because deforestation rates are high (Meyfroidt and Lambin 2011). However, it has recently been shown that habitat degradation in Amazonian rainforests has additive negative effects on biodiversity independent of habitat loss (Barlow et al. 2016). By contrast, forest area in Europe and North America has increased over the last century (Meyfroidt and Lambin 2011), and the loss of dead wood was recognized as a key driver of declining forest biodiversity more than 30 years ago (Maser and Trappe 1984; Harmon et al. 1986;

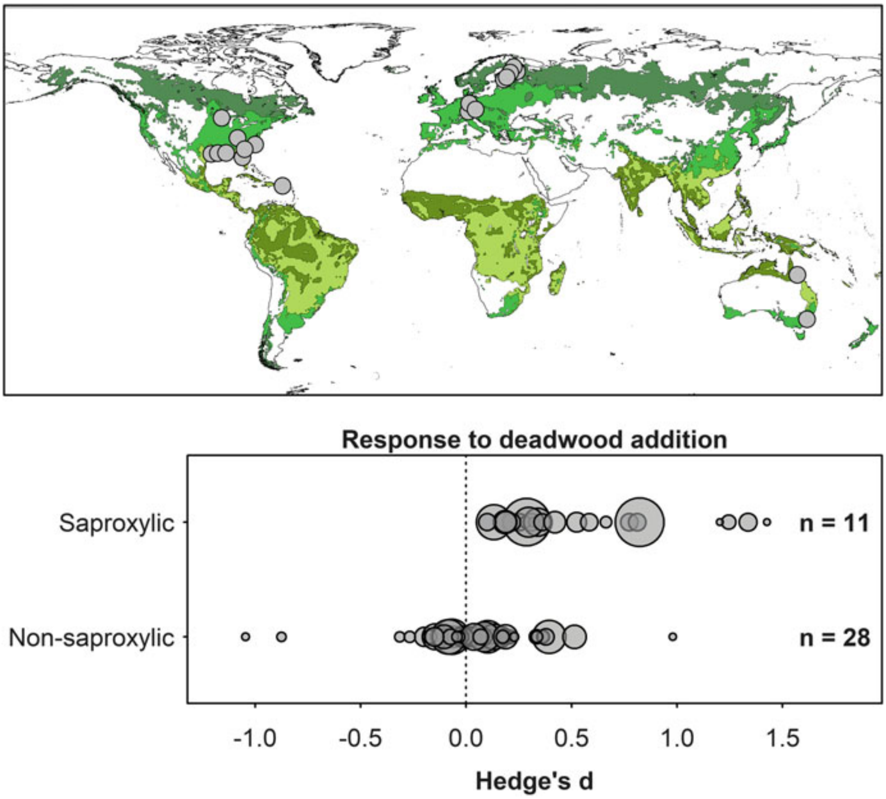


Fig. 18.2 Location of 15 experiments (gray circles on map) that tested effects of added dead wood on saproxylic and non-saproxylic taxa [modified after Seibold et al. (2015a)]. Positive values in the scatterplot indicate higher mean species richness on plots with added dead wood than on control plots; negative values indicate lower mean species richness on plots with added dead wood than on control plots. The positive effect of added dead wood was significant for both groups of taxa. Point size was scaled according to its weight in the meta-analysis. Several points were drawn from the same experiment if it comprised several species groups or years

Speight 1989). Nevertheless, a few studies from subtropical and tropical regions link dead-wood amount and biodiversity, with positive, neutral, or negative relationships. Grove (2002a) has shown that although overall differences in dead-wood amounts between old-growth and managed forests (logged and regrowth) in Queensland, Australia, are subtle, the amount of dead wood of large diameter is clearly higher in old-growth forests. The volume of dead wood of large diameter is the best predictor of saproxylic beetle richness, but the basal area of trees of large diameter is a better predictor of abundance, incidence, and assemblage composition. In Benin, a higher species richness of saproxylic beetles in natural forests compared to plantations can be attributed to higher amounts of dead wood, particularly new dead wood and dead wood of large diameter (Lachat et al. 2006). The experimental addition of dead wood positively affected saproxylic beetles in subtropical USA (Klepzig et al. 2012), but two other experiments conducted in subtropical forests of South Carolina, USA (Ulyshen and Hanula 2009), and Puerto Rico (Richardson et al. 2010; Schowalter et al. 2014) found no significant or mixed effects of added dead wood on arthropod communities. However, saproxylic and non-saproxylic species were mostly analyzed together in the latter studies, which might have obscured the effects of added dead wood on the potentially more sensitive saproxylic fauna.

Overall, the majority of studies have reported positive relationships between the amount of dead wood and the biodiversity of saproxylic taxa (Grove 2002b; Riffell et al. 2011; Lassauce et al. 2011; Seibold et al. 2015a), including saproxylic insects. Minimum thresholds of dead-wood amount have been identified for some regions (e.g., Müller and Bütler 2010). For non-saproxylic taxa, the relationship is more heterogeneous. Although positive effects of dead-wood amount on non-saproxylic taxa have regularly been reported, conservation strategies targeting saproxylic biodiversity need to carefully consider possible negative effects on nontarget species (Riffell et al. 2011; Bouget et al. 2012; Seibold et al. 2015a). The strength of the relationship between dead-wood amount and saproxylic biodiversity, however, seems to differ between biomes, with stronger relationships in boreal forests than in temperate forests (Lassauce et al. 2011) and with possibly the weakest relationships in subtropical and tropical forests (Ulyshen and Hanula 2009; Richardson et al. 2010; Schowalter et al. 2014). Global-scale studies are required to evaluate whether this is caused by a negative interaction between dead-wood amount and climate (Müller et al. 2015); other factors that differ between biomes, such as forest management history (Lassauce et al. 2011); or a combination of drivers. It has often been reported that correlations between dead-wood amount and richness of saproxylic species are weak, particularly in survey studies of heterogeneous mixtures of different types of dead wood (Lassauce et al. 2011). Since species richness differs among tree species, decay stages, and diameter classes (Stokland et al. 2012; Gossner et al. 2016), the power of dead-wood amount as a predictor of species richness might be limited if the abundance of different types of dead wood is not considered. Hottola et al. (2009) have developed a promising measure of dead-wood amount that accounts for the abundance of different types of dead wood, but it has rarely been applied.

To unravel complex interactions between dead-wood amount and other factors, studies have increasingly considered functional traits and phylogenies of saproxylic beetles. Information about, e.g., body size, feeding guild, and preferred dead-wood substrate of a species are combined to test the effects of ecosystem management on saproxylic insect communities. For instance, Gossner et al. (2013) have demonstrated that even near-to-nature forest management affects the functional composition of saproxylic beetle assemblages via changes in the amount of dead wood. They found that when the dead-wood amount increased, the assemblage composition shifted toward larger species and species preferring dead wood of large diameter and in advanced stages of decay. Moreover, the extinction risk of saproxylic beetles

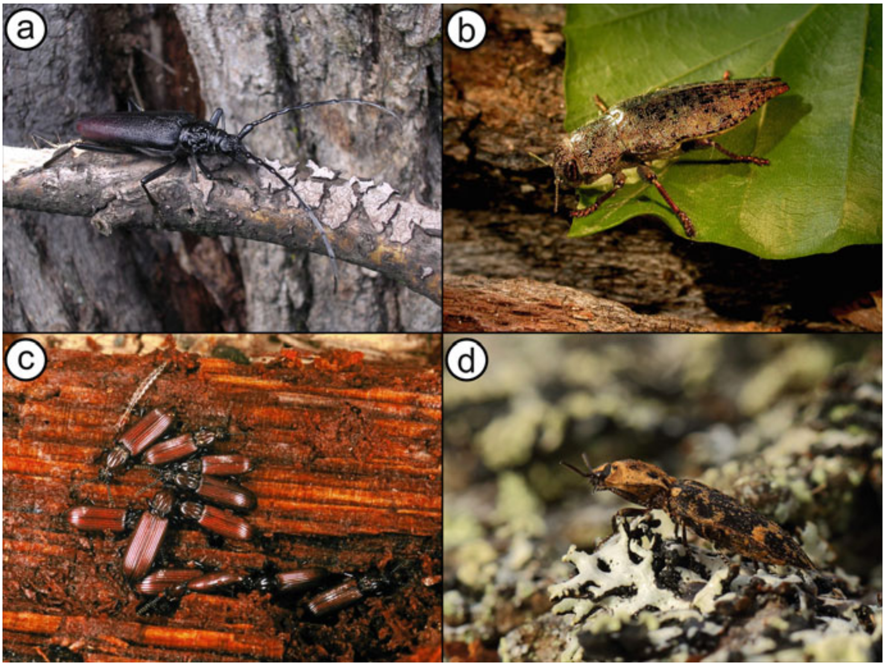


Fig. 18.3 Anthropogenic alteration of natural amounts of dead wood in forests has altered saproxylic diversity in various ways. (**a**) *Cerambyx cerdo* L. has been actively persecuted as a pest species by removing breeding trees. Today, this species is threatened and protected under the European Habitats Directive. (**b**) The loss of sun-exposed dead wood is a threat to sun specialists, such as *Dicerca berolinensis* (Herbst). (**c**) *Rhysodes sulcatus* (F.) has suffered from the drastic reduction in dead wood of large diameter in advanced decay stages. (**d**) A benign-neglect strategy toward natural disturbances has led to strongly increasing populations of *Danosoma fasciata* (L.), which had been considered regionally extinct. Photos: (**a**–**c**) H. Bussler and (**d**) S. Thorn

is strongly connected to species' traits; large species and species that prefer dead wood of large diameter and sun-exposed dead wood have a higher Red List status than others (Fig. 18.3a–c; Seibold et al. 2015b). Traits and phylogenies have also been used to study the effects of green-tree retention (Heikkala et al. 2016) or post-disturbance management on saproxylic insect communities. Post-storm salvage logging predominantly affects species associated with branches and sun-exposed tree parts (Thorn et al. 2014, 2016a). These results led to detailed guidelines for retention in the management of windthrows (Thorn et al. 2016b). While most studies so far have used traits of saproxylic insects measured at the species level, recent approaches considering traits measured at the individual level (i.e., considering intraspecific variation) can provide an additional mechanistic understanding of community responses to forest management (Bouget et al. 2015).

18.5 Interactions Between Dead-Wood Amount and Other Factors

Identifying the importance of dead-wood amount for biodiversity independent of the effects of correlated factors, such as dead-wood diversity, spatial connectivity, and forest continuity, can be challenging. Furthermore, the importance of dead-wood amount can vary along environmental gradients, such as temperature gradients. In the following, we will summarize attempts to disentangle effects of dead-wood amount and other correlated factors on the biodiversity of saproxylic beetles as well as the interaction between dead-wood amount and temperature.

18.5.1 Dead-Wood Diversity

Resource availability is typically correlated to habitat heterogeneity (Wright 1983; Whittaker 1998), as is dead-wood amount and dead-wood diversity (Okland et al. 1996; Similä et al. 2003; Müller and Bütler 2010; Bouget et al. 2013). Species richness of saproxylic species might thus increase with increasing amount of dead wood owing to an increasing resource availability that allows larger populations (*more-individuals hypothesis*) or owing to increasing habitat heterogeneity (*habitat-heterogeneity hypothesis*). Although effects of dead-wood amount on saproxylic communities have been studied more frequently than effects of dead-wood diversity, some of the reported effects of dead-wood amount might actually be attributed to dead-wood diversity due to the correlation of these two variables. Several field survey studies statistically disentangled the effects of dead-wood amount and dead-wood diversity using, e.g., partial correlation or partial least squares regression. These studies found that the number of saproxylic beetle species was better explained by dead-wood diversity than by dead-wood amount (Similä et al. 2003; Brin et al. 2009; Bouget et al. 2013). Moreover, dead-wood diversity is an important driver of the functional composition of saproxylic beetle communities (Janssen et al. 2017).

Experimental manipulation of dead wood is another way to disentangle effects of dead-wood amount and dead-wood diversity. Seibold et al. (2016) created independent gradients of dead-wood amount and dead-wood diversity by adding different amounts of dead wood to 190 experimental plots in southeastern Germany. Each plot received one, two, or four different types of dead wood (logs and branches of *Fagus sylvatica* L. and *Abies alba* Mill.), and saproxylic beetles were sampled using flight-interception and pitfall traps over 3 years. Dead-wood amount positively affected both abundance-corrected species richness (i.e., abundance served as a covariate and recorded species numbers as response; see also Gotelli and Colwell 2001) and species composition of saproxylic beetle assemblages but not abundance. Dead-wood diversity positively affected abundance, abundance-corrected species richness, and species composition. The effect of dead-wood diversity is in line with the *habitat-heterogeneity hypothesis*. But, as dead-wood amount affected abundance-corrected species richness and not abundance, its effect cannot be explained by the *more-individuals hypothesis*, which predicts increasing abundance with increasing resources. Instead, the authors suggest that the direct effect of dead-wood amount on species richness might be attributed to increasing habitat heterogeneity. Since temperature, wood density, water content, fungal colonization, and decay stage can vary on a fine scale within a single dead-wood object, particularly when of large size (Graham 1924; Saint-Germain and Drapeau 2011; Leather et al. 2014), habitat heterogeneity can increase with increasing number of dead-wood objects even if tree species and diameter are constant. This confirms previous non-experimental studies (Similä et al. 2003; Brin et al. 2009; Bouget et al. 2013) and suggests that habitat heterogeneity is a major driver of saproxylic beetle richness. It moreover suggests that both obvious differences between dead-wood objects and cryptic differences within objects contribute to dead-wood diversity. The successive analysis of abundance and abundance-corrected species richness might help to identify underlying mechanisms of species richness and should thus be adopted more frequently.

18.5.2 Forest Continuity

Forest stands that arise from reforestation after conversion to non-forest habitats often have a lower amount and diversity of dead wood than forest stands that have never been deforested (Nordén and Appelqvist 2001; Rolstad et al. 2002; Jonsson et al. 2005; Nordén et al. 2014), but also the opposite has been reported (Brin et al. 2016). This correlation makes it challenging, for example, to identify whether higher species richness in natural forests compared to human-affected forests can be attributed to higher amounts of dead wood (including the abundance of microhabitats related to large old trees) and higher diversity of dead wood, to forest continuity, or to an interaction of these factors. Siitonen and Saaristo (2000) recorded stand structural attributes and the presence of *Pytho kolwensis* (Coleoptera, Boridae) in old-growth forests with unbroken forest continuity in Finland. They found higher amounts of dead wood in stands where the species was present than in stands where the species was absent. A study conducted in the French Alps aimed at disentangling the effects of forest continuity (ancient vs. recent; reference date mid-nineteenth century) and stand maturity (mature vs. overmature) on diversity and functional composition of saproxylic beetle communities (Janssen et al. 2016, 2017). Stand maturity was strongly linked to differences in stand structural complexity, dead-wood amount and diversity, and tree-related microhabitat diversity. The authors found that beetle diversity, even of species with low dispersal ability, was only affected by stand maturity, while the functional composition was affected by an interacting effect of stand maturity and forest continuity. Both studies support the idea that the amount of dead wood is a dominant factor contributing to the importance of natural forests for biodiversity. However, in a study of recent forests with amounts and diversity of dead wood higher than in ancient forests, species number of common saproxylic beetle species was affected by both forest continuity and dead-wood amount, while rare species were only affected by dead-wood amount (Brin et al. 2016). Moreover, the significant interaction between forest continuity and dead-wood amount indicated that species numbers are significantly related to dead-wood amount in ancient forests but not in recent forests. The authors interpret this as a loss of relationship between assemblages and their environment due to dispersal limitation.

18.5.3 Spatial Connectivity

Decreasing spatial connectivity, characterized, for example, by increasing distance between two habitat patches, might limit the ability of dispersing individuals to reach suitable resources and thus have negative effects on populations. Spatial connectivity is, however, strongly linked to the amount of habitat present in a landscape, as the distance between patches increases with decreasing habitat amount (Fahrig 2003, 2013). One possible approach to disentangling the influence of habitat amount on biodiversity from that of connectivity is to select plots with different amounts of habitat, e.g., dead wood, in the landscapes surrounding the plots and to manipulate the patch size, e.g., by adding different amounts of dead wood to plots (Seibold et al. 2017). If connectivity has an effect independent of the total habitat amount (i.e., the total amount of dead wood within surrounding landscapes and on the plot), the slope of the relationship between patch size (i.e., dead wood added to the plots) and the number of species per plot should be steeper for plots with low amounts of dead wood in surrounding landscapes than for plots with high amounts of dead wood. Such a difference in slope is indicated by a significant interaction between patch size and the amount of dead wood surrounding the plots. In a study in a forested region in southeastern Germany, Seibold et al. (2017) found independent positive effects of patch size and the amount of dead wood surrounding the plots on the number of saproxylic beetle species. For all species and for several ecological subgroups that might differ in dispersal ability, the interaction between patch size and dead-wood amount surrounding the plots was not significant. This suggests that the total amount of dead wood available within a given landscape is the main driver of the number of saproxylic beetle species and that the spatial arrangement of dead wood, i.e., connectivity, plays no or only a minor role.

Indirect support for the lack of an island effect comes from the finding that numbers of saproxylic beetle species in recent and ancient forests are similar as long as local dead-wood resources are high (Janssen et al. 2016) and from studies that report low genetic differentiation among populations of saproxylic insects even over hundreds of kilometers (e.g., Ranius and Douwes 2002; Oleksa 2014; Drag et al. 2015). However, the dispersal ability of individuals of two saproxylic beetle species did not differ between forests of different sizes (i.e., a proxy for habitat amount) but was higher in isolated forests than in connected forests (Bouget et al.

2015). It remains to be tested whether connectivity plays a more important role when dead wood is not distributed within a forested region but is distributed within other landscape contexts, such as agricultural or urban regions, and whether its importance is mediated by temporal forest continuity (Nordén et al. 2014; Brin et al. 2016). Finally, some species have disappeared from most forests owing to anthropogenic habitat degradation, and these should be targets of specific conservation measures pursued within extant distributional ranges of the species (Seibold et al. 2017).

18.5.4 Temperature

Temperature is a crucial factor for ectothermic organisms, such as insects; it determines the distribution of species from the microhabitat scale within logs (Graham 1924) to global scales (Schowalter 2006). Effects of temperature on saproxylic insect communities can interact with effects of dead-wood amount. Metabolic and larval development rates increase with temperature, and thus, less dead wood or smaller dead-wood objects might be sufficient to allow larval development to complete in warmer climates. Therefore, species numbers are predicted to increase more strongly with dead-wood amount in cool climates than in warm climates (*temperature-dead-wood compensation hypothesis* (Müller et al. 2015)). The first support of this hypothesis comes from the meta-analysis of Lassauce et al. (2011), who found significantly stronger correlations between dead-wood amount and the numbers of saproxylic beetle species in boreal forests than in temperate forests of Europe. It was then further corroborated by an indicator species analysis in European beech forests (Lachat et al. 2012). The authors found many indicator species of warm forests with low and/or high amounts of dead wood, but indicators for cold beech forests were observed only in combination with high amounts of dead wood. Müller et al. (2015) then tested the hypothesis by analyzing flight-interception trap data from forests with differing amounts of dead wood distributed across a macroclimatic temperature gradient within European beech forests and from a topoclimatic gradient (north- versus south-facing slopes) within a region in Germany. In addition, they reared beetles from wood bundles exposed at different elevations and at north- and south-facing slopes. They found a significant interaction between dead-wood amount and temperature on both the macroclimatic and topoclimatic scale. More saproxylic beetles emerged from bundles at lower altitudes than at higher altitudes and from south-facing slopes than from north-facing slopes. Both results support the *temperature-dead-wood compensation hypothesis*. Insignificant effects of dead-wood amount on saproxylic insects in subtropical and tropical regions (Ulyshen and Hanula 2009; Richardson et al. 2010; Schowalter et al. 2014) might further support this hypothesis. However, positive relationships between dead-wood amount and the number saproxylic insects in other subtropical and tropical studies (Grove 2002a; Klepzig et al. 2012) call for an explicit test of this hypothesis along a global temperature gradient.

18.6 Effects of Natural Disturbances and Salvage Logging on Saproxylic Biodiversity

Positive effects of natural disturbances on forest biota, particularly saproxylic insects, strongly depend on disturbance-created dead wood and biological legacies. Naturally disturbed stands often represent sunny islands rich in dead wood in otherwise intensively managed forests. Hence, disturbed forest stands are of high value for many saproxylic insects (for a review of wind-disturbed forests, see Bouget and Duelli 2004). For instance, saproxylic beetles can be 30–500 times more abundant in windthrow areas than in adjacent intact forest, whereas species numbers are 2–4 times higher in windthrow areas than in intact forests (Wermelinger et al. 2002). Thus, natural disturbances, such as wildfires but also windstorms, have become an important tool to guide the restoration of managed forests toward more natural stages (Attiwill 1994; Angelstam 1998). For instance, prescribed fires have become an important tool for the restoration of intensively managed boreal forest in Finland. As a consequence, the species richness of red-listed or rare saproxylic beetles increased on burned sites (Hyvärinen et al. 2006), with a cascade effect on others species, e.g., woodpeckers (Nappi et al. 2010). Similarly, a benign-neglect strategy in the Bavarian Forest National Park, Germany, enabled an outbreak of the European spruce bark beetle (*Ips typographus* (L.)), resulting in a significant increase in biodiversity, including endangered saproxylic beetles species (Beudert et al. 2015), e.g., *Danosoma fasciata* (L.) (Fig. 18.3d).

Impacts of forest disturbances on biodiversity are closely connected to altered abiotic conditions, e.g., increased insolation, and to an increase in dead-wood amount and diversity (Swanson et al. 2011). Forest biota are commonly adapted to cope with natural disturbances, but multiple disturbances, such as salvage logging following natural disturbances, can push natural systems out of the range of natural variability (Lindenmayer et al. 2017). Not surprisingly, the extensive removal of dead-wood resources by post-disturbance salvage logging leads to a loss of species, depending on the resources. Thus, the combination of natural disturbances and logging often has a greater effect on insects dependent on dead wood than one disturbance alone. For instance, post-fire salvage-logged stands in Canada had a lower species richness of saproxylic beetles than undisturbed, burned, or logged stands (Cobb et al. 2011). These significant impacts can be linked to a decrease in quantity and quality of dead wood. Such changes in the composition of saproxylic beetle assemblages between salvage-logged and unlogged stands can be tracked for 20 years (Norvez et al. 2013). In summary, not only saproxylic beetles but likewise many species groups dependent on dead wood suffer from salvage logging in that it results in a general decrease in the number of saproxylic species [reviewed in Thorn et al. (2018)]. However, salvage logging impacts communities of saproxylic insects not only by removing dead wood but also by altering the dead-wood diversity. For instance, salvage logging in spruce-dominated mountain forests resulted in a loss of saproxylic beetle species that depend on sun-exposed small branches (Thorn et al. 2014). This was due to the deterioration of the logging residuals, which were rapidly overwhelmed by perennial grasses.

18.7 Conservation, Habitat Restoration, and Dead-Wood Enrichment

The first step required to maintain populations of saproxylic species is to reduce deforestation or more generally the loss of trees to maintain sources for dead-wood development. The second step is to maintain levels of dead-wood amount and diversity similar to ones in natural forests. Depending on the disturbance regime, this can include very high amounts produced by stand-replacing natural disturbances. It might not be possible to achieve such high amounts in forests where timber production is the primary goal; thus, protected areas that are spared from salvage and green logging, which interfere with natural ecosystem dynamics, must be established. However, since reserves will only cover a small fraction of the total forest area, production forests are crucial for the conservation of biodiversity (Franklin and Lindenmayer 2009) and thus should contain minimum amounts of dead wood needed to maintain a considerable portion of saproxylic species. Such minimum thresholds, as those identified for temperate and boreal forests of Europe (Müller and Bütler 2010), are a valuable starting point for an evidence-based conservation strategy. More studies are needed to provide similar information for other biomes. However, even if a range of threshold values are developed, they might not fully address the high natural variability in dead-wood amount, for example, in different successional stages (Harmon 2001).

Measures to maintain or increase dead-wood amount can be passive or active. Passive measures include the retention of senescent and dead trees, e.g., often referred as “habitat trees” or “keystone structures,” which are particularly important as they contain slowly developing microhabitats, such as cavities (Davies et al. 2007; Lindenmayer et al. 2012; Müller et al. 2014). Retention of dead wood should be also considered after natural disturbances, particularly in protected areas as pointed out above but to some degree also in production forests (Thorn et al. 2018). The main benefits from salvage logging—pest control and financial returns—that motivate managers can be marginal. Outbreaks of pest species affect only a few tree species, and the economic value of salvage-logged wood is often considerably lower than that of regularly logged timber due to wood of small diameter and damages caused by the disturbance (e.g., fire) or colonizing fungi and insects. Thus, the opportunity costs of retaining dead wood created by natural disturbances can be quite low, and retention might often be a cost-efficient alternative to other forms of dead-wood enrichment (see below). Retention of logging residuals in conventional production forests can also contribute to reaching minimum thresholds of dead-wood amount (Dörfler et al. 2017). However, it is crucial that not only branches of small diameter but also logging residues of large diameter are retained, such as complete tree crowns, including the upper part of the trunk or parts of the trunk that are of low economic value, e.g., due to stem rot (Fig. 18.1). Finally, green-tree retention (Lee et al. 2018; see Chap. 19) is another passive way to allow some trees to become senescent and to develop dead-wood habitats as long as some trees survive the change in environmental conditions caused by the harvest (Langor et al. 2006;

Gustafsson et al. 2010). Owing to increased mortality of retention trees during the first years after the harvest, these trees can also contribute considerably to the provision of dead wood (Heikkala et al. 2014).

Active measures to create or accelerate the development of dead wood are manifold. For instance, high stumps and snags are frequently created by topping trees in Fennoscandia and North America during regular harvesting operations or as a restoration measure (Brandeis et al. 2002; Jonsell et al. 2004; Walter and Maguire 2005; Abrahamsson et al. 2009). Standing dead trees can also be created by girdling, which leads to slow death (Shea et al. 2002; Komonen et al. 2014b), and downed dead wood can be created by cutting complete trees or removing only a part of the trunk of a harvested tree (Komonen et al. 2014b; Dörfler et al. 2017). Active measures also include injuring trees without killing them to initiate the formation of cavities and other microhabitats (e.g., Zapponi et al. 2015). However, saproxylic communities in man-made and natural substrates can differ (Shea et al. 2002; Komonen et al. 2014a), and thus, windthrows have been simulated using excavators or winches (Hekkala et al. 2016), and bark beetles that kill trees have been attracted with pheromones (Shea et al. 2002). Nevertheless, studies in which dead wood is added show that man-made dead wood positively affects saproxylic biodiversity (Seibold et al. 2015a), including red-listed species (Seibold et al. 2016). Therefore, active measures are a meaningful tool to complement passive measures, particularly when rates of natural dead-wood development are low, as in young even-aged stands (Bauhus et al. 2009; Roberge et al. 2015; Hekkala et al. 2016). The decision of which measure to use to create dead wood should consider which types of dead wood are less common than they would be naturally (e.g., dead wood of broad-leaved tree species in forests where conifers have been planted to replace natural broad-leaved species; Ranius et al. 2011; Seibold et al. 2015b).

The efficiency of dead-wood enrichment strategies can be further increased by considering interacting factors. The interaction between dead-wood amount and temperature indicates that more dead wood is needed in cool climates than in warm climates, e.g., more dead wood is needed at higher elevations or on north-facing slopes than in lowlands or on south-facing slopes (Müller et al. 2015). Dead-wood enrichment strategies should not only target specific dead-wood amounts but also high dead-wood diversity (Seibold et al. 2016). Dead-wood diversity can be directly increased, for example, by creating dead wood of locally less abundant tree species or of the full range of diameters of different parts of trees and by considering the full range of canopy openness. This allows managers of production forests who must deal with strong economic restrictions to reduce costs of dead-wood enrichment by providing a high diversity of dead wood while aiming at the lower boundaries of the proposed thresholds of dead-wood amount. In turn, managers whose primary goal is to promote biodiversity should aim at high amounts of dead wood, i.e., above the lower boundaries of the proposed thresholds of dead-wood amount, and high diversity of dead wood by, e.g., retaining or creating complete dying and dead trees.

Consideration of the spatial arrangement of dead-wood enrichment, i.e., selecting forest regions or stands where measures are to be conducted, is both labor and time intensive, requires information about the distribution of species, and restricts the area available for conservation. It should thus only be considered if there is clear evidence that the spatial arrangement of dead wood matters. First results for saproxylic beetles show that the number of species increases locally in proportion to the amount of added dead wood independent of the amount of dead wood already present within the surrounding landscape (Seibold et al. 2017). This indicates that forest managers should increase amounts of dead wood wherever and whenever possible, in landscapes with low or high amounts of dead wood. This would be a faster and less expensive means of reaching the minimum amount of dead wood needed to maintain viable populations of all extant saproxylic beetle species than a detailed spatial planning of conservation measures. Nevertheless, some species require a continuous supply of very high amounts of dead wood and are thus nowadays restricted to a few forest stands with sufficient habitat (Müller et al. 2005). To protect these demanding species, conservation measures must be applied within their extant distributional ranges to allow colonization.

18.8 Research Gaps

Basic limiting factors to all ecological studies are the lack of taxonomical knowledge needed to identify insects at the species level and the lack of information about their ecology needed to classify them as saproxylic or to assign them to trophic groups (Grove and Stork 1999, 2000; Langor et al. 2006). Taxonomic and basic work on the natural history of insects should therefore be supported as a basis for future studies, particularly in those regions underrepresented in the literature today. The vast majority of studies that investigated the contribution of dead-wood amount and diversity to the diversity of saproxylic insects have been conducted in boreal and temperate forests in Europe, North America, and Australia (Grove 2002b; Davies et al. 2007; Seibold et al. 2015a). As a consequence, most compilations and analyses are restricted to these regions and often to only one continent (Müller and Bütler 2010; Riffell et al. 2011; Lassauce et al. 2011; Bouget et al. 2012). The same is true for the effects of natural disturbances and salvage logging on saproxylic insects (Thorn et al. 2018). The interacting effect of temperature and dead-wood amount on saproxylic beetle diversity (Müller et al. 2015) indicates that the relationship between dead-wood amount and saproxylic biodiversity might differ between biomes. Although available knowledge from other biomes might help to reduce the loss of saproxylic biodiversity in subtropical and tropical regions, more studies have to be conducted in these regions to understand general ecological principles and to provide a sufficient basis for conservation. A better understanding of the relationship between dead-wood factors and biodiversity in subtropical and tropical regions is crucial so that conservation strategies in these regions no longer neglect the importance of dead wood and acknowledge that the removal of dead wood causes habitat degradation and biodiversity loss.

Habitat factors, such as dead-wood amount and diversity, habitat continuity, connectivity, disturbance-generated dead wood, and increased insolation simultaneously drive saproxylic communities. Experimental studies have proven successful in resolving these interacting effects and in providing implications for evidence-based and efficient conservation strategies. Trait-based and phylogenetic approaches are other promising ways to provide a better understanding of underlying mechanisms behind biodiversity patterns. However, the collection of trait information of diverse taxonomic groups, such as saproxylic beetles, is laborious and time consuming and might require access to taxonomic collections. We thus strongly encourage that traits be collected following standardized protocols (Moretti et al. 2017) and made publicly available alongside data from the literature (e.g., Bouget et al. 2008). Also, studies that investigate the potential effect of dead-wood amounts on social insects, such as termites and ants, are clearly lacking, despite the important roles of these taxa. From a conservation point of view, studies that investigate how an increase in dead-wood amount can be best implemented in common forest management via socioeconomic studies are lacking. Such studies are essential for providing information on dead-wood amount and diversity for existing and upcoming forest management plans, e.g., for artificially creating dead wood or implementing natural disturbances (Lindenmayer et al. 2010).

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Chapter 19
Conservation of Saproxylic Insect Diversity Under Variable Retention Harvesting

Seung-Il Lee, John R. Spence, and David W. Langor

Abstract Saproxylic (i.e., deadwood-associated) insects are important functional components of biological diversity in forest ecosystems; however, they depend on microhabitats associated with dying, dead, and decaying wood that are dramatically altered by industrial forestry. Habitat loss and fragmentation by activities, such as clear-cutting, salvage logging, and bioenergy extraction, threaten saproxylic biodiversity on forested landscapes through changes in quantity, quality, and dynamics of deadwood. Retention forestry has been proposed and widely applied to support conservation and recovery of biodiversity and the associated ecological function on managed landscapes. In spite of its short history, retention forestry has undoubtedly had positive effects on biodiversity compared to conventional clear-cut harvest. The amount and pattern of retention are two important factors that determine biotic and abiotic responses and thereby influence success of retention approach. We review major findings from several large-scale variable retention experiments that have considered impacts on saproxylic insects. General conclusions from these experiments include the following three points: (1) aggregated retention conserves saproxylic insect faunas better than dispersed retention; (2) mixes of aggregated and dispersed retention have greater conservation value for saproxylic beetles than a single retention type; and (3) inclusion of prescribed burning will improve the conservation performance of retention forestry approaches. Successful conservation of saproxylic insect populations will likely depend on management to ensure availability of a full range of deadwood quantities and qualities in harvested and regenerating forest stands. We argue that variable retention harvesting, which includes sufficient amounts of retained trees as combinations of aggregated and

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dispersed retention, will best support diversity of deadwood habitats in the harvested matrix and promote conservation and local recovery of saproxylic assemblages.

19.1 Ecosystem Roles of Saproxylic Insects

19.1.1 Definition of "Saproxylic" Insects

Saproxylic insects are those that depend on the phloem or wood of wounded, dying, or dead woody plants during some parts of their life cycle (Speight 1989; Alexander 2008; Langor et al. 2008; Stokland et al. 2012; Lee et al. 2014). However, the conceptual boundary between saproxylic and non-saproxylic species is somewhat vague. As deadwood is in direct contact with the forest floor in its later stages of decomposition, and eventually becomes part of the forest floor, many species that inhabit deadwood, particularly that in advanced stages of decay, also use the forest floor as a habitat. For instance, Ferro et al. (2012) showed that 30% of beetle species, including many that would undoubtedly be classified as saproxylic, occurred in both well-decayed angiosperm coarse woody debris (CWD) and leaf litter. Perhaps the most important criterion defining "saproxylic" is that populations of a species contribute significantly to ecological interactions within deadwood communities.

Saproxylic insects have received attention because they are undoubtedly sensitive to industrial forestry (Siitonen and Martikainen 1994; Stokland et al. 2012). Saproxylic species are abundant, are functionally and taxonomically diverse, include many economically important pests such as bark beetles, and provide important forest ecosystem services (Siitonen 2001; Langor et al. 2008; Stokland et al. 2012; Bouget et al. 2014). As significant elements in forest food webs, they can be assigned to the following feeding guilds (e.g., Klimaszewski et al. 2007; Dollin et al. 2008; Lee et al. 2015): detritivores (feeding on decomposing plant and animal tissues), mycetophages (feeding on fungi), myxomycophages (feeding on slime molds), omnivores (feeding on a variety of materials), phloeophages (feeding in phloem tissue), predators (feeding on live invertebrates), and xylophages (feeding on xylem tissue).

Saproxylic insect assemblages also serve as useful indicators of habitat change in forest ecosystems because of their taxonomic and trophic diversity and sensitivity to natural and human disturbances (Siitonen 2001; Langor et al. 2008; Hjältén et al. 2012) (Fig. 19.1). For example, saproxylic beetles (order Coleoptera) have been used as model organisms to test effects of forest management practices such as variable retention harvesting because they are functionally important and species-level analyses are possible (Jacobs et al. 2007a; Tikkanen et al. 2007; Lee et al. 2015; Heikkala et al. 2016a). Nonetheless, significant challenges remain in reliably sampling and identifying saproxylic insects, and these obstacles have undoubtedly deterred serious ecological work on the natural history of these species and their specific roles in forest ecosystems (Martikainen and Kouki 2003).

Fig. 19.1 Diverse saproxylic beetle species found in NW Alberta, Canada: (**a**) Tenebrionidae: *Upis ceramboides* (Linnaeus), (**b**) Cerambycidae: *Xylotrechus undulatus* (Say), (**c**) Cerambycidae: *Rhagium inquisitor* (Linnaeus), (**d**) Lycidae: *Dictyoptera aurora* (Herbst), (**e**) Trogossitidae: *Peltis fraterna* (Randall), and (**f**) Pythidae: *Pytho seidlitzi* Blair (Photo credits: Seung-Il Lee)

19.1.2 Importance of Deadwood and its Diversity

Deadwood, especially in the form of coarse woody debris (CWD), includes logs, snags, stumps, large branches, and decayed roots. The lower limit of CWD in published studies is varied from 2 to 10 cm, depending on researchers and research objectives (Harmon et al. 1986, 1999; Siitonen et al. 2000; Keller et al. 2004; Lee et al. 2015). However defined, CWD is an important functional component of nutrient dynamics and soil structure in forest ecosystems and also provides substrate and habitat for the saproxylic biota (Siitonen 2001; Grove 2002; Stokland et al. 2012). For example, CWD holds moisture, provides seedbeds for plant germination, slowly releases nutrients into the soil, reduces soil erosion, and serves as food, habitat, and shelter for many forest organisms (Harmon et al. 1986; Stevens 1997). Furthermore, the range of different decompositional stages of CWD promotes biodiversity by providing the variety of microhabitats required by a diverse range of forest arthropods (Esseen et al. 1997). Therefore, deadwood management is now widely accepted as an essential component for sustainable forest management (Franklin et al. 1987; Hagan and Grove 1999; Lindenmayer and Franklin 2002; Jacobs et al. 2007a; Hjältén et al. 2012).

CWD may be either standing or downed, and these structural types are not ecologically equivalent. Hammond et al. (2004), for example, found that boreal aspen (*Populus tremuloides* Michaux) snags and logs harbored quite different assemblages of saproxylic beetles in Alberta, Canada. Franc (2007) concluded that logs of European oaks (*Quercus* spp.) in Sweden supported more species of saproxylic beetles than did snags. Similarly, Ulyshen and Hanula (2009) concluded that logs of *Quercus nigra* L., *Pinus taeda* L., and *Liquidambar styraciflua* L. had generally higher species richness of saproxylic beetles than were found in snags in the mixedwood forests of South Carolina, USA. In contrast, Bouget et al. (2012b) found that saproxylic beetles in European oak had higher species richness and abundance in snags than in logs. However, species richness of red-listed saproxylic beetles was similar in logs and snags in boreal forests of Finland (Tikkanen et al. 2006). Thus, there is apparently no general pattern of difference among saproxylic assemblages of standing and fallen CWD, and explanation of local patterns must be rooted in local context.

We have come to understand that forest CWD is not a uniform entity. Different decay stages occur within a single piece of deadwood in the same stand, and each is characterized by different fungal associations and chemical/structural conditions, therefore presenting a variety of habitats for saproxylic invertebrates (Grove et al. 2011; Stokland et al. 2012). Thus, to facilitate study, various CWD decay classification systems have been proposed to accommodate different research objectives as well as to consider differences in decompositional characteristics of various tree species and types (Maser et al. 1979; Sollins 1982; Hofgaard 1993; Enrong et al. 2006; Lee et al. 2014; Kunttu et al. 2015). Decay classification systems vary from three to eight classes, and criteria are based on physical and biological characteristics of CWD, such as percentage of bark remaining, shape in cross section, and percentage of plant and moss covering (McCullough 1948; Fogel et al. 1973; Hofgaard 1993; Hale and Pastor 1998; Wood 2012; Lee et al. 2014). Some researchers have also used average depth of knife penetration to CWD in determining decay class together with other characteristics indicated above (Næsset 1999; Zielonka 2006; Sahlin and Ranius 2009).

19.1.3 Threats to Saproxylic Insects

Habitat degradation, fragmentation, and loss due to human activities, particularly forest management in some parts of the world, directly threaten biodiversity on forested landscapes (Hjältén et al. 2012), and only a small amount of the global forest estate is protected (Schmitt et al. 2009). Among forest biota, saproxylic organisms are widely thought to be more sensitive to deforestation than other groups of organisms (Siitonen and Martikainen 1994; Stokland et al. 2012). The reasoning is straightforward: these creatures depend on deadwood microhabitats and forest exploitation, and management leads to a significant decline of CWD quantities and changes in qualities (Grove 2002; Siitonen 2012). For example, in Finland, there are 814 threatened forest-dwelling species (IUCN categories: critically endangered, endangered, and vulnerable), and for 21% of these, lack of deadwood is thought to be the main cause of threat (Rassi et al. 2010). Siitonen (2012) identified four principal threat factors for saproxylic species: forest loss, forest management, intensifying land use, and biomass harvesting for energy. Since all types of forestry alter within-stand microclimates, destroy or alter deadwood in situ, and remove live trees from forest stands, thereby disrupting long-term supplies of deadwood, forestry practices clearly have detrimental effects on saproxylic biota (Grove and Stamm 2011; Jonsson and Siitonen 2012; Lee et al. 2015).

Significant losses in deadwood volume after harvest compared to natural disturbances such as wildfire cause abrupt changes in species composition of saproxylic insect assemblages (Hammond et al. 2017). Since most trees are removed from stands during clear-cut harvesting, harvested areas remain different in terms of amount and quality of deadwood for significant periods. In contrast, natural disturbances like wildfire leave most trees in place as injured stems or as standing, downed, or burnt deadwood (Jonsson 2000; Kouki et al. 2001; Gibb et al. 2005; Grove et al. 2009), leading to a post-disturbance surfeit of deadwood and different deadwood dynamics than after harvest. In addition, deadwood volumes are much lower in intensively managed forests than in natural forests throughout postharvest succession. This has been clearly associated with local extinction and serious decline in population size of saproxylic organisms in Fennoscandian countries where timber harvesting has a long history (Siitonen 2001; Similä et al. 2002; Gibb et al. 2005; Jonsson and Siitonen 2012). Conservation methods have been proposed to address such effects. For example, in Sweden, creation of man-made high stumps is becoming more popular in harvested areas for conservation of saproxylic organisms (Abrahamsson and Lindbladh 2006).

Insects respond to variation in deadwood, with different species using different kinds of deadwood, i.e., different decay stages, species, orientation, and diameters (Esseen et al. 1997; Tikkanen et al. 2006; Vanderwel et al. 2006; Wardlaw et al. 2009; Ulyshen and Hanula 2010; Ferro et al. 2012; Lee et al. 2014). Thus, forestry activities that affect these characteristics may also profoundly affect saproxylic assemblages. Furthermore, conventional clear-cut harvests, followed by establishment of even-aged regeneration or plantations, alter natural ranges of deadwood characteristics, homogenizing deadwood habitats in terms of microhabitats compared to preharvest conditions. This narrow range of deadwood characteristics benefits only a small cross section of the saproxylic fauna (Similä et al. 2003; Jonsson and Siitonen 2012; Hammond et al. 2017). For example, early and advanced decay stages of CWD are dramatically reduced after harvest, and Lee et al. (2015) reported that the CWD left at harvest was completely dried out and mostly unsuitable for saproxylic species after a decade. This leads to dramatic reductions of population size in early colonizing and late-successional saproxylic organisms or even to local extirpation (Hammond et al. 2017). These adverse effects are expected to be more severe in regions where exotic trees are planted for strictly economic purposes, because many native saproxylic species associated with specific local tree species may not colonize novel hosts (Jonsson and Siitonen 2012; Ulyshen et al. 2018).

Large-scale salvage logging after catastrophic natural disturbances, such as wildfires, storms, and insect outbreaks, also has negative ecological and biological impacts on forest stands (Lindenmayer et al. 2008). For example, Cobb et al. (2011) found that the effects of wildfire and logging on saproxylic beetles were synergistic, negatively affecting species richness and composition of beetle assemblages. Similarly, biomass harvesting for bioenergy production negatively affected biodiversity in deadwood because of reductions in deadwood volume (Grove 2002; Siitonen 2012). In a simulation study, Johansson et al. (2016) showed that increasing bioenergy extraction also increased landscape-level extinction risks for many saproxylic species, and this negative effect was stronger for rare than common species.

In short, all forestry activity that reduces quantity of CWD on significant scales, or alters its composition and characteristics, will cause changes in saproxylic invertebrates. Two fundamental questions facing those concerned about meeting the biodiversity criteria for sustainable forest management are as follows: (1) What harvest levels will conserve the saproxylic fauna? and (2) What conservation targets are appropriate for landscapes subject to industrial forestry? Around the globe, variable retention harvest is emerging as the strategy favored to meet economic and conservation objectives.

19.2 Retention Forestry

19.2.1 Definition and Goals of Retention Forestry

Retention forestry was initially proposed and applied commercially in the Pacific Northwest of the USA and Canada and has been subsequently developed as a new approach to conserve biodiversity on managed forest landscapes more widely in North and South America, Australia, and Fennoscandian countries (Franklin et al. 1997; Bunnell et al. 1999; Lindenmayer and Franklin 2002; Aubry et al. 2009; Gustafsson et al. 2010; Work et al. 2010; Baker 2011; Baker and Read 2011; Lencinas et al. 2011; Gustafsson et al. 2012). The general approach that we refer to as "retention forestry" in this chapter has been variously termed "variable retention," "green tree retention," "tree retention," and "retention harvesting" (Franklin et al. 1997; Spence 2001; Mitchell and Beese 2002; Aubry et al. 2009; Gustafsson et al. 2012; Lindenmayer et al. 2012; Pinzon et al. 2012; Simonsson et al. 2015). Although there may be subtle differences in emphasis, these terms all refer to the practice of leaving merchantable trees and associated microhabitats of preharvest stands, including deadwood, behind at harvest as legacy elements (Gustafsson et al. 2012).

Retention forestry aims strategically to retain a significant level of continuity in forest structure, composition, and complexity at harvest to maintain both biodiversity and ecological functions in an overall landscape context (Gustafsson et al. 2012; Lindenmayer et al. 2012). However, the retention forestry approach is meant to complement but not replace large permanent reserves. Thus, the planned retention is not necessarily expected to provide habitats for all species, but overall conservation still depends on a decent permanent reserve network (Lindenmayer et al. 2012; Lachat and Müller 2018). Those practicing retention forestry also frequently attempt to emulate natural disturbance patterns in harvest designs (see Sect. 19.2.2), hoping to conserve natural processes in fostering spatiotemporal heterogeneity in forests reminiscent of those shaped by natural disturbance regimes (Lindenmayer et al. 2012; Gustafsson et al. 2012).

The most important thing that distinguishes retention forestry from other harvesting approaches, such as uneven-aged selection management or even-aged shelterwood and seed tree systems, is that there is no plan to remove retained forest structures in future harvests (Spence 2001; Lindenmayer et al. 2012). This is intended to promote long-term continuity of forest structures and organisms. Unlike conventional forestry that has focused on timber production and rapid regeneration, retention forestry attempts to strike a balance between timber production and biodiversity conservation by moderating, at least to some extent, the most local impacts of harvest (Lindenmayer et al. 2012; Fedrowitz et al. 2014; Simonsson et al. 2015). Increasingly, in such silvicultural systems, emphasis is placed on promoting rapid faunal recovery (Pinzon et al. 2016; Bergeron et al. 2017) to supplement benefits of in situ preservation (Franklin et al. 1997; Baker et al. 2013).

19.2.2 Forest Management to Emulate Natural Disturbance Regimes

Although using natural disturbance regimes as models for forest management was proposed more than a century ago (Lindenmayer et al. 2012), broad popularity of the modern natural disturbance-based approach began with Hunter's (1993) seminal paper. This paper provided clear motivation for change centered on biodiversity conservation and natural disturbance emulation (NDE) as the principal guidance for improving forest management over conventional clear-cutting. NDE meshed nicely with the more explicitly stand-level strategy of conserving biological legacies at harvest, being developed by Franklin and his colleagues in the Pacific Northwest, by promoting a broader landscape context for harvest design and planning (Franklin et al. 1997; Lindenmayer and Franklin 2002).

The NDE approach to forest management is based on an understanding that forest organisms have evolved with natural disturbances and thus posits that forest biota and important ecosystem functions can be maintained by emulating natural disturbance regimes (Hunter 1993; Lindenmayer et al. 2012). Under this approach, patches of living trees, including microhabitats such as standing and downed deadwood, are retained on harvested landscapes specifically to leave legacy structures similar to those left by natural disturbances (e.g., unburned fire-skips) that promote recovery of biodiversity and ecosystem functions (Lindenmayer and Franklin 2002; Lindenmayer et al. 2012; Pinzon et al. 2012). The number and spatial patterns of residual trees are generally adjusted to accommodate specific management goals (Gustafsson et al. 2012; Fedrowitz et al. 2014). Furthermore, with evolution of the approach, a central element of the strategy is to incorporate a variable amount and pattern of retention among harvest blocks in an attempt to at least coarsely emulate variable patterns of natural disturbances such as wildfire (Work et al. 2003; Lee et al. 2015).

Despite the appeal of the NDE paradigm, there are significant differences between the natural disturbances that reset forest succession (e.g., wildfire, windthrow, and insect outbreaks) and forest management based on NDE. Natural disturbances leave (1) various sizes and shapes of disturbed and undisturbed areas, contributing to the structure of complex forest landscapes (Bergeron et al. 2002; Andison 2004); (2) huge amounts of deadwood in burned areas, insect outbreaks, or blowdowns (Hunter 1993); and (3) trees with various characteristics, including healthy living, damaged, dying, and dead, depending on the intensity of fire, insect attack, or wind events (Hunter 1999). Under the present NDE approach, however, harvest planners leave only relatively small numbers of live and dead trees in the harvested matrix, still a significant departure from “natural” (Hunter 1993).

Retention levels within stands vary among countries and forestry companies, ranging from 0 to 45% (Baker 2011; Gustafsson et al. 2012). In many countries, however, the average retention level is less than 10% of the preharvest timber volume (Gustafsson et al. 2012), which is rather poor emulation of the range of natural disturbance regimes. Therefore, the NDE approach to forest management likely does not retain all important processes and structures intrinsic to natural disturbances (Heikkala et al. 2016a). At present, we do not know how much this matters, and thus, relatively long-term experimental tests (see Sect. 19.3) of the basic NDE hypothesis are required to test our hypotheses about conservation of forest biodiversity (Pinzon et al. 2012). In spite of its short history, however, retention forestry has shown, without any doubt, positive effects on biodiversity compared to conventional clear-cut harvest, based on a meta-analysis (Fedrowitz et al. 2014).

19.2.3 Different Roles of Aggregated and Dispersed Retention

Residual trees may be retained in harvested areas as aggregations (patches) or as more or less singularly dispersed trees. Different conservation advantages seem to flow from the two ends of this spectrum of retention pattern. Aggregated retention, also known as clumped retention and group retention, refers to groups of live trees preserved at the time of harvest, usually with location and area/size predetermined (Franklin et al. 1997; Lindenmayer and Franklin 2002) (Fig. 19.2a). Aggregated retention patches of sufficient size contribute to long-term persistence of live trees, interior forest species, and microhabitats, such as undisturbed soils and understory plants (Franklin et al. 1997; Baker 2011; Pinzon et al. 2012) (Table 19.1). Aggregated retention can be strategically located to sites where conservation values are high, e.g., areas known to harbor rare or sensitive elements.

In contrast, dispersed retention refers to the pattern of leaving individual trees or small clumps consisting of several trees throughout a harvested area (Franklin et al. 1997) (Fig. 19.2b). It better maintains connectivity of belowground biota such as ectomycorrhizal fungi, ensures a future wide distribution of deadwood over a cut block when retained trees eventually die and fall over, and contributes to maintenance of forest aesthetics that appeal to public perception (Lindenmayer and Franklin 2002; Baker and Read 2011) (Table 19.1). However, dispersed retention generally fails to conserve interior forest species (Pinzon et al. 2012; Lee et al. 2017). For instance, Halaj et al. (2008) concluded that even 40% dispersed retention did not conserve forest-dependent invertebrate predators. Work et al. (2010) also demonstrated that higher levels of dispersed retention (i.e., >50%) than are economically feasible were required to preserve local beetle assemblages that represent late-successional stages.

Studies of relationships between sizes of aggregated retention patches and biodiversity have shown that relatively small patches ($\leq$1 ha) are generally insufficient to conserve whole assemblages of ground-dwelling (epigeic) invertebrates because of edge effects that penetrated into the center of patches (Matveinen-Huju et al. 2006; Aubry et al. 2009). In the mixedwood boreal forest of Western Canada, Pyper (2009) suggested that at least 2 ha coniferous and 3 ha deciduous forest patches were required for effective conservation of epigeic beetle assemblages, which included many species also associated with deadwood habitat. Several studies have concluded that even 3 ha patches were ineffective to conserve certain carabid beetles and spiders in coniferous forests (Halme and Niemelä 1993; Pearce et al. 2005). Although there have been few direct studies that assessed the value of patch retention for saproxylic insects, Lee et al. (2015) showed that retention of large spruce patches (>3.3 ha) alleviated negative edge effects and benefited saproxylic beetle assemblages. Understanding edge effects is key to determining the effective size and shape of aggregated retention patches. In fact, edge effects can extend as much as 1 km or

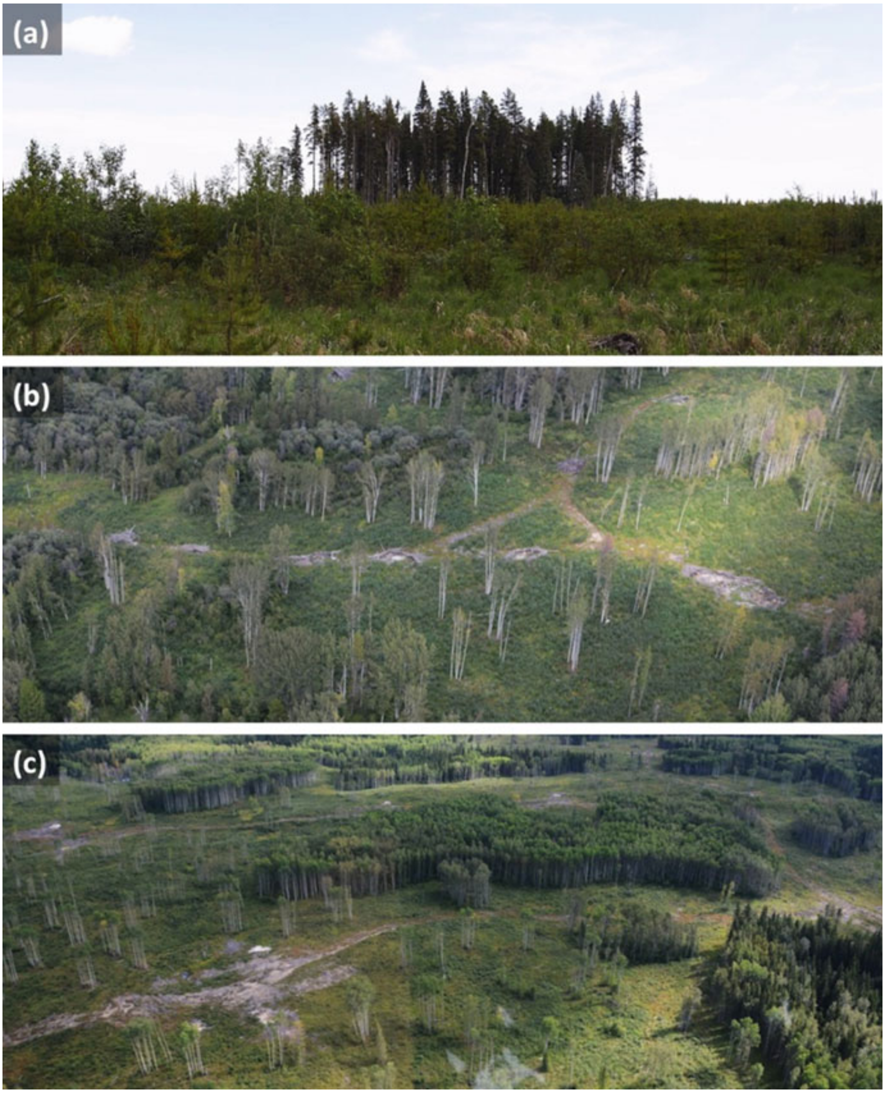

Fig. 19.2 Different types of retention in the boreal forest of Alberta, Canada: (**a**) aggregated retention, (**b**) dispersed retention, and (**c**) combination of aggregated and dispersed retention (Photo credits: Seung-Il Lee)

more into the forest if matrix characteristics are largely dissimilar to those of existing forests, e.g., forest-grassland edges (Laurance 2000; Ewers and Didham 2008). However, if the matrix consists of regenerating forests, edge effects are known to fade within 100 m into the forest, especially for invertebrates (Baker et al. 2007). Thus, determining minimum size of retention patches requires consideration of

Table 19.1 Summary of advantages and disadvantages of aggregated retention (AG) and dispersed retention (DP)

Advantages	AG	DP
Maintenance of overstory and multiple canopy levels	Yes	No
Maintenance of undisturbed soil and leaf litter	Yes	No
Maintenance of original microclimate conditions	Yes	No
Reduction in tree mortality	Yes	No
Conservation of original fauna and flora	Yes	No
Promotion in growth of seedlings	No	Yes
Aesthetics for public perceptions	No	Yes
Connectivity of belowground biota	No	Yes
Evenly distributed CWD as trees naturally fall down	No	Yes
Protection of surrounding aggregated retention	–	Yes

diverse factors, such as study organisms, matrix characteristics, and time since harvest.

Structural persistence of retention is also considered for determining how benefits vary with patch size and pattern of retained trees. It is known, for example, that dispersed retention is more susceptible to windthrow than is aggregated retention (Scott and Mitchell 2005). It is also known that small aggregated retention patches ($\leq$1 ha) are highly susceptible to windthrow in some forest types (Jönsson et al. 2007; Aubry et al. 2009; Urgenson et al. 2013). Windthrow risk, thus, factors into decisions to use aggregated over dispersed retention in some areas such as Vancouver Island, Canada (Baker 2011). Patches too small to persist until the time that regenerating forests start to provide deadwood habitats for harvest-sensitive species likely have little long-term conservation value (Heikkala et al. 2014). In addition to patch-level characteristics, tree-level properties seem to have major influence on retention tree dynamics as tree species and diameter affect mortality rates of retained trees (Hämäläinen et al. 2016). Such information can be used to guide retention practices, aiming to maximize conservation benefits in early-successional stages of the surrounding matrix (Hämäläinen et al. 2016).

In an effort to maximize positive effects of both aggregated and dispersed retentions on biodiversity in the face of uncertainty, some forestry companies are implementing a combination of both aggregated and dispersed retention practices (“mixed retention”) in an adaptive management framework (Fig. 19.2c). In Alberta, Canada, for example, Daishowa-Marubeni International Ltd. applies such a mix of retention tactics on all harvested areas of its Forest Management Agreement area (Daishowa-Marubeni International Ltd. 2013). In fact, balancing these tactics in an overall strategy appears to be the main approach to delivering so-called new or “green” forestry in Western Canada (Work et al. 2003).

19.3 Large-Scale Variable Retention Experiments and Saproxylic Insect Response

The recognized need for experimental tests of the effectiveness of variable retention for biodiversity conservation has led to the initiation of a number of such experiments around the world (Gustafsson et al. 2012). However, only a subset of these projects has considered impacts on saproxylic organisms and, in particular, covered highly diverse saproxylic assemblages at the species level. We review the results available to date about saproxylic insects from large-scale experiments in retention forestry.

19.3.1 Ecosystem Management Emulating Natural Disturbance (EMEND) Experiment, Canada

The Ecosystem Management Emulating Natural Disturbance (EMEND) experiment is located in the boreal forest of northwestern Alberta, Canada. EMEND is among the earliest and most extensive attempt to explore multiple effects of stand cover type, disturbance type, and tree retention level on a wide variety of forest response variables using a rigorous experimental design implemented on a modestly large industrially harvested landscape of about 1000 ha (see Spence et al. 1999; Work et al. 2010, and www.emendproject.org for details).

The EMEND design is fully factorial with eight treatments and three replications within each of four cover types (i.e., deciduous dominated, deciduous with spruce understory, mixed, and coniferous dominated), for a total of 96 experimental compartments. Harvest treatments include clear-cuts, four levels of retention harvest, and uncut "control" compartments (Fig. 19.3). Harvest treatments were applied during the winter of 1998–1999 to ca. 10 ha compartments in each cover type. The clear-cut treatments included ca. 2% dispersed retention, as is typical of this practice in western Canada. The experimental design called for retention prescriptions designed to leave 10%, 20%, 50%, and 75% of the original basal area as dispersed retention. The design also included two sizes of aggregated retention patches (ellipses of 0.20 ha and 0.46 ha) embedded in each 10 ha compartment and surrounded by different dispersed retention prescriptions (Fig. 19.3). Uncut "control" compartments were used to specify biodiversity recovery targets after harvest. Burn treatments are part of the overall design, but their implementation was delayed because weather was too dry for prescribed burns at the time that harvest treatments were delivered, and the limited data about saproxylic insects presently available from these treatments will not be discussed here (Fig. 19.3).

Research on invertebrate biodiversity on the EMEND landscape since 1999 has focused on a wide range of taxa, including both epigeic and more strictly saproxylic species. For epigeic carabid beetles (Work et al. 2010) and spiders (Pinzon et al. 2016), >50% dispersed retention was required to conserve species assemblage

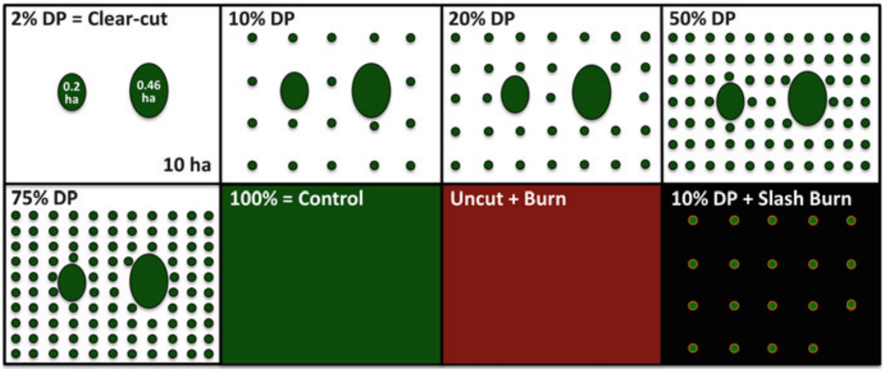

Fig. 19.3 A schematic diagram of the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment, showing six levels of harvest treatments (2%, 10%, 20%, 50%, 75%, 100%) and two levels of burn treatments. Each 10 ha harvesting treatment has two sizes (0.20 and 0.46 ha) of aggregated retention patches. Note that all treatments have been applied to four different forest cover types, representing successional chronosequence of boreal forests categorized as deciduous dominated, deciduous with spruce understory, mixed, and coniferous dominated stands. Abbreviation: *DP* dispersed retention

characteristics of unharvested forests based on 5-year and 10-year postharvest data, respectively. Negative impacts on biodiversity of both groups were relatively more severe in the late-successional coniferous forest, dominated by white spruce, *Picea glauca* (Moench) Voss, compared to the early-successional deciduous forest, dominated by trembling aspen and balsam poplar, *Populus balsamifera* L.

Initial studies about saproxylic insects at EMEND focused on responses of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) due to their economic importance. For example, Wesley (2002) studied parasitism of the spruce beetle, *Dendroctonus rufipennis* (Kirby), 1–2 years after harvest treatments. Although spruce beetle populations were greater in low levels of retention, there was no clear impact of harvesting treatments on percent parasitism. Park and Reid (2007) showed that abundance of the striped ambrosia beetle, *Trypodendron lineatum* (Olivier), increased with increasing numbers of live host trees and stumps.

Jacobs et al. (2007b) investigated whole saproxylic beetle assemblages 1–2 years after treatments in white spruce stands and found that mycetophages were the only group expressing sensitivity to low (10–20%) levels of dispersed retention. They concluded that quality and quantity of CWD were more important determinants in shaping initial structure of these boreal saproxylic beetle assemblages after harvest than were retention treatments.

Lee et al. (2017) studied combined effects of aggregated and dispersed retention on saproxylic beetle assemblages 10–11 years postharvest of white spruce. They found that small aggregated retention patches (0.46 ha or less) surrounded by clear-cut matrix were significantly impacted by blowdown and, as a result, did not conserve saproxylic beetle assemblages typical of unharvested forests. However, aggregated retention functioned well as a lifeboat for whole assemblages when embedded within 20% or higher levels of dispersed retention, especially for predatory species that were most sensitive to the absence of surrounding dispersed retention. They also found no clear benefit for any trophic group of increasing dispersed retention to 50% as compared to 20% (Lee et al. 2017).

19.3.2 Demonstration of Ecosystem Management Options (DEMO) Study, USA

The Demonstration of Ecosystem Management Options (DEMO) experiment was initiated in the mid-1990s in Western Oregon and Washington, USA. It explores the effects of the tree retention level and pattern on a range of forest response variables using a randomized complete block design. Specifically, DEMO addresses the effects of variable retention on aspects of the physical environment, hydrology, public perception, and also on various groups of forest organisms, such as arthropods, birds, small mammals, amphibians, mycorrhizal fungi, and vegetation in forests dominated by Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco (see Aubry et al. 1999, 2009; Halpern et al. 2005 and www.fs.fed.us/pnw/research/demo/).

The DEMO experiment includes six treatments, i.e., three levels of aggregated retention (15%, 40%, 75% of original basal area), two levels of dispersed retention (15%, 40% of basal area), and unharvested controls (Fig. 19.4). In addition, the clear-cut matrix surrounding aggregated patches has been used for many comparisons since a specific clear-cut treatment was not included in this experiment. Each treatment covers 13 ha area, replicated at six different locations. In blocks with 15% and 40% aggregated retention, two and five circular 1 ha aggregates were retained, respectively. In blocks with 75% aggregated retention, three circular 1 ha gaps were created (Aubry et al. 2009) (Fig. 19.4).

Most published research from the DEMO experiment has focused on the initial responses to harvest (1–7 years postharvest). Biological responses of taxa such as bryophytes, vascular plants, mycorrhizal fungi, epigeic arthropods, and small mammals were strongly affected by retention level, but in general these were not strongly affected by retention pattern (Aubry et al. 2009). Nonetheless, the results suggested that aggregated retention better preserved species characteristic of interior forests than did dispersed retention. In addition, 15% retention, regardless of pattern, was not enough to accommodate conservation of biodiversity, forest microclimates, or public perceptions. Thus, more than 15% retention is required to meet conservation goals in mixtures of both aggregated and dispersed retentions in these Douglas fir forests.

In the DEMO research most relevant to saproxylic insects, Halaj et al. (2009) used a subset of experimental treatments to test effects of aggregated and dispersed retention on bark-dwelling arthropods using crawl traps installed on 280 live trees and 260 snags 5–6 years after harvest. Interestingly, spiders and major groups of

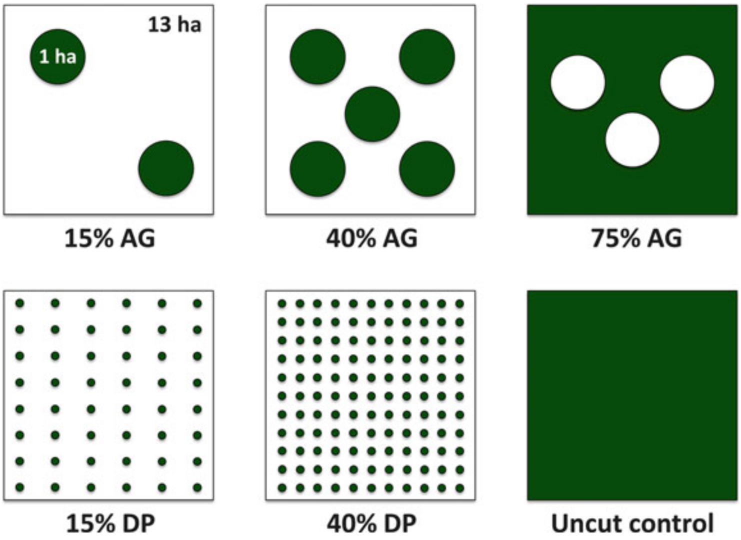

Fig. 19.4 A schematic diagram of the Demonstration of Ecosystem Management Options (DEMO) experiment, showing three levels of aggregated retention (AG: 15%, 40%, 75%), two levels of dispersed retention (DP: 15%, 40%), and unharvested control

insects, such as Coleoptera, Diptera, and Hymenoptera, showed increasing activity-density with a decreasing level of retention. However, there were no differences in activity-density between aggregated and dispersed retentions for most arthropod groups, except for the spider families Linyphiidae and Thomisidae.

19.3.3 Warra Silvicultural Systems Trial (Warra SST), Australia

The Warra Silvicultural Systems Trial (Warra SST) is located within the Warra Long-Term Ecological Research (Warra LTER) site in southern Tasmania, Australia. This trial was established in 1997 to test the effects of various silvicultural techniques on social acceptability, worker safety, economics, regeneration success, and biodiversity, such as plants, bryophytes, mammals, birds, fungi, and ground-active beetles in wet eucalypt, *Eucalyptus obliqua* L'Hér., forests (Hickey et al. 2006; Baker and Read 2011; Baker et al. 2009, 2017).

The Warra SST includes two replicates of each of eight treatments in one study area of 200 ha and includes several retention treatments. Treatments are as follows: (1) clear-fell, burn, and sow (CBS), (2) CBS with four understory islands (CBS+UI), (3) stripfell, (4) 10–15% dispersed retention, (5) 30% aggregated retention with small patches of 0.5–1.0 ha in size, (6) single-tree/small-group selection, (7) group selection, and (8) unharvested controls (Fig. 19.5).

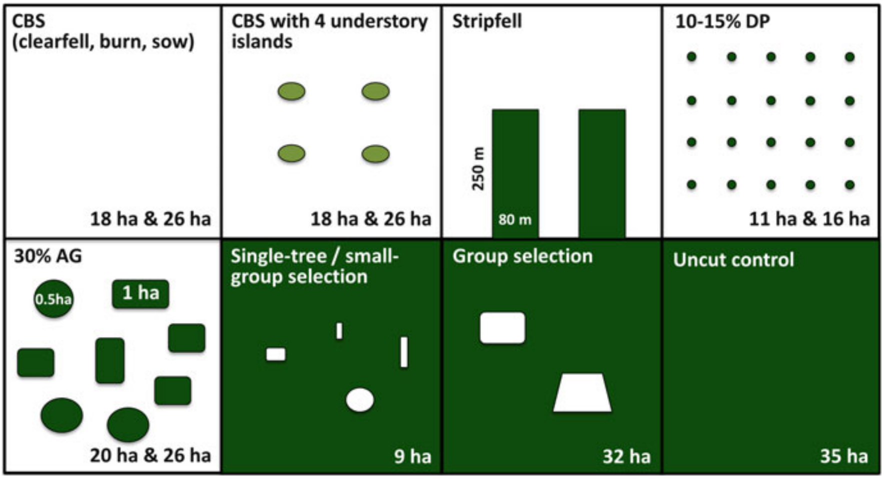

Fig. 19.5 A schematic diagram of the Warra Silvicultural Systems Trial (Warra SST), showing clear-fell, burn, and sow (CBS), CBS with four understory islands, stripfell, 10–15% dispersed retention (DP), 30% aggregated retention (AG) with small patches of 0.5–1.0 ha in size, single-tree/small-group selection, group selection, and unharvested controls. Note that the understory islands were embedded within the clear-fells, so they are not actually a separate treatment

Although published research from the Warra SST to date has focused on the first 3 years postharvest, it showed clear advantages of aggregated retention over dispersed retention for biodiversity of forest organisms, such as ground beetles, birds, vascular plants, bryophytes, lichens, and ectomycorrhizal fungi (Baker and Read 2011). For example, Baker et al. (2009) studied effects of CBS, CBS+UI, aggregated retention, and dispersed retention on ground-active beetles (i.e., Carabidae, Curculionidae, Leiodidae), many of which were appropriately considered as saproxylics. They concluded that aggregated retention best conserved these beetle assemblages that are similar to unharvested forests. Aggregated retention also had more hollow-bearing trees and snags that are important habitats for saproxylic organisms compared to dispersed retention (Baker and Read 2011). Although not strictly related to this silvicultural trial, the saproxylic beetle fauna of eucalypt logs has been extensively investigated in the Warra LTER site, highlighting the importance of large-diameter logs for biodiversity conservation (Grove and Forster 2011a, b).

19.3.4 Fire and Tree Retention Experiment (FIRE), Finland

The Fire and Tree Retention Experiment (FIRE) is located in eastern Finland. FIRE was initiated between 1999 and 2000 to understand the impacts of both fire and tree retentions on the biota of forests dominated by Scots pine, *Pinus sylvestris* L. (see Hyvärinen et al. 2005 and http://forest.uef.fi/~jkouki/project_fire.htm). The project has a two-way fully factorial design, following the before-after-control-impact (BACI) principle. The first factor of the experiment is the presence or absence of fire delivered as controlled burns at the end of June 2001. The second factor is the tree retention level after harvest in winter (2000–2001), including treatments of 0, 10, and 50 m^3/ha and unharvested controls (Fig. 19.6). In the retention level of 50 m^3/ha, 8–13 aggregates were retained, each group accommodating about 30 trees (den Herder et al. 2009). Retention levels of 10 m^3/ha and 50 m^3/ha are typical for Fennoscandia (see Gustafsson et al. 2012), corresponding to ca. 4% and 17% of the preharvest volumes, respectively. Each treatment combination was applied to a forest stand of 3–5 ha, a cutblock size typical for the region, and replicated three times over 24 sites (Fig. 19.6). To maintain statistical independence, most experimental units were separated by more than 1 km in a landscape that covered ca. 20 × 30 km.

The FIRE experiment has focused on both short-term (2–3 years posttreatment: Hyvärinen et al. 2005, 2006, 2009; Martikainen et al. 2006a, b; Heikkala et al. 2016b) and longer-term (10 years posttreatment: Heikkala et al. 2014, 2016a, 2017) responses of saproxylic organisms. Since half of the experimental sites contain prescribed burning treatments, to which pyrophilous organisms are attracted, the design offers possibilities to test simultaneously the effects of retention and (prescribed) fire. Hyvärinen et al. (2006) sampled beetles before and immediately after fire and retention treatments. They found that the number of individuals of red-listed and rare saproxylic (RRS) beetles dramatically increased in the burned sites. Also, controlled burning was the most important factor shaping different saproxylic beetle assemblages in comparison to unburned sites. In another study (Hyvärinen et al. 2009), species composition of saproxylic beetles strongly differed among years and

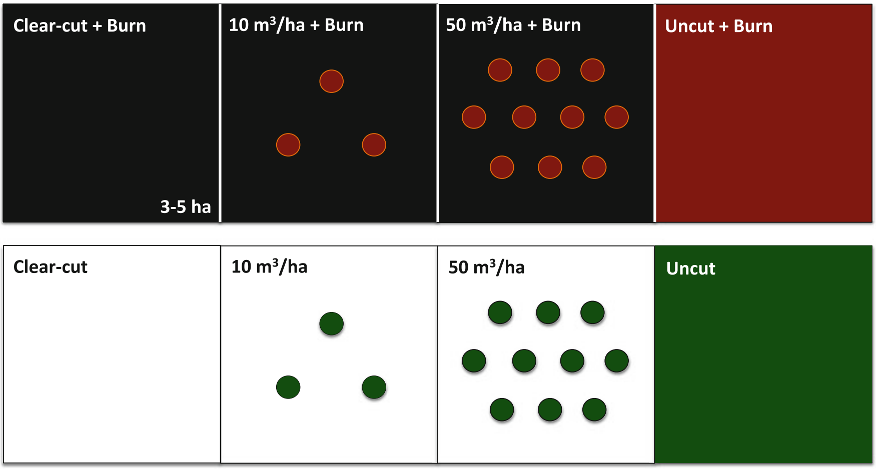

Fig. 19.6 A schematic diagram of the Fire and Tree Retention Experiment (FIRE). The first factor of the experiment is fire (controlled burning and no burning). The second factor is the tree retention level (0, 10, 50 m^3/ha and unharvested control)

between burned and unburned sites. It was also noted that the initial negative effects of burning on some non-saproxylic beetle groups were transient, and the authors concluded that both retention and fire benefited threatened saproxylic beetles.

Short-term effects on functional-phylogenetic diversity of saproxylic beetles were studied by Heikkala et al. (2016b). The results showed strong differences in functional characteristics of species assemblages among prescribed burning, tree retention, and clear-cut harvest treatments, suggesting the importance of both prescribed burning and retention forestry for conservation of saproxylic beetle assemblages.

The commonly held idea that retention harvests and burning will negatively affect harvested stands and adjacent forests by promoting population outbreaks of pest species has been also studied at FIRE. For example, Pitkänen et al. (2008) studied bark- and cambium-feeding pine weevils, *Hylobius* spp. (Coleoptera: Curculionidae: Molytinae), potential pests of pine seedlings, and found that they occurred commonly in both burned and retention sites. Interestingly, however, damage of pine seedlings caused by the weevils appeared to be lower when the retention level was high (50 m^3/ha). Additionally, Martikainen et al. (2006b) showed that the treatments did not affect the damage level on mature pines by two pine shoot beetles, *Tomicus piniperda* (L.) and *T. minor* (Hart.) (Coleoptera: Curculionidae: Scolytinae), the main local forest insect pests on Scots pine.

In a longer-term, decadal study at FIRE, Heikkala et al. (2014) showed that small amounts of retention led only to very short-term availability of fresh deadwood, and thus the harvest prescriptions employed likely have little immediate conservation value. Heikkala et al. (2016a) showed that effects of fire on beetles were dependent on retention level; however, none of the harvest and burn combinations could fully mimic effects of natural disturbances on saproxylic species assemblages. However, generally, small amounts of retention maintained more saproxylic species 10 years after harvest than did clear-cuts. The threatened pyrophilous flat bugs, *Aradus* spp. (Heteroptera: Aradidae), were completely dependent on fire, but the effect was transient (Heikkala et al. 2017). Thus, conservation of pyrophilous species will require a landscape-level approach because single harvested and burned stands provide only short-term refuges for such species. Overall, results from FIRE underscore the significance of retention trees for conservation of saproxylic invertebrates and have further shown that combining retention with prescribed burning is potentially effective in reducing negative impacts of forest harvest on the biota, including saproxylic insects.

19.4 Future of Retention Forestry and Saproxylic Insect Conservation

19.4.1 Mixes of Aggregated and Dispersed Retention

Although clear-cutting remains the most prevalent harvesting method for forests throughout the world, various silvicultural approaches such as variable retention are being promoted by scientific investigation as better alternatives for conservation of forest biodiversity (Franklin et al. 1997; Lindenmayer and Franklin 2002; Gustafsson et al. 2012; Fedrowitz et al. 2014; Baker et al. 2016). Among these alternatives, aggregated retention has been strongly advocated over dispersed retention as an effective way of maintaining biodiversity because it is thought to best maintain intact forest structures and associated microhabitats necessary to conserve a range of interior forest species (Franklin et al. 1997; Baker 2011), depending on the quantity and quality of the retention.

A general conclusion drawn from results about a variety of taxa in large-scale variable retention experiments is that low levels of dispersed retention are ineffective for ameliorating negative effects of forest harvest on native biodiversity (Aubry et al. 2009; Work et al. 2010). In fact, even 50% dispersed retention, a level that is unlikely to be economically viable, does not maintain even the epigeic arthropod species characteristic of interior forest habitats (Work et al. 2010; Pinzon et al. 2012). Dispersed retention of 75% may preserve some interior forest species in situ (Work et al. 2010; Pinzon et al. 2012); however, it is not practical or cost-efficient to retain so many uncut trees in most industrial harvests. There are few data about saproxylic taxa relevant to this matter, but what data are available suggest that low amounts of large tracts of dispersed retention will lead to losses of old-forest-associated species mainly because conservation of deadwood resources will be insufficient to meet conservation goals for saproxylic species.

Although the prevailing opinion is that dispersed retention alone does not conserve characteristics of interior forest and the species that depend upon them, dispersed retention is a practical component of modern “green forestry.” For example, Lee et al. (2017) showed that dispersed retention provided benefits for postharvest recovery of western Canadian boreal mixedwood landscapes that aggregated retention alone could not provide. Dispersed retention strengthens connectivity on harvest blocks between adjacent aggregated retention patches and surrounding intact forests (Lindenmayer and Franklin 2002), and belowground processes and organisms benefit from such connectivity (Franklin et al. 1997). Evenly dispersed live trees eventually die and supply standing and fallen deadwood continuously throughout harvest blocks, at least during the early phases of forest regeneration (Solarik et al. 2012; Heikkala et al. 2014), and such CWD will provide an array of decay classes and diverse habitats in the regenerating stands to help biodiversity recover following harvest. These are important features of dispersed retention, missing from conventional clear-cut harvests. Moreover, dispersed retention can play a pivotal role in providing windbreaks that minimize blowdown of aggregated retention at least 10 years postharvest (Lee et al. 2017).

Fortunately, dispersed retention can be applied together with aggregated retention to maximize conservation impact as the combination is likely to provide diverse “habitat value” for forest biota (e.g., Pinzon et al. 2012; Hämäläinen et al. 2016; Lee et al. 2017). In fact, many forestry companies have recently implemented this combined approach to enhance biodiversity conservation (Baker 2011). Despite the emerging practice of combining aggregated and dispersed retention on harvested blocks, only a few studies have tested the hypothesis that combinations of dispersed and aggregated retention promote superior conservation results, e.g., for birds (Lencinas et al. 2009), understory plants (Lencinas et al. 2011), spiders (Pinzon et al. 2012), and saproxylic beetles (Lee et al. 2017). Based on published work known to us, only the EMEND project has experimentally tested the conservation value for saproxylic organisms of combining dispersed and aggregated retention; however, the limited size of retained patches at EMEND (i.e., 0.20 and 0.46 ha) is likely too small to fully evaluate these effects and to provide a firm basis for recommending harvest prescriptions. Thus, additional field experiments on the surrounding operational landscape are needed to test the combined effects of aggregated and dispersed retention using larger patch sizes. Given the clearly demonstrated and functionally significant adverse effects of forestry practices on biodiversity of saproxylic organisms, such work should receive high priority.

19.4.2 Importance of Deadwood for Conservation of Saproxylic Insects

As presently understood, the greatest threat to saproxylic insects is the combination of forestry practices that result in habitat loss and fragmentation of forested landscapes (Stokland et al. 2012). Because many of the Earth's original forests are subjected to harvesting cycles to meet continued human demand for wood fiber, local biotas dependent on forested habitats will be affected, and many species will suffer some level of extirpation. Clearly, the biodiversity of saproxylic species in wide areas of Northern Europe has dramatically decreased coincident with a long history of extensive fiber extraction (Siitonen 2001; Djupström et al. 2008; Stokland et al. 2012). In the European work to date, efforts to retain deadwood by leaving logs and snags in harvested areas and the practice of creating high stumps and snags have contributed to conservation of saproxylic biodiversity (Siitonen 2001; Jonsson et al. 2005; Franc 2007; Jonsell et al. 2007; Stokland et al. 2012; Bouget et al. 2014).

Managing deadwood effectively to conserve the rich saproxylic insect assemblages of natural forests will require maintenance of the full range of sizes and decompositional stages of deadwood (Similä et al. 2003; Langor et al. 2008; Ferro et al. 2012; Wood 2012; Lee et al. 2014). However, this aspect of deadwood management, in conjunction with its associated value for biodiversity conservation, is difficult to achieve through traditional forestry practices. Thus, success in saproxylic insect conservation will likely depend on how well we are able to manage and maintain the range of deadwood quantity and quality in the harvested matrix. Well-informed application of variable retention that deploys dispersed and aggregated retention together shows the best present promise of supporting diversity of deadwood habitats on harvest blocks to promote conservation and recovery of local saproxylic assemblages. In addition, the use of large permanent reserves effectively connected to blocks harvested under variable retention provides a promising avenue to maintain overall biodiversity (Lindenmayer et al. 2012).

19.5 Final Thoughts and Future Research

Research about the trade-offs inherent in retention forestry is becoming increasingly important. Most results published to date about this new conservation-oriented approach to forest management have focused on short-term responses of forest organisms; however, future research is likely to reveal significant and interesting medium- to long-term findings as the quality of harvested areas changes (see Heikkala et al. 2014, 2016a; Baker et al. 2015; Pinzon et al. 2016). Among important issues related to biodiversity conservation, we suggest that future work can contribute significantly to improved forest management through focus on the following nine areas related to variable retention:

1. Publication of modern faunistic information about saproxylic organisms for regions significantly affected by forestry, including effective and well-illustrated keys. This provides baseline information and diagnostic tools that will encourage increased interest and enable research on this diverse fauna (Langor et al. 2008).
2. Testing the combined effects of aggregated and dispersed retention, particularly on large operational landscapes, since combinations of these two tactics appear to be beneficial in an overall strategy for biodiversity conservation in forest management (Lencinas et al. 2011; Lee et al. 2017).
3. Defining an operationally effective range of retention levels and patch sizes in specific forest types that will satisfy the needs of species characteristic of interior habitats, concentrating on patches larger than 1 ha, through applications of systematic experimental designs (Aubry et al. 2009; Lee et al. 2015).
4. Further investigations of variation in deadwood quality among different sizes of retention patches in relation to maintenance and recovery of interior forest species, especially those dependent on CWD in later stages of decomposition (Heikkala et al. 2014; Lee et al. 2014, 2015).
5. Long-term studies of edge effects and forest influences on biodiversity over a range of retention forestry treatments (Baker et al. 2013, 2015).
6. Exploring variable retention options in forests targeted for bioenergy production and defining effective conservation objectives, especially for saproxylic species (Bouget et al. 2012a).
7. Examining long-term effects of planned CWD creation, including man-made high stumps, on harvested landscapes to test effects on the persistence of saproxylic organisms. Although this is an area of intense investigation in northern Europe (e.g., Abrahamsson and Lindbladh 2006; Hjältén et al. 2010), such tactics remain relatively unexplored elsewhere in the world.
8. Exploring the effects of linking local retention together with large reserves to conserve regional biodiversity in a landscape perspective (Lindenmayer et al. 2012; Heikkala et al. 2017).
9. Determining potentially unique contributions of various natural disturbances (e.g., fire and windstorm) to maintenance of biodiversity and developing management approaches that emulate those that are important (Hyvärinen et al. 2005; Heikkala et al. 2016b).

We underscore the importance of the first point. Only in Europe it is likely that taxonomic and natural history resources are sufficient to support the sort of work that is badly needed to conserve saproxylic biotas (Siitonen 2001). Despite clearly established threats from anthropogenic forces, this faunal element is poorly studied elsewhere because work at the species level, as required for rigorous biodiversity focus, remains formidable. As with all living organisms, conservation of the saproxylic biota depends on understanding its elements and their diversity.

Many researchers have argued that there is no single "best" approach to retention forestry that can be universally applied for satisfying all forest biota (e.g., Serrouya and D'Eon 2004). In fact, this is the raison d'être for variable retention strategies. The fundamental idea of variable retention is to leave postharvest landscapes with variation among resulting stands that is closer to that left by natural disturbances than is a patchwork of clear-cuts. Clearly, conservation of all species or maintenance of high species diversity in *all* sites cannot be the main purpose of retention forestry. Instead, retention forestry aims to support recovery and continuity of the heterogeneity characterizing the original forest structure and composition that maintains native biodiversity and ecological functions on larger forest landscapes (Lindenmayer et al. 2012).

The variable retention approach flows from a particular environmental ethic or value system. It is rooted in the concept that conservation of forest biodiversity is properly focused on maintenance of the original forest species that are most threatened by anthropogenic disturbance (Diamond 1976) and *not* on maximizing biodiversity. Early-successional and less-sensitive species can be easily conserved as a natural result of efforts to preserve large forest patches or to introduce combinations of retention and prescribed fire, because many of these species prosper in either whole small patches or at the edges of large patches (Swanson et al. 2011; Lee et al. 2015; Heikkala et al. 2016b). However, late-successional and sensitive saproxylic species that depend on diverse deadwood habitats found in forest interiors may not maintain their populations in small patches where negative edge effects compromise the value of the whole area as habitat (Lee et al. 2015). Under a variable retention approach, the appropriate biodiversity targets are taken to be the structure and composition of preharvest communities. Of course, under climate change, history may be a less useful guide for setting targets, underscoring the purpose of variation and continued study of biotic response. We cannot count on simple emulation of the past to conserve sensitive species into the future. We must seek to understand the processes that generate and maintain saproxylic assemblages so that we may work and evaluate conservation efforts within these constraints.

In summary, we favor forest management ground rules that include leaving unharvested patches of aggregated retention mixed with areas harvested with dispersed retention on landscapes that also include large protected reserves with features of old-growth forests. We argue that this is critical for conservation of saproxylic insects and likely for the forest biota as a whole. Strict emulation of the size distribution left by historical fires is likely less important in achieving both biodiversity and fiber goals than is leaving patches large enough to maintain local populations of deep forest saproxylic species (Lee et al. 2015). With continued study of the resulting landscapes, we can move closer to a goal of explicitly understanding trade-offs that must be managed to develop retention forestry that satisfies both our economic need for timber production and fiber extraction and our ecological and ethical focus on conservation of biodiversity on a changing planet.

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Chapter 20
Saproxylic Insects and Fire

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Abstract Fire plays a prominent role in many biomes, but the natural fire regime has been influenced by silvicultural management, changes in land use, climate changes, and fire suppression. Fire clearly induces profound changes in both habitat characteristics and assemblages of saproxylic insects. However, our current understanding on this is strongly biased toward coniferous boreal and temperate systems and specific taxonomic groups, e.g., beetles, whereas the information from other biomes and saproxylic groups is limited at best. Knowledge from coniferous boreal and temporal systems might not be applicable in other biomes; therefore, studies in those areas should have high priority. Although natural fire regimes vary among ecosystems, saproxylic insects adapted to fire, both with respect to physiology and behavior, can be found in many different ecosystems. Changes in fire regimes can therefore have strong effects on saproxylic species, especially specialist pyrophilous species. For example, disruption of fire regimes in the boreal region, due to silvicultural management, changes in land use, and fire suppression, is a serious threat to saproxylic species, and restoring natural fire regimes is of the essence. Fire has been used as an active management tool to benefit saproxylic species in Fennoscandia. However, the effects of fire on saproxylic species are rather short-lived which should be considered in landscape planning. It has also been suggested that some fire-adapted species must be able to maintain viable populations in the unburned forest matrix if it is of sufficient quality. Thus, our ability to maintain viable populations of pyrophilous and fire-favored saproxylic species might depend on the sum of all conservation efforts on the landscape level rather than fire restoration efforts alone.

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20.1 Geographical Distribution of Fires

Fire occurs with varying frequency and intensity in most terrestrial biomes, with major exceptions in barren cold and/or arid ecosystems. Determinants of fire include availability and quality of fuels, climate, and human influence (Krawchuk et al. 2009; Archibald et al. 2013). Bradstock (2010) conceptualized the interplay of fire-regulating factors as a set of "switches": (1) Enough biomass fuel must be produced, (2) the fuels must be in a combustible state, (3) weather conditions must be favorable for ignition and fire spread, and (4) there must be sources of ignition. The degree to which each of these switches constrain fires varies across ecosystems, creating a global mosaic of different fire regimes. The relationships among regulating factors are complex, including feedback loops (Bowman et al. 2014), but result in reoccurring patterns. In analogy with the biome concept, Archibald et al. (2013) used satellite data and correlations among fire traits (fire return intervals, fire intensities, fire sizes) to classify fire regimes into five different "pyromes" (Table 20.1). Four of these pyromes (frequent-intense-large, FIL; frequent-cool-small, FCS; rare-intense-large, RIL; rare-cool-small, FCS) are representative of more or less "natural" fire regimes, whereas the remaining category (intermediate-cool-small, ICS) seems to be tightly coupled to humans (prescribed burnings, slash-and-burn agriculture/silviculture, etc.).

Several authors (e.g., Krawchuk and Moritz 2011; Pausas and Ribeiro 2013) describe a hump-shaped relationship between ecosystem productivity and fire. Fires tend to be most frequent in ecosystems with intermediate to high productivity but decrease in frequency toward both extremes of the productivity gradient. In unproductive systems, fires tend to be fuel limited, whereas high productivity is associated with wet climates making fuels less combustible (Bradstock 2010; Pausas and Ribeiro 2013; Krawchuk and Moritz 2011). High fire frequencies often coincide with distinct wet and dry seasons. Fuel loads build up during the wet season, and with the arrival of the dry season, fuels dry out and the probability of fire increases. Along similar lines, fire frequencies are raised by strong interannual variation in precipitation (e.g., effects of the El Niño-Southern Oscillation). The length of the "fire season" is also important, and we can observe an apparent trend of increasing fire return intervals (longer time between fires) with decreasing fire season length (Archibald et al. 2013).

Fire regimes vary among biomes, but there is not a one-to-one correspondence between biomes and pyromes. Individual pyromes are, however, distinctly more common in certain biomes (Table 20.1). Among the terrestrial biomes containing significant proportions of woody vegetation (and potentially saproxylic insects), there are sharp contrasts between fire-prone savanna/shrubland ecosystems (fire return intervals of a few years) and more infrequently burned forest ecosystems across the world (fire return intervals on scale of several decades). There are also distinct differences among forest biomes. In tropical broad-leaved forests, the majority of fires are of human origin (ICS pyrome). In contrast, Mediterranean forests and tropical coniferous forests show more frequent fire activity (estimated

Table 20.1 Dominant pyromes, occupying at least 20% of a biome, and a number of journal articles relating to fire effects on saproxylic hexapods across terrestrial biomes containing vegetation with trees and/or shrubs (excluding mangroves, because they do not burn). Pyromes occupying more than 50% of a biome are indicated by a bold capital X. Pyromes are delineated according to fire return interval (frequent, intermediate, rare), fire radiative power (intense, cool), and fire size (large, small). Pyrome definitions and data are from Archibald et al. (2013). Journal articles published between the years 1945 and 2017 were retrieved using Web of Science (see Sect. 20.2 for details). All studies with a focus on fire effects on insects/hexapods and where saproxylic taxa could be identified among the studied organisms were included. The studies are classified as manipulative (field and/or laboratory experiments) or observational and whether they explicitly classify studied taxa as saproxylic (expl. saproxylic). A few papers includes results from both manipulative and observational approaches. Some studies include two or more taxonomic groups

	Xeric	TrMoist	TrDry	TrConif	TempBrMix	TempConif	Boreal	TrSavi	TempSav	FlSav	Montane	MedFor	Total
Pyromes													
Frequent-intense-large (FIL)[a]								x		x			
Frequent-cool-small (FCS)[b]			x					x					
Rare-intense-large (RIL)[c]	x					x	x		x			x	
Rare-cool-small (RCS)[d]	x	x			x	x	x		x		x	x	
Intermediate-cool-small (ICS)[e]	x	**X**	**X**	**X**	x	x		x	x	x	x	x	
Taxa													
Collembola	0	0	0	0	0	0	2	0	0	0	0	0	2
Coleoptera	0	1	0	1	8	43	46	0	0	0	0	12	111
Diptera	0	0	0	0	7	6	3	0	0	0	0	1[f]	17
Hemiptera	0	0	0	0	0	5	7	0	0	0	0	1	12
Hymenoptera	0	4	0	0	8	11	6	12	2	0	0	7	60
Isoptera	0	2	1	0	1	2	NA	3	0	0	0	2	11
Neuroptera	0	0	0	0	0	3	0	0	0	0	0	1[f]	4

(continued)

Table 20.1 (continued)

	Xeric	TrMoist	TrDry	TrConif	TempBrMix	TempConif	Boreal	TrSavi	TempSav	FlSav	Montane	MedFor	Total
Psocoptera	0	0	0	0	0	0	1	0	0	0	0	0	1
Thysanoptera	0	0	0	0	0	0	1	0	0	0	0	0	1
Studies													
Observational	0	6	1	1	10	30	27	9	2	0	0	17	103
Manipulative	0	1	0	0	9	20	29	6	0	0	0	3	68
Studies	0	7	1	1	19	50	56	15	2	0	0	20	171
Studies (expl. saproxylic)	0	5	1	1	10	43	55	3	0	0	0	11	130

Biomes according to Olson et al. (2001): *Xeric* deserts and xeric shrublands; *TrMoist* tropical and subtropical moist broadleaf forests; *TrDry* tropical and subtropical dry broadleaf forests; *TrConif* tropical and subtropical coniferous forests; *TempBrMi*x temperate broadleaf and mixed forests; *TempConif* temperate coniferous forests; *Boreal* boreal forests; *TrSav* tropical and subtropical grasslands, savannas, and shrublands; *TempSav* temperate grasslands, savannas, and shrublands; *FlSav* flooded grasslands and savannas; *Montane* Montane grasslands and shrublands; *MedFor* Mediterranean forests, woodlands, and scrubs. *NA* Not applicable

[a] Median fire return interval (FRI) 3 years, median maximum fire radiative power (FRP) 473 MW, median maximum fire size (FS) 414 km^2

[b] FRI 1 year, FRP 197 MW, FS 25 km^2

[c] FRI > 50 years, FRP 476 MW, FS 83 km^2

[d] FRI > 50 years, FRP 187 MW, FS 4 km^2

[e] FRI 12 year, FRP 224 MW, FS 9 km^2

[f] Included although taxa are only resolved to family level. The families (Mycetophilidae and Berothidae) contain, however, a significant proportion of saproxylic species

fire return intervals in the range of 2–10 years for some areas). The boreal forest and most of the temperate coniferous and temperate broad-leaved and mixed forests burn relatively infrequently (>50 years between fires) from a global perspective, and the RIL and RCS pyromes tend to dominate these ecosystems (Krasutskiy 1996; Krawchuk et al. 2009; Bedia et al. 2015; Archibald et al. 2013).

20.2 Geographical and Taxonomic Clustering of Studies

To assess the geographic distribution of studies of fire effects on saproxylic insects (including the “non-insect” hexapods in Entognatha), a thorough literature survey[1] was conducted which covered articles published from 1945 to 2017 (Table 20.1). Papers were included if saproxylic species could be identified among the studied taxa. A total of 171 papers, excluding reviews, news articles, editorial material, conference proceedings, and pure modeling studies, were found. There were almost twice as many observational than manipulative studies in the sample.

The survey revealed a pronounced bias toward Coleoptera in both boreal and temperate coniferous forest ecosystems. In particular, economically important beetle taxa within Buprestidae, Cerambycidae, and Scolytinae are relatively well studied. Other taxonomic groups and biomes are sparsely represented, although studies of ants (Formicidae) in tropical and temperate savanna/open forest ecosystems contribute a substantial proportion (~16%) of the published papers. The proportion of papers referring to fire effects on saproxylic termites (Isoptera) was small (~7%) despite their importance in many tropical ecosystems. Bugs (Hemiptera) and flies (Diptera) are also represented in a fair number of studies, while Collembola, Neuroptera, Psocoptera, and Thysanoptera occur in a handful of papers only. Three insect orders with saproxylic taxa (Raphidioptera, Zoraptera, Lepidoptera) and three biomes with woody plants (deserts and xeric shrublands; flooded grassland and savannas; montane grasslands and shrublands) are completely absent from the literature sample.

Taxa are not explicitly classified as saproxylic in all of the collected papers. This is especially pronounced in the ant studies which, in general, tend to partition the studied assemblages according to functional groups based on climate affiliations and

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[1] Based on searches in Web of Science™ Core Collection made during the first 2 weeks of April 2017. Search strings were built by combining the phrase (burn* OR fire OR wildfire) and (NOT “fire ant” OR “fire ants”) with each of the following 36 words or phrases: insect OR insects; arthropod OR arthropods; invertebrate OR invertebrates; saproxylic; “wood living” OR “wood inhabiting”; xylophages OR xylophagous; “coarse woody debris” OR “dead wood” OR “deadwood”; Collembola; Coleoptera; Diptera; Hemiptera; Hymenoptera; Isoptera; Neuroptera; Psocoptera; Thysanoptera; Raphidioptera; Zoraptera; Lepidoptera; bug* OR *bug OR *bugs; planthopper OR planthoppers; sawfly OR sawflies; bee*; ant OR ant; wasp*; beetle*; termite OR termites; moth OR moths; lacewing OR lacewings; psocid* OR booklice OR barklice OR barkflies; snakefly OR snakeflies; thrips OR thunderfly OR thunderflies OR “thunderfly” OR “thunderflies”; zorapterans OR “angel insect” OR “angel insects”; fly OR flies; midge OR midges; gnat OR gnats).

competitive abilities. Only a handful (5 out of 29) of the ant studies explicitly refer to species microhabitats (e.g., deadwood). This contrasts sharply with the Coleoptera studies, where almost all papers (~94%) explicitly refer to the taxa as saproxylic. The bias in the literature toward boreal and temperate ecosystems and Coleoptera means that our results and conclusions will be biased toward these biomes and this group of insects.

20.3 Human Influence on Fire Regimes

Fire plays a prominent role in many forested regions (Table 20.1), but in some, e.g., the boreal region, the natural fire regime has been influenced by silvicultural management, changes in land use, changes in climate, fire suppression, and prescribed burning to reduce hazardous fire conditions (Cyr et al. 2009; Wallenius 2011; Prichard et al. 2017). For example, fire regimes have been disrupted to different degrees in large parts of North America, and fire restoration is needed to maintain natural functioning and structured ecosystems (Brown and Smith 2000). Compared to the preindustrial period, there has been a reduction in the annual burned area in the conterminous USA in most habitat types (Leenhouts 1998). Fire suppression is even more pronounced in part of Europe, e.g., Fennoscandia. For example, the forest area burned annually in Finland averaged 500 ha between 1980 and 2010, while during the fire peak years in late nineteenth century, the land area burned annually was as high as 70,000 ha. Over large areas in Fennoscandia, stand-replacing natural disturbances such as fire have been replaced with stand-replacing clear-cutting, which resulted in habitat conditions that are very different from those in burned areas (Heikkala et al. 2016b). After fire the volume of deadwood may reach several hundred cubic meters and deadwood diversity increases greatly (Eriksson et al. 2013; Hekkala et al. 2016), in contrast to clear-cutting where most deadwood is removed. Fire also creates numerous unique microhabitats that cannot be created with any other management method. Human-induced changes in fire regimes can therefore have profound impacts on forest ecosystems including saproxylic communities (McCullough et al. 1998; Stokland et al. 2012; Ulyshen 2013). In many other biomes, e.g., savanna systems and in Australia, prescribed burning is used as a tool to control and reduce fire hazards rather than for biodiversity management. The challenge is to combine these two goals as fire management for the purpose of reduced fire hazard has the potential to negatively affect biodiversity (Holland et al. 2017; Williams et al. 2017). Williams et al. (2017) demonstrated the potential of scenario analyses and optimization modelling for spatial planning to support decision-making through the prioritization and scheduling of controlled burns and quantifying trade-offs among multiple objectives. Climate change-driven wildfire risks will increase the need for adaptive fire management for multiple objectives.

20.4 Fire and Habitat Change

In many ecosystems throughout the world, mounting evidence points to the existence of fire-driven alternative stable vegetation states (Pausas and Ribeiro 2013). From the tropics several authors describe how feedbacks between fire regimes and plant composition operate to structure a mosaic of savanna vegetation and closed-canopy tropical forests (Hoffmann et al. 2012; Murphy and Bowman 2012). For example, Dantas et al. (2013) show how frequent fires in the neotropical Cerrado promote an open savanna/shrubland vegetation with highly flammable conditions but that longer fire intervals/fire suppression and increasing canopy closure promote a shift in vegetation composition toward more shade-tolerant and less flammable species. Similar feedbacks between fire regimes and vegetation have also been observed in other forest ecosystems across the globe. From the cold temperate region of Patagonia, Paritsis et al. (2015) describe how positive fire-vegetation feedbacks induce changes from fire-resistant *Nothofagus* forests to fire-prone shrublands. Odion et al. (2010) demonstrate how self-reinforcing fire regime feedbacks drive alternative community states in the Klamath Mountains of the Western United States. Regularly occurring high-severity fires maintain dry and pyrogenic sclerophyll shrublands, but with longer fire return intervals, the vegetation shifts toward a much more fire-resistant closed-canopy mixed forest consisting of evergreen conifers and shade tolerant hardwood species.

Depending on the fire regime, fire can conserve park-like stands through repeated low-intensity fires like the *Pinus ponderosa* forests in the Southwestern United States and the dry *Pinus sylvestris* forests in Northern Europe (Moore et al. 1999; Weaver 1951; Zackrisson 1977). In the Eastern United States, regularly occurring fires maintained relatively open and flammable oak/pine forests and savannas/woodlands, but long-term fire suppression has resulted in shifts to relatively fire-resistant closed-canopy forests dominated by mesophytic hardwood species (Nowacki and Abrams 2008). In many ecosystems, fire interacts with other disturbances to shape the post-fire succession (Herder et al. 2009; Smith et al. 2016; Foster et al. 2016). Co-occurring disturbances can interact to produce distinctly different outcomes from what would be expected based on individual effects. This means that altered disturbance regimes may result in changed successional pathways and forest structure (Didham et al. 2007; Tylianakis et al. 2008; Royo et al. 2010). For example, in the presence of alternative stable vegetation states, disturbances (e.g., droughts) that temporarily increase the probability of fire in otherwise fire-resistant late successional communities can allow fires to spark and induce shifts to more fire-prone vegetation states (Pausas 2015).

Fire can affect the habitat of saproxylic species by creating new substrates, creating competition-free substrates on existing deadwood by destroying pre-fire colonizers, changing the microclimate by opening the canopy, and providing not only dead but also weakened and dying trees over years after a fire (Bassett et al. 2015; Harmon et al. 1995; Azeria et al. 2012; Stokland et al. 2012; Wikars 1997). Warmer microclimates increase activity (Wikars 1997) and most likely reduce the development time of larvae, especially in colder climates. Furthermore, both competition and predation risk can be temporally reduced following fire (Wikars 2002; Holliday 1991). Moreover, the substrates created by the fire, such as burned sapwood, could themselves be necessary for pyrophilous insects and provide them with a niche that few other saproxylic insects use (Holliday 1991; Wikars 2002; Stokland et al. 2012).

The deadwood created by fire provides diverse physical and biological properties and suitable microclimatic conditions for many saproxylic species. Standing dead trees can serve as important structures and substrates for saproxylic species for considerable periods of time, especially at higher latitudes, where decomposition can be extremely slow, e.g., for black spruce snags in northern Quebec (Boulanger and Sirois 2006), mountain hemlock in the Pacific Northwest (Acker et al. 2013), and Scots pine forests in Northern Europe (Shorohova and Kapitsa 2014). Eventually, however, these snags fall and contribute to the pool of logs which often decompose faster than snags but still could contribute to the deadwood pool for centuries (Acker et al. 2013; Boulanger and Sirois 2006; Shorohova and Kapitsa 2014).

After stand-replacing fires in boreal forests, the accumulation of deadwood usually follows a U-shaped curve (Brassard and Chen 2006; Siitonen 2001). Immediately after fire, vast amounts of deadwood of both logs and snags are formed, providing saproxylic insects a surplus of habitat of different niches. Forests become characterized by open habitats that are not dominated by trees but have high levels of structural diversity and spatial heterogeneity and retain legacy materials in the forms of snags, logs, and dying trees from the old stand (Esseen et al. 1997; Swanson et al. 2011). Furthermore, within a fire area, there is considerable variation in fire intensity resulting from differences in ground conditions (e.g., ground moisture), topography, and structural forest properties. In areas with low-intensity fires, a large proportion of the trees in boreal forests might survive, and fire therefore helps produce a variable landscape with different habitat types (Kuuluvainen 2009).

During the decades after a fire in boreal forests, deadwood is slowly decaying, but little new deadwood is formed. However, when the stand matures, new deadwood can be formed, slowly increasing deadwood volumes. Fire also influences forest succession, resulting in regeneration of primary tree species such as birch and aspen in boreal biomes (Brassard and Chen 2006; Lilja and Kuuluvainen 2005; Rouvinen and Kouki 2002; Siitonen 2001; Uotila et al. 2002; Östlund et al. 1997). For example, aspen regeneration in Northern Europe is dependent on fire, and the current distribution of aspen, a keystone species and important habitat for many saproxylic insects, is probably a legacy of historical fires (Lankia et al. 2012).

Data from the southern slopes of the Swiss Alps show that fire impacts habitats for saproxylic species on both small and large scales. At small spatial scales, fire serves to maintain highly structured and relatively open stands with large amounts of deadwood and big oak trees. At large spatial scales, fire favors a mosaic of forest habitats and successional stages (Moretti and Barbalat 2004). In areas where fires are intensive and stand-replacing, a succession occurs with new tree species colonizing the newly burned area replacing the species associated with the pre-fire environment.

In North America intensive fires benefit early successional species such as aspen over late successional climax-stage conifers (Duchesne and Hawkes 2000). Changes in fire regimes can therefore have long-term impacts on forest structure and as a consequence saproxylic communities.

On a smaller scale, fire modifies both living and deadwood structure, ground vegetation, and soils, thereby affecting various species adapted to fire. For early colonizing saproxylic species, the deadwood created by fire is of great importance, but over the long term, fungi growing on burned wood appears to be the most important feeding habitat for many mycophagous saproxylic species (Wikars 1997, 2002). Fire also promotes flowering plants and can be an important habitat for pollinators such as flower-visiting bees and wasps (Rubene et al. 2014) as well as for some saproxylic long-horned beetles where the adults use flower nectar/pollen as food source. The promotion of flowering plants by using fire could potentially benefit these species as well (Campbell et al. 2007). In many savanna/woodland ecosystems, fire benefits plants with extrafloral nectaries and triggers the production of extrafloral nectar which is an important source of food for many species of deadwood-inhabiting arboreal ants (Fagundes et al. 2015).

20.5 Fire Adaptations in Saproxylic Insect Species

Fire is a reoccurring event in many biomes (Table 20.1), and consequently some saproxylic species have adapted to this type of disturbance. These species are often referred to as pyrophilous, fire-dependent, or fire-favored, depending on the degree of fire dependence. Pyrophilous ("fire-loving") saproxylic species are those that (1) have evolved traits in response to fires, (2) mainly occur in burned areas, and (3) to a large extent depend on fire to maintain viable populations (Wikars 1997). The number of species exhibiting all these characteristics (pyrophilous species) is relatively small, but many other species exhibit one or two of these traits and are referred to as fire-favored species. This group is quite large and hard to define (Wikars 1997). Pyrophilous species are found in Coleoptera, Diptera, Heteroptera, and Lepidoptera (Wikars 1997, 2002) and have evolved independently several times in insects, even within the same family (Schmitz et al. 2000, 2010; Wikars 1997).

Fire creates specific conditions that might favor species with certain traits. Large amounts of deadwood are usually produced by fire, and this might benefit species that can find and colonize burned areas quickly. Deadwood with specific characteristics, such as burned sapwood and deadwood colonized by certain fire-favored species of wood fungi, could also provide specialist saproxylic insects with a niche that few other saproxylic insects use (Danks and Footit 1989; Wikars 2002; Schmitz and Bousack 2012). Thus, both competition and predation risk can be temporarily reduced following fire, and most pyrophilous species are early colonizers and regarded as poor competitors (Wikars 1997; Schmitz et al. 2000; Stokland et al. 2012). Furthermore, a warmer microclimate increases activity (Stokland et al. 2012;

Wikars 2002) and most likely reduces development time of larvae, especially in colder climates.

It is difficult to define fire adaptations, as certain traits might be adaptive, increasing fitness without having evolved as a response to fire (Wikars 1997). However, some specific adaptations have been found in pyrophilous species that are considered adaptations to fire. One such adaptation is sensory organs that enable the insects to detect fire making it possible to detect the ephemeral resource of a burned forest. In some Coleoptera and Heteroptera species, photomechanical infrared (IR) receptors have evolved (Klocke and Schmitz 2012; Schmitz et al. 2000). Beetles in the genus *Melanophila* (Buprestidae) and flat bugs (Heteroptera) of the genus *Aradus* have these receptors, but species-specific differences in receptor placement and function in beetles suggest that they must have evolved independently (Schmitz et al. 2000, 2010). Saproxylic species with these receptors are widely distributed and can be found in Europe, North America, and Australia (Schmitz et al. 2000; Klocke and Schmitz 2012). These species can detect fires at considerable distances (Schmitz and Bousack 2012).

In addition to adaptations that allow them to detect fires, many pyrophilous beetles have excellent dispersal abilities which allow them to colonize burned areas that often occur haphazardly across the landscape. Strongly fire-favored and pyrophilous species seem to be able to respond quickly and over large distances to the occurrence of fire (Schmitz and Bousack 2012). Based on numerous anecdotal reports, Schmitz and Bousack (2012) estimated that *Melanophila* beetles must be able to detect and disperse to fires more than 60 km away. Most saproxylic insects are not able to disperse such distances, and some non-pyrophilous saproxylic taxa are clearly restricted in their dispersal (Brunet and Isacsson 2010; Ranius 2006; Schiegg 2000a, b; Stokland et al. 2012). For example, Ranius and Hedin (2001) found that most *Osmoderma eremita* remained in their natal trees and that dispersal distances never exceeded 190 m. However, Saint-Germain et al. (2013) did not detect any dispersal limitations in saproxylic species colonizing a large burn. Saproxylic assemblage composition did not differ between the core of the burn and the edge of the burn 8 km way. This indicates that early colonizing non-pyrophilous saproxylic species probably have a dispersal potential higher than generally expected for mycophagous, and other saprophagous species associated with deadwood (Saint-Germain et al. 2013). Ultimately, there is a trade-off between dispersal ability and reproduction. Species with well-developed wing muscles often produce fewer eggs which reduces their reproduction potential (Jonsson 2003; Stokland et al. 2012; Wikars 1997) and thus potentially also their competitive ability.

Fire occurrence is unpredictable in both time and space. It has therefore been suggested that the intraspecific variation in developmental time, e.g., resulting in *Melanophila acuminata* DeGeer larvae from the same brood emerging in different years, can potentially be a bet-hedging strategy to deal with the stochasticity of fire occurrence (Wikars 1997). Furthermore, prolonged swarming in pyrophilous insects can be found in many regions of the world and is probably a way to deal with the stochastic occurrence of fires (Wikars 1997). The swarming period of the Australian pyrophilous beetle *Merimna atrata* (Gory and Laporte) ranges from August to

December, and several boreal pyrophilous species, e.g., *Henoticus serratus* (Gyll.) and *M. acuminata*, have prolonged swarming periods potentially allowing them find and colonize fire areas throughout the fire season (Wikars 1997). In comparison, the activity period in other saproxylic species can be very restricted, in some cases only spanning 1 week (Jonsell et al. 2003). In addition, many pyrophilous species have cryptic coloration, e.g., black or charcoal-colored, and this have been suggested to be an adaptation to reduce predation risk in fire areas (Wikars 1997).

It is clear that pyrophilous species have adapted in different ways to the ephemeral and haphazardly occurring resource that fire constitutes. This is especially true in biomes experiencing frequent burns, e.g., boreal forests, temperate shrublands and woodlands, and tropical seasonal forests and savannas. These adaptations include the ability to detect and disperse to fire but also developmental adaptations (Schmitz et al. 2010; Schmitz and Bousack 2012; Wikars 1997, 2002). As all adaptations involve trade-offs, pyrophilous species depend on reoccurring fires and are most likely sensitive to changes in disturbance regimes (McCullough et al. 1998; Saint-Germain et al. 2004a; Siitonen 2001; Stokland et al. 2012; Wikars 2002).

20.6 Fire Effects on Assemblage Composition and Species Richness

Fire results in profound changes to habitat characteristics that benefit some species while harming others, resulting in mixed effect of fire on biodiversity (Thom and Seidl 2016). In a review, Thom and Seidl (2016) found that in boreal and temperate forest ecosystems, fire had an overall positive effect on biodiversity but also that the effect varied depending on the group of organism, time, and ecosystem studied. However, they did not detect any differences between natural and prescribed fires; both had generally a positive effect on biodiversity indices (e.g., species richness). A similar pattern with generally positive effects of fire on species richness has also been shown for saproxylic beetles (Azeria et al. 2012; Boucher et al. 2012; Hjältén et al. 2017).

The reason for the positive effect on saproxylic diversity could partly be explained by changes in light and temperature following fire but also by changes in the availability and quality of the deadwood substrates, reduced competition, and reduced predation pressure (Stokland et al. 2012; Ulyshen et al. 2010; Wikars 2002). Although a lot of deadwood is created by fire, fire also seems to reduce the quality of deadwood for many saproxylic species, due to destruction and drying out of the cambium (Wikars 2002; Boucher et al. 2012; Saint-Germain et al. 2004b). This could also affect species higher up in the food chain (Hilszczanski et al. 2005). Toivanen and Kotiaho (2010) reported reduced abundances of cambium consumers on burned compared to unburned spruce trees, whereas the opposite pattern was found for fungivores and wood borers. By contrast, they found that species richness of saproxylics including cambivores was consistently higher on burned trees. Furthermore, Hyvarinen et al. (2009) reported an increase in both species richness and abundance of saproxylic beetles following prescribed burns. However, these seemingly contradictive results could potentially be explained by the choice of sampling methods. Toivanen and Kotiaho (2010) used tree trunk window traps, and Hyvarinen et al. (2009) used free hanging window traps, whereas Wikars (2002) and Ulyshen et al. (2010) reared beetles from burned and unburned logs. These latter studies reported a decreased abundance on burned logs but no differences in species richness [see also Boucher et al. (2012)]. Thus, it is likely that the partial destruction of the cambium on burned deadwood reduces saproxylic abundance at the substrate level but that this is compensated by the large amounts of deadwood created in many fires, resulting in an increased abundance of saproxylics at the stand level.

For saproxylic species in tropical ecosystems the results are not as straightforward, and the literature is scarce with the exception of studies focusing on termites (Isoptera) and ants (Formicidae). The termite literature points in different directions but suggests either negative or neutral effects of fire on wood-feeding termites which could be regarded as saproxylic. From a tropical forest ecosystem, Neoh et al. (2016) report a 40% decrease in termite diversity following a peat fire, although the impacts on the wood-feeding groups were mixed across genera. On the other hand, Avitabile et al. (2015) found that termites in Malle vegetation, in southeastern Australia, were highly resistant to fire at multiple spatial scales. These mixed results of termite responses to fire are a general feature of the existing literature. In a recent review, Neoh et al. (2015) summarized findings from several ecosystems and found results showing positive effects (Indonesian dry dipterocarp forests) and negative effects (Australian and African savanna), as well as studies showing no effect (Cerrado in Brazil and longleaf pine savanna in Florida) of fire on wood-feeding termites. There also appears to be difference in fire resistance among genera, with mound-building termites showing a higher resistance and resilience to fire (Peterson 2010).

General patterns on the effect of fire on saproxylic ants in tropical forest and savanna ecosystems are difficult to establish, due to the fact that the ant literature rarely explicitly classify species as saproxylic or not. There are, however, several saproxylic species among arboreal and litter dwelling ants, and available studies show mixed responses depending on species and context. Studying the effects of fire-induced transition from tropical forest to Cerrado woodland, Paolucci et al. (2017) were unable to detect any impact of fire on the abundance of arboreal ants (a group containing several deadwood-nesting species, e.g., *Cephalotes* spp.), although they observed a general shift from forest specialists to open habitat species at the community level (including also the non-saproxylics). On the other hand, Frizzo et al. (2012) showed fairly strong short-term negative effects of fire on the arboreal ant fauna in Cerrado vegetation but could also show a striking resilience with abundances recovering to pre-fire levels within a single year following the fire. When studying the effects of fire in long-unburnt Australian savanna woodlands, Parr and Andersen (2008) found negative effects of fire on the arboreal (and paper nest building) ants in the genus *Papyrius* as well as other ants associated with closed forest vegetation. Results from the literature do however suggest that litter dwelling saproxylics (e.g., twig-nesting species) may be more negatively affected by fire. For example, Paolucci et al. (2016) found sharp reductions in both species richness and abundance of litter dwelling ants as a response to fuel addition and burning in a South American tropical evergreen forest.

There are also results showing positive effects of fire on saproxylic ants in tropical ecosystems. Costa-Milanez et al. (2015) report on certain deadwood-nesting *Crematogaster* spp. tied to open, disturbed habitats colonizing rapidly after fire in a Cerrado woodland. Evaluating a long-term experiment with different fire return intervals, Maravalhas and Vasconcelos (2014) found positive responses within deadwood-associated ant genera, with some species of *Azteca* and *Cephalotes* being more abundant with more frequent burns in Cerrado ecosystems (burnt every 2 or 4 years over 16 years vs. unburned for 37 years).

However, abundance and species richness per se might be a blunt tool for evaluating the effect of fire on saproxylic organisms, as fire will induce distinct changes in the assemblage composition but will often have a weaker effect on species richness (Hjältén et al. 2017; Toivanen and Kotiaho 2010; Hyvarinen et al. 2009; Boucher et al. 2012; Saint-Germain et al. 2004a). Studies from different continents and forest types show consistent patterns with both wildfire and prescribed burning having significant effects on the composition of saproxylic assemblages (Boucher et al. 2012; Hjältén et al. 2017; Hyvarinen et al. 2009; Johansson et al. 2011; Komonen et al. 2014; Saint-Germain et al. 2004a; Toivanen and Kotiaho 2010; Wikars 1997; Hammond et al. 2017). In general, fire favors early successional saproxylic species with good dispersal abilities but disfavors species associated with old-growth forest conditions (Stokland et al. 2012; Toivanen and Kotiaho 2010).

The general pattern in saproxylic insect responses to fire in boreal forests is that some functional groups (e.g., cambivores, fungivores, and predators) benefit from fire (Hjältén et al. 2017). The increase in available cambium following fire benefits cambivores (Hjältén et al. 2017) and changes in wood-dwelling fungal community (Suominen et al. 2015) may benefit fungivores (Wikars 2002). Wikars (2001) found that the increased occurrence of fruiting bodies of *Daldinia loculata,* which is a fire-favored species, was correlated with an increased species richness of fire-favored beetles. Several beetle species live in the fruiting bodies of *Daldinia*, suggesting that indirect effects of fire on other associated species could benefit pyrophilous insect species. Predators are known to track changes in prey availability (Azeria et al. 2012; Johansson et al. 2007), and predators are often attracted to the same volatiles as their prey, which might explain their increased abundance in burned areas (Hulcr et al. 2006; Schroeder 2003). Some fire specialist bugs, beetles, flies, and moths breed more or less exclusively in burned forests one or a few generations after fire (Hyvarinen et al. 2006; Stokland et al. 2012; Wikars 2002; Hjältén et al. 2006). Many of these species are threatened due to reduced fire frequencies in the forest landscape (Hekkala et al. 2014; Siitonen 2001; Stokland et al. 2012). For example, a high proportion of flat bugs are pyrophilous or strongly fire favored (Hjältén et al. 2006; Hägglund et al. 2015; Johansson et al. 2010; Heikkala et al. 2017). However, it should be noted that many species attracted to burned areas are not true fire specialists but merely early successional generalists which benefit from the large amount of deadwood and more open conditions created by fires (Stokland et al. 2012; Wikars 1997).

20.7 Fire as a Tool to Restore and Conserve Saproxylic Insect Diversity

Fire has been used as an active management tool in several biomes and for several reasons, e.g., to decrease the fire hazard in overly dense forests, to prepare the seedbed for silviculturally important trees, to prepare fields for cultivation in slash-and-burn management, and to remove invasive species (Löf et al. 2015; Andersen et al. 1998). However, in Fennoscandian boreal forests, fire has been increasingly used to benefit saproxylic and pyrophilous species (Halme et al. 2013; Johansson et al. 2013). Therefore, in this chapter we define restoration burning as *an active management operation to benefit biodiversity*, to distinguish it from actions to restore forest cover or other actions mentioned above. Restoration burning may be preceded by tree removal to either increase or decrease fire intensity or to pay for the costs of the action. In general, restoration burning is aimed to mimic natural fire, and it should therefore generate varying amounts of deadwood by killing and weakening or wounding standing trees and simultaneously generate habitat for fire-dependent and saproxylic organisms. Thus, restoration burning should include a certain degree of tree retention. However, Hyvarinen et al. (2009) found that even if higher volumes of tree retention in burned stands maintained the composition of assemblages closer to unharvested and burned stands, assemblages still differed from unharvested and burned stands. In addition, burning after clear-felling without tree retention or post-fire salvage logging can serve as an ecological trap or sink habitat for saproxylic insects as they are attracted to the burned area but will be unable to find substrate suitable for reproduction or if breeding substrate is harvested before the larvae have developed (Stokland et al. 2012; Wikars 1997; Cobb et al. 2011).

Restoration burning is used in some areas to benefit biodiversity, but at a global scale, the area in need of restoration burning is rather small, as natural fires still frequently occur in most parts of the world (Global Forest Watch 2017). For example, in Canada the annually burned area was almost 4 million ha in 2015, and there seems to be no decrease in the number or size of fires (National Forestry Database 2017). However, in some areas of the world, fire regimes have been disrupted and Dajoz (1998) expressed concern that pyrophilous species may become rare or extinct due to fire suppression occurring in the USA since the early 1900s. In Finland and Sweden, there are good historical records of fire-dependent or fire-adapted species, especially beetles, and many have been listed as threatened due to changes in fire regimes or forest management (Westling 2015; Wikars 2006; Rassi et al. 2010). In Finland, active management of fire-dependent and saproxylic species started in the late 1980s, and several large-scale experiments using fire as a tool were established. While these Fennoscandian countries have become model examples of effectiveness in timber production (Cyr et al. 2009), they are also acting as pioneers in using restoration burning to benefit biodiversity of saproxylic insects. Therefore, the lessons learned in Fennoscandia should be applied where relevant to other parts of the world, before it is too late (Halme et al. 2013). With increasing effectiveness of salvage logging after fire in North American and Russian forests, these areas may experience decreases in the biodiversity of pyrophilous saproxylic insects (Boucher et al. 2016; Cobb et al. 2011).

The spatial and temporal aspects in restoration implementation are of the essence because when restoring habitat, we assume that the "Field of dreams hypothesis"(Palmer et al. 1997), predicting that target species will find and colonize restored habitats, is valid. That may not be true, if the species have already disappeared from the landscape within the distance of dispersal. Kouki et al. (2012) showed that forest management history at least partly determines the success of restoration burning. The shorter the forest management history in the landscape, the more pyrophilous and red-listed species were able to disperse to stands subjected to prescribed burning. The high-value (i.e., old-growth forest) landscape matrix around restoration areas is probably very important for many pyrophilous species, possibly more important than fire continuum within the landscape (Saint-Germain et al. 2008). Thus habitat loss may have caused an extinction debt that even restoration cannot pay back, unless continuity is provided. For example, the influence of a long forest management history in boreal Sweden (see studies of Hjältén et al. 2017; Kärvemo et al. 2017) and Estonia (Laarmann et al. 2013) may explain why restoration burning did not benefit red-listed saproxylic species as clearly as in studies conducted near Russia (Hyvarinen et al. 2006; Hekkala et al. 2014; Heikkala et al. 2017), where natural fires still occur and forest management has not reached the effectiveness of western countries. The same was partly seen in a southern Finnish study by Toivanen and Kotiaho (2007). Even though the species overall richness was comparable to that documented by Hyvarinen et al. (2006), the count of red-listed species was clearly lower. These differences were possibly due to differences in the history of forest management or in the surrounding landscape composition (Toivanen and Kotiaho 2007).

Furthermore, when applying restoration burning, we should be aware that the effects of fire on saproxylic species are generally expected to be short-lived for many species (Hyvarinen et al. 2009). In boreal forests the occurrence of many saproxylic species is restricted exclusively to the first few years after fire (Jonsell et al. 1998), with abundances of some early successional species (Scolytidae and Elateridae) being significantly reduced in just a few years after fire (Saint-Germain et al. 2004b). Boulanger and Sirois (2007), using a 29-year chronosequence of burned sites, report fast initial changes in saproxylic assemblages but that a second colonization occurs only after dead trees fall to the ground. Ranius et al. (2014) reported that the pyrophilous, red-listed beetle species *Stephanopachys linearis* (Kug.) inhabited burned forests for 15 years, although the probability of occurrence and colonization decreased with time since fire. Similarly, Heikkala et al. (2016a) found that a few pyrophilous species persisted on burned and unlogged stands 10 years after burning, while logged stands were not suitable. This suggests that the fire effect might be more long lasting for some pyrophilous species. Regardless of this, it is likely that reoccurring fires in a landscape are necessary to maintain intact assemblages of pyrophilous insects (Heikkala et al. 2017). To maintain the populations of the most demanding pyrophilous species, we need to ensure temporal availability of burned habitat in the landscape.

Thus, it has been questioned if current restoration efforts using prescribed fires are sufficient to mitigate the long-term effect of fire suppression in, e.g., Fennoscandia (Johansson et al. 2013). However, efforts to practice restoration and retention forestry in Finland and Sweden have led to the reevaluation of many species that were red-listed in the early 2000s (Rassi et al. 2001; Gärdenfors 2005). As a result of increased knowledge gathered in large-scale experiments and by increasing suitable habitats for species, several species that were threatened in the 1990s are nowadays only near-threatened or of least concern (Rassi et al. 2010; ArtDatabanken 2015). This is at least an indication that prescribed burning, if properly planned, could help maintain viable populations of pyrophilous and fire-favored saproxylic species. However, biodiversity management in non-burned forests may also play an important role. It has been suggested that some, albeit not all, fire-adapted species must be able to maintain viable populations in the unburned forest matrix if it is of sufficient high quality (Saint-Germain et al. 2008) as fire frequency is extremely low in many landscapes. Thus, our ability to maintain viable populations of pyrophilous and fire-favored saproxylic species might depend on the sum of all conservation efforts at the landscape level rather than only on fire restoration efforts (Hjältén et al. 2017; Johansson et al. 2013; Saint-Germain et al. 2008).

20.8 Knowledge Gaps

Most studies of fire effects on saproxylic species and assemblages are short term. Only a few of the experimental studies are longer term, and no follow-up study exceeds 10 years in published literature. Thus, there is an urgent need for more long-term studies of saproxylic insect responses to fire to get a better knowledge of the persistence of fire effects, which is essential for landscape planning. We also need to better understand the degree to which pyrophilous species utilize the unburned matrix and what constitutes a good habitat for them in unburned areas. Furthermore, fire studies are strongly biased toward boreal and temporal forests, and our understanding of fire effect on saproxylic species in many other areas of the world where fire frequently occurs is limited at best. Thus, we have very limited knowledge of the occurrence of pyrophilous saproxylic species in, e.g., savanna systems and whether these are affected by changes in fire regimes. We also found a strong bias toward studies of specific taxonomic groups, e.g., beetles. This could result in biased recommendations for fire restoration due to specific traits of this taxonomic group, e.g., good dispersal activity. Studies comparing the responses of different taxonomic groups should therefore be prioritized.

20.9 Conclusions and Future Directions

Fire occurs in most biomes and undoubtedly has profound effects on the habitat and assemblages of saproxylic insects. Many saproxylic species benefit from fire but as many also have specific adaptations to fire disturbance they are sensitive to changes in fire regimes. However, our understanding of the long-term effects of changes in fire regimes in all but a few biomes (coniferous boreal and temperate forest) and taxonomic saproxylic groups (e.g., beetles) is very limited. Long-term or chronosequence studies involving a multitude of taxonomic saproxylic groups and biomes are therefore valuable. At the same time, we should be aware that from a landscape perspective, it is the sum of all land use activities including conservation and restoration efforts that influences the viability of saproxylic insect populations. We therefore need to apply a more holistic approach to the management of saproxylic insects.

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Chapter 21
Saproxylic Insects in Tree Hollows

Estefanía Micó

Abstract Tree hollows are fascinating microcosms that host a rich saproxylic insect assemblage. One of the most peculiar characteristics of this habitat is that both biotic and abiotic factors affect the evolution of the cavity making each unique and able to host a specialized fauna. Tree hollows are patchy habitats that provide a stable abiotic environment and long-lasting resources to a complex assembly of species from different trophic guilds (xylophagous, xylomycetophagous, saproxylophagous, saprophagous, predators, etc.), where species interactions seem to be an important piece of the puzzle of tree hollow diversity. Fourteen orders of insects and more than 800 species have been reported from tree hollows (primarily from Europe), with Coleoptera being the most diverse, followed by Diptera. However, knowledge of tree hollow insects and their requirements is still very asymmetric both geographically and taxonomically.

Forest reduction and fragmentation, climatic change, forestry and the abandonment of cultural practices are causing a decrease in tree hollow availability in natural and seminatural habitats, threatening the survival of the species that depend exclusively on them. Conservation and retention of hollowed trees has crucial importance for forest diversity maintenance worldwide; thus, actions should be urgently adopted.

21.1 Saproxylic Insects in Tree Hollows

Speight (1989) described overmature trees as the "arboreal megalopolis" representing a multiplicity of habitats for saproxylic organisms of many different taxonomic groups and a surprisingly large number of species. Among them, tree hollows are fascinating microcosms in which a variety of physical, biotic and abiotic factors will determine the cavity evolution and the living assemblage inside.

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Tree hollows are often characterized by a confined space with unique microclimatic conditions. Much like cave environments, values of temperature and moisture are generally more constant and stable than ambient conditions (Park and Auerbach 1954). However, this depends highly on entrance size, cavity depth and wall thickness (Gibbons and Lindenmayer 2002).

Food stability is another important hollow feature; microbes, fungi and animals produce nutrients inside the hollow due to their activity. Carbon (C), nitrogen (N) and phosphorus (P) are essential nutrients to achieve synthesis of metabolites for the biota, and the mean values of these elements can vary highly among cavity types. The N content of the cavity substrate is between 1% and 2%, which is three to six times higher than undecayed wood and two or three times higher than in decayed wood as a result of the organism's activity inside (Kelner-Pillault 1974; Jönsson et al. 2004; Micó et al. unpublished data), and the same occurs with P. Carbon content also varies among cavities, but in this case, values tend to be slightly lower than in undecayed wood contributing to a still lower C/N ratio as a consequence of the digestion of polysaccharides by insects and other organisms (Sánchez et al. 2017; Micó et al. unpublished data).

To some extent tree hollows could be compared with caves, as both are discontinuous (patchy) habitats inside a major habitat and both have their own microclimate, nutrient inputs and fauna. Moreover, some cavities in large living trees can become an exceptionally long-lasting dead wood microhabitat as they can remain for several hundred years (Siitonen 2012).

21.2 The Hollow: A Burst of Microhabitats for Saproxylic Insects

With the exception of some Neotropical pioneer species (e.g. *Cecropia*), which are naturally hollow trees (Ruxton 2014), cavities in live trees are formed primarily by the action of heart rot fungi when they access the heartwood in the trunk, branches or roots. Heart rot fungi do not grow on sapwood; instead, they are specialized in decaying the inner heartwood of mature trees forming hollows as result of the decay (Siittonen and Jonsson 2012).

Although fungi are the main agent of decay for most tree species, animals also contribute to the decay process in aged trees (Gibbons and Lindenmayer 2002). In this way, galleries made by woodborer insects such as beetles (Anobiidae, Brentidae, Buprestidae, Cerambycidae and Scolytinae, among others) and ants (*Lasius*, *Camponotus*, etc.; see Douwes et al. 2012) facilitate the further spread of decay fungi (Perry et al. 1985), as well as provide access for other taxa unable to excavate their own tunnels (Siittonen and Jonsson 2012). Termites (Blattodea) play a major role in the development of hollows in the tropics (Gibbons and Lindenmayer 2002) as they can create hollows within living trees whether there are openings to the outside or not (see Apolinário and Martius 2004; N'Dri et al. 2011 and Werner and

Prio 2007 from South America, Africa and Australia, respectively). Termites often excavate trunks by creating internal cavities inaccessible from the outside (Werner and Prio 2007), however, with limited colonization opportunities for other insects. Among vertebrates, woodpeckers (Picidae) are the most important group of primary cavity nesters in almost all regions, with the exception of Australia and New Zealand where they are absent (Siittonen and Jonsson 2012) (see next section).

In general, hollow occurrence in mature trees can be predicted by tree age and tree diameter (Gibbons and Lindenmayer 2002; Ranius et al. 2009; Horak 2017). However, this depends highly on tree species, as not all species are equally likely to be colonized by heart rot fungi (e.g. living conifers have fewer cavities than broadleaved trees) (Siitonen 2012; Milberg et al. 2014). Furthermore, environmental conditions (Wormington and Lamb 1999) and disturbance history (e.g. fire, cultural practices such as pollarding, etc.) not only favour the hollow formation process but also determine the type of cavity (Ranius et al. 2005).

21.3 Types of Hollows and Microhabitats

Not all cavities are equal; the causative agent of the hole and the position of the hollow in the living tree will primarily define the type of hollow. Although there are hollow trees without a connection to the outside (e.g. those formed by termites in tropical areas or natural hollow trees such as some *Cecropia* trees), in this chapter I limit my discussion of tree hollows to those that have an opening to the outside and that can consequently be colonized by the saproxylic fauna more easily. Depending on the size and exposure of the opening, cavities can be dry, moist or wet, and this will, in turn, affect species composition of fungi and insects (Siitonen 2012). The biotic character of dead wood becomes as much dependent upon which saproxylics have occupied it previously, as upon other factors. Hence, the hollow communities of saproxylics occurring in different parts of a tree will likely become further and further differentiated as the decomposition process proceeds (Speight 1989). In addition, as each cavity develops throughout time, it becomes larger and structurally more complex, offering in turn different niches that will be occupied by their own distinctive fauna (Speight 1989). Kraus et al. (2016), in their catalogue of tree microhabitat in temperate European forests, distinguished five categories of cavity—woodpecker cavities, insect galleries and bore holes, trunk and mould cavities, branch holes and dendrotelms, each one with their own subcategories.

21.3.1 Woodpeckers

Woodpeckers excavate their own nest holes in trees with heart rot, and these are used by other secondary hole-nesting birds (Siitonen 2012), mammals and invertebrates such as bees and social wasps. The shape, size and position of these kinds of cavities depend on the woodpecker species, and some can last for decades. This type of cavity, as with all vertebrate nesting cavities, has high nitrogen inputs coming from faeces, food remains and carcasses (e.g. dead nestlings) that enrich the habitat for invertebrate colonization (Siittonen and Jonsson 2012). The importance of woodpeckers as cavity suppliers varies among regions. They produce more than 77% of nesting cavities in North America but only 26% in South America and Eurasia (Cockle et al. 2011; Bhusal et al. 2015). However, in spite of the frequency of this type of hollow in some regions, studies on their ecological relevance are focused on vertebrates (Gibbons and Lindenmayer 2002; Cockle et al. 2011), and there is little information on the kind of insect assemblage that they host.

21.3.2 Insect Galleries and Bore Holes

Insect galleries and bore holes are also special microhabitats that host their own distinctive fauna. Holes made by borers are used by many wood-nesting solitary wasps and bees (Siitonen 2012) and are also important as hibernation sites of many other insects such as moths (Speight 1989). Galleries are also an important hunting place for saproxylic predators and provide access routes for saprophagous and saproxylophagous species. Micó et al. (2015) showed that in Mediterranean tree hollows, beetle assemblages associated with the presence of *Cerambyx* can be dominated by predators (50% of the species). Moreover, these debris-filled tunnels may be used by many other species (e.g. some Cetoniinae and Tenebrionidae species) as entrance routes and habitats (Palm 1959; Buse et al. 2008; Micó et al. 2015).

21.3.3 Trunk and Mould Cavities

Trunk and mould cavities are the main saproxylic microhabitat in veteran trees. Heartwood decayed by fungi is subsequently colonized by invertebrates and microorganisms that will physically and chemically modify the cavity. The boring action of many saproxylophagous and xylophagous beetle larvae expands the cavity by feeding on the wood of the walls and converting the wood into frass—borings, excrement and carcasses—that accumulate at the bottom of the cavity together with the external inputs of leaves, twigs and seeds (Ranius 2002; Jönsson et al. 2004; Siitonen 2012). The main substrate of the cavities is the resulting wood mould (Ranius and Nilsson 1997; Dajoz 1998; Siitonen 2012) that has also been referred to as tree hole mould (Park et al. 1950) and tree humus (Speight 1989). Wood mould of different cavities can vary greatly in volume and quality depending on the moisture inside, the main decomposer fungi and the invertebrate action. The openness of the cavity can determine to a great extent the moisture of the wood mould inside, but in addition, the height of the cavity in the trunk affects its microenvironmental conditions and nutrient inputs. In this way, the presence of bird nests, with everything that entails, is more frequent in higher cavities (Nilsson 1984; Ranius and Wilander 2000). Moreover, wood mould composition varies in its percentage of soil and litter, depending on distance to the ground (Taylor and Ranius 2014). Hollows formed at the base of trees are also called basal hollows or butt hollows (Fig. 21.1), and the existence of ground contact confers them special conditions that shape a different saproxylic assemblage from fungi to animals (Siitonen 2012). In many regions, basal hollows are mainly created by fire scars and subsequently favoured by human action (Gibbons and Lindenmayer 2002).

21.3.4 Branch Holes

Branch holes originate from branch breakage and can also become important saproxylic microhabitats. Many of them are small cavities (5 cm of opening diameter) with a horizontal opening in or near to the crown. Nevertheless, tree management such as pollarding or coppicing can generate horizontal cavities bigger than 10 cm in diameter with a varying amount of wood mould inside. They are open cavities that can develop a tubular prolongation inside the existing branches or that can remain even in a totally hollow tree (Fig. 21.1). The horizontal position of this kind of cavity allows it to easily collect rain water and leaves, and, depending on tree species and the depth of the hollow, they can become cavities temporally filled by water.

Fig. 21.1 Horizontal tree hollow (left) and basal tree hollow (right) (Photo E. Micó)

21.3.5 *Dendrotelms*

Dendrotelms (from the Greek *dendron* = tree and *telm* = pond) are a kind of phytotelm that have been reported in most parts of the world and, in many places, form an important part of the aquatic environment for insects (Kitching 1971). In the tropics they are more frequent than in other regions; however, the high number of other phytotelms reduces their relative importance as aquatic habitat. On the contrary, they are by far the most common type of phytotelm in the temperate zone (Kitching 1971). These tree holes hold water mixed with tree exudates, woody debris and leaf litter that form a special kind of habitat for saproxylic insects. These kinds of saproxylic aquatic or semiaquatic assemblages are dominated by larvae of Diptera that feed on a variety of fungi, bacteria and protozoan (Srivastava and Lawton 1998). The water-filled tree holes may be thought of as semi-permanent habitats that can potentially persist for the whole life of a mature tree (Kitching 1971).

To the diversity of existing hollow types, we should add the stage of cavity development which is closely linked with both biotic (fungi, microbials and animals) and abiotic factors, making each cavity unique and able to host a specialized fauna. Furthermore, as mature cavities become more structurally complex, they should be better considered as “multi-habitats” as they offer different trophic resources such as dead wood, saproxylic fungi, sap exudates and wood mould to the inhabiting fauna.

21.4 Sampling Tree Hollow Fauna

Tree hollows have been noted as a keystone habitat for saproxylic organisms in natural and seminatural forests. They host special assemblages consisting of both facultative and obligatory species, including endangered species, so the knowledge of species richness and composition of tree hollows has special relevance in forest management and conservation decisions.

Tree hollow faunas have received the interest of entomologists for a long time, but only recently have they been studied with quantitative methods (Ranius and Jansson 2002). In general, the choice of an adequate method will depend on the main objective of the survey and on the target group. In addition, it is important to consider the difficulties associated with accessing some kinds of cavities (e.g. those high above the ground (Ranius and Jansson 2002) or those very deep within the trunk). Another important consideration is the fact that species adapted to habitats providing long-lasting resources and stable abiotic environments, such as tree hollows, appear to have low dispersal propensity as compared with species associated with other microhabitats such as snags, logs, bark, dying branches, etc. (Stokland et al. 2012).

21.4.1 Wood Mould Sampling

Wood mould sampling is a direct, absolute method that implies that a certain amount of wood mould from each tree is examined. The extracted volume can be analysed directly in the field by searching through the material on a sheet when target species are easily recognizable (Ranius and Jansson 2002) or can be studied in the laboratory where different methods to extract the fauna can be used depending on the target group (Nageleisen and Bouget 2009). As with all direct methods, this provides valuable information on the species biology; however, it is time-consuming, and a large fraction of the individuals sampled can be larvae which greatly complicates species identification.

21.4.2 Vacuum Cleaning Method

Vacuuming is another a direct, absolute method that has been used to monitor saproxylic insects in tree hollows (Bußler and Müller 2009). The method consists of a vacuum cleaner carried on the back and a suction tube that is introduced into the cavity. The sample is limited by the size of the collecting bag (see Bußler and Müller (2009) for more details). This method saves time with respect to the wood mould sampling and deals better with cavities in which access to wood mould is difficult. However, it provides less information on species biology unless each stratum is separated during the sampling. Both methods can be very intrusive if wood mould samples are carried to the lab for processing.

21.4.3 Pitfall Traps

Pitfall traps have been widely used in studies of arthropods active on the ground (Bonneil et al. 2009), but they can also be used in quantitative assessments in tree hollows, alone or combined with other methods (Jansson 2009). Pitfall traps consist of containers buried in the substrate so that the opening is level with substrate surface in order to collect species that are actively moving inside the cavity (see Ranius and Jansson (2002) for more details). It is an indirect and relative method but also easily standardizable. The trap can be filled with a preservative agent (e.g. non-toxic propylene glycol), but sampling may be done without the use of a preservative agent if the goal is only to detect the presence of target species and/or to minimize mortality. Unlike both wood mould sampling and vacuum cleaner sampling that give a picture of the whole species assemblage at a given moment, pitfall traps allow more frequent visits and thus longer monitoring periods.

21.4.4 Emergence Traps

Emergence traps provide an indirect, absolute method for quantitative assessment of hollow diversity. Modified from Colas (1974), these traps are for collecting species that inhabit tree hollow microhabitats (Gouix and Brustel 2012; Quinto et al. 2013). The trap consists of nylon mesh stapled over the opening of the cavity and with a container attached (Fig. 21.2). This kind of trap allows saproxylic species (including both flying and nonflying species) to be recorded shortly after their emergence from immature stages. Consequently, this method prevents species underestimation as only adults are collected instead of larvae that are normally unidentifiable (Gouix and Brustel 2012) and provide information about species phenology and co-occurrence. A preservative agent such as propylene glycol can be used, but sampling may be considered without the use of preservative agents.

Fig. 21.2 Hollow emergence trap (Photo E. Micó)

21.4.5 Flight Interception Traps

Flight intercept traps were first designed to study flying beetles, especially scolytids (Chapman and Kinghorn 1955), and are the most commonly used trap for saproxylic flying beetles in general. Window flight traps consist of transparent plastic vanes of variable dimensions positioned above a collection chamber (Økland 1996; Ranius and Jansson 2002). This kind of trap is placed near the trunk beside or in front of a hole entrance. Different types of flight intercept traps are commonly used: single vane traps, transparent cross-vane traps and black cross-vane traps (Bouget et al. 2008b; Redolfi de Zan et al. 2014). These traps are the least selective, collecting also fauna living in other microhabitats outside of the cavity, and it is biased towards flying beetle species. However, it allows one to more easily survey cavities at a greater height on the trunk as they can be lifted up in the canopy near a cavity entrance without climbing.

21.5 The Hollow Inhabitants

The first documented studies on cavity inhabitants date from the early twentieth century, but most of them were referred to as dendrotelms, motivated by the study of breeding sites of mosquito species that affect human health (Keilin 1927; Kitching 1971). However, more attention has been paid to hollow assemblages since the popularization of the "saproxylic" concept that has also involved a more precise definition of the saproxylic microhabitats, including living trees (Dajoz 1966; Speight 1989; Alexander 2008).

The importance of hollows that host rich saproxylic assemblages is now indisputable. Several researchers highlight that cavities containing wood mould are keystone habitats for saproxylic conservation as they host endangered species (Ranius and Jansson 2000; Sirami et al. 2008; Micó et al. 2010; Chiari et al. 2012; Gouix et al. 2015). Moreover, cavities seem to be more diverse functionally and phylogenetically than other woody resources (Müller et al. 2013). Hollow assemblages are not only important for individual species but also for species interactions (Quinto et al. 2012, 2014). In this way, it should be kept in mind that in the reduced space of a mature cavity, species belonging to different trophic guilds (saprophagous, saproxylophagous, xylomycetophagous, predators and parasitoids) live together and interact in different ways among them and/or with the woody substrates. Regarding this, tree hollows could be considered as hotspots of saproxylic insect diversity. However, knowledge on the diversity of hollow assemblages varies greatly among taxa and regions.

The main gap in the study of insect diversity within hollows occurs at a geographical level; tree hollow insect assemblages have not been equally studied in all regions (see Table 21.1) regardless of the density of hollow occurrence. Density of tree hollows seems to increase from the poles to the equator (Boyle et al. 2008).

Table 21.1 Insect taxa reported in tree hollows

Order	Family	Genus (n° spp)	Reference
Blattodea			9
Coleoptera	Aderidae	*Aderus (1)*	3, 14, 17
		Cnopus (1)	14, 17
		Euglenes (2)	3, 15, 29
		Otolelus (1)	14, 17
		Vanonus (1)	3
	Anthicidae	*Notoxus (1)*	16
	Anthribidae	*Anthribus (1)*	15
		Dissoleucas (1)	15
		Noxius (1)	4
		Platyrhinus (1)	15
		Tropideres (1)	15
	Biphyllidae	*Biphyllus (1)*	22
		Diplocoelus (1)	14, 15, 17, 22
	Bostrichidae	*Apate (1)*	4
		Scobicia (1)	4, 22
		Sinoxylon (1)	4
		Xylopertha (1)	15
	Bothrideridae	*Dastarcus (1)*	4
		Oxylaemus (1)	3, 10
	Buprestidae	*Acmaeodera (3)*	1, 4, 17
		Agrilus (8)	1, 4, 15, 21
		Anthaxia (3)	1, 4
		Chrysobothris (1)	15
		Coraebus (1)	3
		Eurythyrea (1)	10, 14, 17
		Nalanda (1)	1
	Cantharidae	*Malthinus (1)*	15
		Malthodes (2)	15
	Carabidae	*Agonoderus (1)*	16
		Bembidion (1)	16
		Calosoma (1)	16
		Clivina (1)	16
		Dicaelus (1)	16
		Platynus (1)	16
		Tachymenis (1)	16
		Trechus (1)	22
	Catopidae	*Catops (1)*	16
	Cerambycidae	*Acmaeops (2)*	3
		Akimerus (1)	10
		Alocerus (1)	14, 17
		Alosterna (1)	15, 21, 22

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Anaglyptus (1)	3, 15
		Cerambyx (3)	1, 3, 10, 14, 17
		Chlorophorus (2)	1, 4
		Clytus (3)	4, 15
		Corymbia (2)	15
		Ergates (1)	1
		Exocentrus (1)	1
		Grammoptera (2)	15, 21
		Hesperophanes (1)	4
		Leiopus (1)	15, 21
		Leptura (1)	15
		Mesosa (2)	3, 15
		Nathrius (1)	4
		Necydalis (2)	3, 10
		Niphona (1)	4
		Oxymirus (1)	15
		Phymatodes (2)	15, 21, 22
		Pogonocherus (1)	15
		Prinobius (1)	17
		Prionus (1)	3, 15
		Pyrrhidium (1)	15
		Rhagium (2)	3, 15
		Rhamnusium (1)	3, 15
		Saperda (2)	3, 15
		Stenidea (1)	4
		Stenostola (1)	15
		Stenurella (1)	15
		Stictoleptura (3)	3, 14, 17
		Stromatium (1)	4
		Tetropium (1)	3
		Trichoferus (1)	4, 14, 17
		Vadonia (1)	1
		Xylotrechus (1)	15
	Cerophytidae	*Cerophytum (1)*	3, 10
	Cerylonidae	*Cerylon (4)*	3, 15, 16, 17, 21, 22
		Philothermus (2)	1, 3
	Chrysomelidae	*Glyptina (1)*	16
	Ciidae	*Cis (12)*	3, 14, 15, 16, 17, 22
		Ceracis (1)	16
		Ennearthron (1)	15
		Hadreule (1)	3
		Orthocis (2)	15

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Sulcacis (2)	15
		Xestocis (1)	16
	Clambidae	*Calyptomerus (1)*	17
		Clambus (1)	17
	Cleridae	*Denops (1)*	4
		Korynetes (3)	1, 3, 20
		Opilo (3)	1, 3, 14, 15, 17
		Thanasimus (1)	15
		Tilloidea (1)	1
		Tillus (1)	15, 21
		Trichodes (2)	1
	Corylophidae	*Arthrolips (1)*	3, 22
		Orthoperus (3)	3, 15, 16
		Sericoderus (1)	22
	Cryptophagidae	*Anchicera (1)*	16
		Atomaria (4)	3, 14, 20, 21
		Coenoscelis (2)	3
		Cryptophagus (24)	3, 14, 15, 17, 20, 21, 22
		Cryptophilus (1)	16
		Loberus (1)	16
	Cucujidae	*Laemophloeus (1)*	16
		Prostomis (1)	27
	Curculionidae	*Camptorhinus (3)*	10, 14, 17
		Cossonus (1)	15
		Ernoporicus (1)	15
		Gasterocercus (1)	14, 17
		Leperisinus (1)	15
		Phloeophagus (2)	15, 29
		Platypus (1)	14, 15, 17, 22
		Rhyncolus (3)	14, 21, 22
		Scolytus (2)	15
		Stereocorynes (1)	15
		Taphrorychus (1)	15
		Xyleborinus (1)	14, 17, 22
		Xyleborus (5)	1, 4, 14, 15, 17, 22
		Xylosandrus (2)	4, 22
		Xyloterus (2)	15
	Dasytidae	*Aplocnemus (5)*	14, 15, 17
		Dasytes (4)	14, 15
		Mauroania (1)	14, 17
		Trichoceble (1)	21
	Dermestidae	*Anthrenus (9)*	1, 14, 16, 17, 20, 21

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Attagenus (7)	1, 14, 17, 20
		Ctesias (3)	1, 15, 21
		Dermestes (6)	1, 14, 17, 20
		Globicornis (2)	1, 20, 21
		Megatoma (2)	1, 15, 21
		Orphilus (1)	1, 14, 17
		Trogoderma (1)	1
	Elateridae	*Adelocera (1)*	1, 4
		Aeolus (1)	16
		Agriotes (1)	16
		Ampedus (12)	6, 10, 14, 15, 17, 19, 20, 21, 29
		Brachygonus (2)	10, 15
		Calambus (1)	15
		Cardiophorus (2)	1, 4, 27
		Crepidophorus (1)	15, 20, 29
		Denticollis (1)	15
		Drapetes (1)	1
		Ectamenogonus (1)	1, 14, 17
		Elater (3)	10, 14, 16, 17, 19, 20, 21, 27, 29
		Elathous (2)	1, 14, 17
		Haterumelater (1)	1
		Hypoganus (1)	15
		Ischnodes (1)	1, 10, 14, 17
		Lacon (3)	1, 4, 10, 14, 17
		Limoniscus (1)	1, 10, 11, 14, 17
		Ludius (1)	6
		Megapenthes (1)	10, 14, 17
		Melanotus (10)	1, 4, 6, 14, 15, 16, 21, 22
		Mulsanteus (2)	1, 4
		Nothodes (1)	1
		Peripontius (1)	1
		Pittonotus (1)	1, 4
		Podeonius (1)	10
		Procraerus (1)	14, 15, 17, 19, 20, 21, 29
		Reitterelater (1)	1
		Stenagostus (1)	15
	Endomychidae	*Mycetaea (1)*	14, 17
		Symbiotes (2)	14, 17, 22
	Erotylidae	*Dacne (1)*	15
		Triplax (2)	15, 22
	Eucinetidae	*Nycteus (1)*	14, 17

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
	Eucnemidae	*Dirhagus (2)*	15
		Eucnemis (1)	15, 22
		Hylis (2)	15
		Isorhipis (1)	15
		Melasis (1)	15
	Geotrupidae	*Anoplotrupes (1)*	22
	Histeridae	*Abraeus (3)*	14, 15, 17
		Aeletes (1)	16, 17
		Atholus (1)	17
		Bacanius (1)	16
		Carcinops (2)	1, 16
		Dendrophilus (3)	1, 2, 14, 15, 16, 20, 21
		Epierus (2)	1, 16
		Gnathoncus (4)	1, 2, 14, 17, 20, 21
		Hetaerius (1)	14, 17
		Hololepta (1)	16
		Isolomalus (1)	16
		Margarinotus (3)	2, 14, 17
		Merohister (1)	1, 14, 17
		Paromalus (3)	1, 14, 15, 17, 21, 22
		Platylomalus (2)	1, 14, 17
		Platysoma (3)	1, 14, 17
		Plegaderus (2)	14, 15, 20, 21, 22
		Xestipyge (1)	16
	Laemophloeidae	*Cryptolestes (1)*	14, 17
		Laemophloeus (2)	15, 17, 22
		Placonotus (1)	14, 17
	Latridiidae	*Cartodere (1)*	16
		Corticaria (1)	17
		Dianerella (1)	17
		Enicmus (5)	15, 17, 22
		Latridius (2)	15, 17
		Metophthalmus (1)	16
		Stephostethus (1)	15
	Leiodidae	*Agathidium (2)*	15, 17
		Anisotoma (2)	15
		Dreposcia (1)	20
		Nemadus (1)	2, 15, 20, 21, 29
	Lucanidae	*Dorcus (2)*	1, 6, 14, 15, 17, 22
		Platycerus (1)	15
		Sinodendron (1)	15
	Lycidae	*Dictyoptera (1)*	27

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
	Lymexylidae	*Hylecoetus (1)*	15
		Lymexylon (1)	21
	Melandryidae	*Abdera (1)*	15
		Conopalpus (2)	15, 21
		Melandrya (1)	15
		Orchesia (2)	1, 14, 15, 17, 21
		Phloiotrya (1)	15
	Melyridae	*Anthocomus (1)*	14, 17
		Axinotarsus (1)	14, 17
		Falsomelyris (1)	17
		Hypebaeus (2)	14, 15, 17, 21
		Malachius (1)	15
		Troglops (2)	1, 14, 17
	Monotomidae	*Rhizophagus (5)*	14, 15
	Mordellidae	*Mordella (1)*	15
		Mordellistena (1)	4
		Mordellochroa (1)	15
		Tomoxia (1)	15, 22
	Mycetophagidae	*Litargus (2)*	14, 15, 17, 22
		Mycetophagus (8)	1, 10, 14, 15, 16, 17, 20, 21
		Triphyllus (1)	22
	Nitidulidae	*Amphotis (1)*	14, 17
		Carpophilus (1)	1, 17
		Cryptarcha (3)	1, 15, 22
		Cychramus (2)	15
		Epuraea (5)	14, 15, 17, 22
		Glischrochilus (1)	15
		Ischnomera (1)	1
		Soronia (1)	1, 14, 17, 22
	Oedemeridae	*Ischnomera (4)*	14, 15, 17, 29
	Pselaphidae	*Batrisus (1)*	2
	Ptiliidae	*Acrotrichis (1)*	16
		Micridium (1)	16
		Ptenidium (2)	15, 16, 29
		Pteryx (1)	16
		Ptiliolum (1)	16
		Ptinella (1)	29
	Ptinidae	*Anobium (3)*	15, 21
		Caenocara (1)	1
		Dignomus (1)	1, 17
		Dorcatoma (9)	1, 14, 15, 17, 21
		Falsogastrallus (1)	1

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Gastrallus (1)	15, 21
		Hedobia (2)	1, 15
		Hemicoelus (1)	14
		Lasioderma (1)	1
		Mesothes (2)	1
		Oligomerus (2)	1, 14, 17
		Ptilinus (1)	15
		Ptinus (15)	1, 4, 15, 17, 20, 21
		Rhamna (1)	14, 17
		Stagetus (5)	1, 14, 17
		Stegobium (1)	1
		Xestobium (2)	14, 15, 21
		Xyletinus (1)	1
	Pyrochroidae	*Pyrochroa (1)*	15
		Schizotus (1)	15
	Rhipiceridae	*Zenoa (1)*	16
	Rhizophagidae	*Rhizophagus (1)*	17
	Ripiphoridae	*Ripidius (1)*	29
	Salpingidae	*Rabocerus (1)*	15
		Salpingus (2)	15
		Vincenzellus (1)	15
	Scarabaeidae	*Cetonia (2)*	6, 14, 15, 17
		Gnorimus (1)	6, 20
		Oryctes (1)	1, 14, 17
		Osmoderma (2)	6, 13, 19, 20, 21, 27
		Propomacrus (1)	1, 4
		Protaetia (7)	1, 2, 14, 17, 19, 20, 21, 29
	Scirtidae	*Prionocyphon (2)*	12, 14, 15, 17, 26, 29
	Scraptiidae	*Anaspis (8)*	4, 14, 15, 17
		Pentaria (1)	17
		Scraptia (3)	14, 17, 20, 21, 29
	Scydmaenidae	*Acholerops (1)*	16
		Cephenium (1)	17
		Connophron (1)	16
		Euthiconus (1)	29
		Nevraphes (1)	29
		Palaeostigus (1)	17
		Scydmaenus (2)	14, 17, 20, 29
		Scydmoraphes (1)	29
		Stenichnus (2)	14, 15, 17, 20
	Silphidae	*Ptomaphagus (1)*	16
	Silvanidae	*Ahasverus (1)*	14, 17

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Airaphilus (1)	17
		Oryzaephilus (1)	14, 17
		Silvanus (1)	17
		Uleiota (1)	14, 15, 17
	Sphindidae	*Aspidiphorus (1)*	15
		Odontosphindus (1)	22
	Staphylinidae	*Atheta (1)*	16
		Batrisodes (4)	16, 20
		Bibloporus (3)	15
		Bolitochara (1)	15
		Bryoporus (1)	16
		Conosoma (1)	16
		Euplectus (6)	15, 16, 17, 20, 21
		Euryusa (2)	15, 29
		Geopsephalus (1)	17
		Gyrophaena (1)	15
		Hapalaraea (1)	15, 20, 21, 29
		Haploglossa (2)	29
		Hesperus (1)	15
		Ischnoglossa (1)	15
		Leptusa (2)	15
		Melba (1)	16
		Nudobius (1)	15
		Omalium (1)	16
		Philonthus (1)	16
		Phloeocharis (1)	15
		Phloeopora (3)	15
		Phyllodrepa (1)	15
		Placusa (2)	4, 15
		Plectophloeus (2)	15, 20
		Quedius (7)	15, 16, 20, 21, 29
		Scaphisoma (3)	15, 22
		Sepedophilus (1)	15
		Tachinus (1)	16
		Thesium (1)	16
		Thiasophila (1)	29
		Thoracophorus (1)	16
		Trichonyx (1)	29
		Velleius (1)	15, 20, 21
		Xantholinus (1)	16
	Tenebrionidae	*Allecula (4)*	1, 4, 6, 10, 15, 19, 20, 21
		Alphitophagus (1)	1

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Blaps (1)	1
		Bolitophagus (1)	15
		Capnochroa (1)	16
		Corticeus (2)	14, 15, 17
		Cylindronotus (1)	1
		Dendarus (1)	14
		Diaclina (1)	15
		Diaperis (1)	1, 4, 21
		Eledona (1)	21
		Eledonoprius (1)	14, 17
		Enoplopus (1)	22
		Entomogonus (1)	1
		Helops (2)	1, 22, 27
		Hymenalia (4)	1, 6
		Hymenorus (1)	16
		Hypophloeus (1)	10
		Isomira (4)	1, 14, 17, 22
		Mycetochara (9)	1, 4, 14, 15, 17, 20, 21, 22, 29
		Mycetocharina (2)	1, 4
		Nalassus (1)	14
		Neatus (1)	1
		Odocnemis (1)	1
		Opatroides (1)	1
		Palorus (1)	1, 14, 20
		Pentaphyllus (1)	1, 20, 21
		Platydema (2)	15, 16
		Prionychus (5)	1, 4, 6, 14, 17, 19, 20, 21, 29
		Probaticus (2)	1, 14, 17
		Pseudocistela (1)	1, 14, 17, 19, 20, 21
		Stenohelops (2)	14, 17
		Strongylium (1)	4
		Tenebrio (5)	1, 14, 16, 17, 19, 20, 21
		Uloma (1)	22
	Tetratomidae	*Tetratoma (1)*	15
	Trogidae	*Trox (2)*	1, 2, 14, 16, 20, 21
	Trogossitidae	*Grynocharis (1)*	21
		Nemosoma (1)	15
		Temnochila (1)	14, 17
		Tenebroides (1)	14, 17
		Thymalus (1)	15
	Zopheridae	*Bitoma (1)*	15

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
		Colobicus (1)	1, 14, 17
		Colydium (1)	14, 17
		Corticus (1)	22
		Endophloeus (1)	14, 17
		Synchita (1)	22
Collembola	Entomobryidae		16
	Poduridae		16
	Sminthuridae		16
Diptera	Cecidomyiidae		16
	Ceratopogonidae	*Bezzia*	26
		Dasyhelea	12
	Chironomidae	*Metriocnemus (1)*	12, 26
	Culicidae	*Aedes (1)*	12, 26
		Anopheles (1)	12, 26
		Toxorhynchites (1)	8
	Dolichopodidae	*Systenus (1)*	25
	Drosophilidae	*Drosophila*	16
	Muscidae	*Phaonia (1)*	25
	Mycetobiidae	*Mycetobia (1)*	25
	Mycetophilidae		16
	Psychodidae	*Psychoda*	26
	Stratiomyidae	*Odontomyia*	26
	Syrphidae	*Anasimya*	26
		Blera (1)	23, 25, 28
		Brachyopa (1)	17, 23
		Brachypalpoides (1)	17, 28
		Brachypalpus (1)	17, 23, 28
		Callicera (5)	17, 18, 23, 25, 28
		Ceriana (1)	17, 18, 23, 28
		Chalcosyrphus	28
		Criorhina (2)	17, 23, 28
		Ferdinandea (4)	17, 18, 23
		Mallota (3)	17, 18, 23, 25, 28
		Milesia (1)	17, 28
		Monoceromyia (1)	24
		Myathropa (1)	12, 17, 18, 26, 28
		Myolepta (4)	17, 18, 23, 28
		Pocota	23, 28
		Polybiomyia (1)	24
		Sphiximorpha (2)	17, 23, 24
		Spilomyia (1)	17, 18, 23, 28
		Xylota	23, 28

(continued)

Table 21.1 (continued)

Order	Family	Genus (n° spp)	Reference
Hemiptera (Cicadomorpha)	Cicadellidae	*Erythroneura (1)*	16
Hemiptera (Heteroptera)	Tingidae		16
	Veliidae	*Paravelia (1)*	8
Hymenoptera	Apidae	*Hypotrigona (1)*	7
		Trigona (10)	7
	Belytidae		16
	Ceraphronidae		16
	Formicidae	*Aphaenogaster (1)*	16
		Camponotus	30
		Lasius (1)	16
		Leptothorax (1)	16
		Monomorium (1)	16
		Ponera (1)	16
		Strumigenys (1)	16
	Ichneumonidae		16
	Tenthredinidae		16
Neuroptera	Ascalaphidae		16
	Myrmeleontidae	*Dendroleon (1)*	5
Odonata	Aeshnidae	*Gynacantha (1)*	8
	Coenagrionidae	*Mecistogaster (2)*	8
	Pseudostigmatidae	*Megaloprepus (1)*	8
Orthoptera	Gryllidae		9
Phasmatodea			9
Protura	Acerentomidae	*Acerentulus*	16
		Acerentomon	16
	Eosentomidae	*Eosentomon*	16
Thysanoptera			16
Thysanura	Campodeidae		16

This is a list of genera (number of species in brackets) reported from papers explicitly focused on the study of natural tree hollows. It also includes species that are not true hollow specialists. After each reference the country of the study is provided:
[1]Atay et al. (2012), Turkey; [2]Binon et al. (1998), France; [3]FRISBEE data base: Bouget et al. (2008a), France; [4]Buse et al. (2013), Israel; [5]Colombo et al. (2013), France; [6]Dajoz (1998), Europe; [7]Eltz et al. (2003), Malaysia; [8]Fincke (1999), Panama; [9]Gibbons and Lindenmayer (2002), Australia; [10]Gouix and Brustel (2012), France; [11]Gouix et al. (2015), France; [12]Kitching (1971) UK; [13]Landvik et al. (2015), Finland; [14]Micó et al. (2015), Spain; [15]Müller et al. (2013), Germany; [16]Park and Auerbach (1954), USA; [17]Quinto et al. (2014), Spain; [18]Rámirez-Hernández et al. (2014), Spain; [19]Ranius (2002), Sweden; [20]Ranius and Jansson (2002), Sweden; [21]Ranius and Jansson (2000), Sweden; [22]Redolfi De Zan et al. (2014), Italy; [23]Reemer (2005), Netherlands; [24] Ricarte et al. (2007), Brazil, Costa Rica; [25]Rotheray et al. (2001), Scotland; [26]Schmidl et al. (2008), Germany; [27]Speight (1989), Europe; [28]Speight (2016), Europe; [29]Svedrup et al. (2010), Norway; [30] Douwes et al. (2012), Sweden

In tropical areas, although trees persist on average for fewer years relative to temperate forests (Losos and Leigh 2004), high decomposition rates potentially result in more decay-caused cavities (Gibbs et al. 1993; Boyle et al. 2008). Hence tree hollow density is high in tropical forests, e.g. from 16 tree cavities per hectare in the subtropical forest of Nepal (Bhusal et al. 2015) to 77 tree cavities per hectare in tropical dry forests in México (Vázquez and Renton 2015), 79 in wet tropical lowland in Costa Rica (Boyle et al. 2008) or even 105 in old-growth tropical forest in Thailand (Pattanavibool 1993). However, with the exception of dendrotelms, hollow insect assemblages have been poorly studied in tropical areas (Fincke 1999, Grove and Stork 1999). Vázquez and Renton (2015) pointed out that arthropods (mainly ants and bees) were the most frequent occupants (58% of occupied cavities) in tropical dry forests. In Australia, although the density of tree hollows per hectare is moderately high (3–7 in disturbed forests and 13–27 in relatively undisturbed ones) and they are recognized as key elements for biodiversity conservation in both managed and unmanaged landscapes, hollow studies have focused mainly on vertebrates, and little is known about invertebrates and insects in particular (Gibbons and Lindenmayer 2002). In comparison, patterns of cavity distribution in temperate forests are well studied; in North America, Goodburn and Lorimer (1998) showed that cavity tree density averaged 11 trees/ha and that old-growth stands have more cavities than younger ones. The insect faunas in old oak tree hollows have received more attention in Europe, in both temperate and, more recently, Mediterranean forests (Table 21.1) where cavities of large old oaks have been widely studied.

At least 14 orders of insects have been reported from tree hollows (Table 21.1). However, other important asymmetries in tree hollow insect fauna studies concern taxonomical groups; springtails (Collembola)—together with mites (Acari)—have been reported as the most abundant taxa in wood mould, while beetles (Coleoptera) are dominant in terms of biomass (Park and Auerbach 1954). Coleoptera and Diptera (Fig. 21.3) are the most diverse groups among saproxylic organisms; however, in comparison with Coleoptera, saproxylic Diptera are poorly known and generally underestimated (Stubbs 1982; Rotheray et al. 2001). Park and Auerbach (1954)

Fig. 21.3 Cetoniinae larva (Coleoptera, Scarabaeidae) (Photo E. Micó) (left) and aquatic saproxylic syrphid larva (Diptera) (Photo E. Galante) (right)

showed that 72% of the arthropods of a cavity are beetles and the number of species that a single cavity can host varies widely depending on the kind of cavity, volume and maturity. In a single hollow, up to 63 different species of beetles have been identified (data from 105 hollow trees of *Quercus* and *Fraxinus* Spain, unpublished data). More than 64 families, 380 genera and 720 species of Coleoptera have been reported from tree hollows, most of them associated with different kinds of cavities (see Table 21.1). Staphylinidae (including Pselaphinae) (>60 spp), Elateridae (>58 spp) and Tenebrionidae (>70) were the richest families (Table 21.1). In beetle assemblages, wood-dependent (including xylophagous, saproxylophagous and xylomycetophagous) are the predominant cavity inhabitants, some of them with high functional relevance such as Cetoniinae (Scarabaeidae) (Jönsson et al. 2004; Micó et al. 2015). However, predators seem to be very noteworthy in tree hollows (Pilskog et al. 2016). Quinto et al. (2014) found that more than 30% of the identified beetle species were predators, and many of them are obligatory saproxylic. Among predatory elaterids, some remarkable species are the near-threatened *Crepidophorus mutilatus* (Rosenhauer 1847), the vulnerable *Ischnodes sanguinicollis* (Panzer, 1793), the endangered *Podeonius acuticornis* (Germar, 1824) or the near-threatened *Elater ferrugineus* (Linnaeus, 1758), the biggest European elaterid that preys on cetonid larvae (Scarabaeidae, Cetoniinae) and a flagship for conservation (Bouget et al. 2008b; Müller et al. 2013; Micó et al. 2015). Park and Auerbach (1954) described Pselaphinae (Staphylinidae) beetles as hole specialists predating mites and collembolans. Moreover, other predator arthropods such as Araneae (Gouix 2011) and Pseudoscorpionida (Ranius and Wilander 2000) are also important members of the hollow invertebrate community. Moreover, predators, as they are in the top of the trophic chain, act also as a good indicator of cavity biodiversity. Nevertheless, the most important flagship species for tree hollow conservation in European countries are nonpredator wood mould inhabitants such as *Osmoderma* species (Box 21.1) and *Limoniscus violaceus* (Müller 1821). In this way *O. eremita* and *L. violaceus* are both included in Annex II of the EU "Habitats" Directive (Council of the European Community 1992, Nieto and Alexander 2010).

Box 21.1 *Osmoderma*—An Umbrella for the Protection of Tree Hollow Communities

Osmoderma (Coleoptera: Scarabaeidae: Cetoniinae) has a Holarctic distribution with 14 species across Europe, Asia and North America (see list below). The name of the genus, from Greek *osmos* = odour and *derma* = skin, refers to the distinctive odour that males emit as a pheromone to attract females. They are quite big beetles, about 18–36 mm long (Hoffmann 1939; Ranius et al. 2005; Audisio et al. 2007; Bezborodov 2015), and are among the most impressive beetle species living in tree hollows. The body is usually wide, oval and slightly flattened dorsally, and the pronotum is characterized by a distinct relief especially in the male (Medvedev 1960; Bezborodov 2015). Adults are

(continued)

Box 21.1 (continued)

lymphophagous and partly anthophagous (Medvedev 1960; Bezborodov 2015). Larvae are saproxylophagous, and their functional importance in the tree hollows is indisputable (see chapter main text). They develop in hollows of mature oaks, limes, beeches and many other deciduous tree species, including fruit trees, in both natural and urban environments (Hoffmann 1939; Carpaneto et al. 2010; Siitonen 2012), but also in warm-temperate evergreen forest in Japan (Seguchi and Sawahata 2016).

Although *Osmoderma* species are good flyers and can disperse over 1000 m, studies on *O. eremita* dispersion show that 85% of adults remain in their natal trees (Ranius and Hedin 2001; Ranius 2007). In Europe, there is evidence of a strong decline suffered by this taxonomic group throughout its distribution range owing to habitat loss and intensive forest management (Audisio et al. 2009). Due to the rarity and vulnerability of the taxa, many *Osmoderma* species have been included in Red Books in the Palearctic region (Audisio et al. 2007; Bezborodov 2015; Seguchi and Sawahata 2016), and one species, *O. eremita*, is protected by European laws (Annex II of the EU “Habitats” Directive, Council of the European Community 1992) (Nieto and Alexander 2010). In the Nearctic region, the conservation status of the three known species of *Osmoderma* deserve more attention, as they could be probably suffering a similar decline as in Europe. In this way, although *Osmoderma* Nearctic species can be locally abundant, they are rare in most part of their range (Ratcliffe 1971, 1991), and there are no current data on the evolution of their populations and habitat.

Osmoderma is considered among the most charismatic tree hollow inhabitants and, in the last decades, has become a flagship species for conservation in Europe (Audisio et al. 2007; Bezborodov 2015). Ranius (2002) demonstrated the value of *O. eremita* as an indicator of saproxylic beetle richness in tree hollows and concluded that it can be used as an “umbrella species” because measures taken to conserve the species will also favour many other hollow inhabitants. However, more studies are needed to check if *Osmoderma* species can act as “umbrella species” for the protection of the local saproxylic communities in all the Holarctic region as *O. eremita* currently does for beetle assemblages in Europe.

***Osmoderma* species list and distribution** (from Audisio et al. 2007, 2009 and Bezborodov 2015):

Osmoderma barnabita Motschulsky, 1845—Europe (*Osmoderma sikhotense* Boucher, 2002—Asia (Russia Far East)—has been considered a synonym of *O. barnabita*; see Audisio et al. 2007)

Osmoderma brevipenne Pic, 1904—Asia: Turkey

(continued)

Box 21.1 (continued)

Osmoderma caeleste (Gusakov, 2002)—Asia: Russia Far East, Korea, China

Osmoderma christinae Sparacio, 1994—Europe (Calabria and Sicilia)

Osmoderma dallieri Pic, 1945—*Nomina dubia* (distribution unknown)

Osmoderma davidis Fairmaire, 1887—Asia (Russian Far East, China)

Osmoderma eremicola (Knoch, 1801)—North America (Canada, USA)

Osmoderma eremita Scopoli, 1763—Europe (*Osmoderma coriarium* DeGeer, 1774, has been considered a synonym of *O. eremita*; see Audisio et al. 2007)

Osmoderma italica Sparacio, 2000—Europe (South Italy)

Osmoderma lassallei Baraud & Tauzin, 1991—Europe (Greece, European Turkey)

Osmoderma opicum Lewis, 1887—Japan, Russia Far East, Korea

Osmoderma richteri Medvedev, 1953—Europe (Georgian Caucasus)

Osmoderma scabrum (Palisot de Beauvois, 1807)—North America (Canada, USA)

Osmoderma subplanata Casey, 1915—North America (USA)

Far from the prolific data on Coleoptera, at least 12 families, 32 genera and more than 48 species of Diptera have been identified as tree hollow inhabitants (Table 21.1). Among Diptera, Syrphidae is the richest family (70% of saproxylic Diptera species, Table 21.1), and although, in general, tree hollows are not the most important microhabitat for saproxylic Diptera (Rotheray et al. 2001), there are syrphids such as *Callicera* and *Mallota* species that are specialized to exploit tree rot holes (Speight 1989, 2016). Among them, we highlight *Mallota dusmeti* Andreu, 1926, a vulnerable species exclusive to wet cavities whose populations have been favoured from tree management in Spain (Quinto et al. 2014). Although most saproxylic Diptera are saprophagous, we also find the predaceous habit among tree hollow specialists such as the larvae of the Dolichopodidae genus *Systenus* that are confined to rot-hole pools where they predate ceratopogonid midge larvae (Speight 1989). However, in contrast to Coleoptera requirements, the majority of saproxylic Diptera need measures to conserve wet microhabitats for breeding. Beetles frequently require veteran (large, old) trees, but although veteran trees often have more wet microhabitats than young trees, they are not essential for saproxylic Diptera in Northern Europe (Rotheray et al. 2001). The same is true of tropical forests, where there is an abundance of wet microhabitat besides tree hollows (Kitching 1971). Nevertheless, in drier climatic areas, tree hollows can be the most important of the very few wet resources for saproxylic organisms during late spring and summer, as occurs in the Mediterranean region (Marcos-García et al. 2011).

Reports of other insect orders in tree hollows are still scarce (Table 21.1). However, in certain latitudes, ants (Hymenoptera) and termites (Blattodea) are functionally important groups in tree cavities that provide habitat for a diverse fauna of beetles (Gibbons and Lindenmayer 2002). In tropical water-filled cavities, Odonata is also a relevant group that predates mosquito larvae (Fincke 1999) (Table 21.1) as larvae of *Ocyptamus* (Diptera, Syrphidae) do in other kinds of phytotelmata such as bromeliads (Rotheray et al. 2000). Moreover, besides the asymmetry in the study of taxonomical groups inhabiting tree hollows, there is also a gap in the knowledge of biology of many species. In this peculiar microhabitat, knowing the role of the species has a special relevance, as species composition can change widely from one region to another, but functions in the assemblage are generally preserved by different taxa.

21.6 Variables Affecting Tree Hollow Insect Assemblages

In the same way that diversity of microhabitats (large trees, cavities, fruiting bodies of saproxylic fungi, tree crown dead wood, sap runs, logs and snags) favour species diversity at the forest level (Bouget et al. 2014), tree hollow heterogeneity (e.g. caves of different sizes and trunk positions) at a local level seems to drive tree hollow species diversity as different tree cavities can host different assemblages, thus increasing species turnover (Ranius 2002; Schmidl et al. 2008; Gouix et al. 2015; Quinto et al. 2014). García–López et al. (2016) compared species turnover among emergence traps within and among forests and deduced a stronger relationship between these species and the micro-variables of the tree hollow, compared to the forest environment.

Many variables can characterize a tree hollow, including physical, biotic and chemical ones (Micó et al. 2015). However, it is difficult to depict the thin line that delimits the boundaries of the effects of each kind of variable on tree hollow assemblages—e.g. Cetoniinae (Coleoptera, Scarabaeidae) larvae have been largely recognized as ecosystem engineers that can modify the volume and chemical composition of wood mould (Jönsson et al. 2004; Micó et al. 2011). With regard to the main physical variables, the presence or absence of semi-permanent water and deepness, the area of the entrance of the cavity and its orientation, the hollow volume (size of the cavity), the wood mould volume and the cavity height, among other variables, affect at least some components of the saproxylic assemblage inhabiting tree hollows (Ranius 2002; Schmidl et al. 2008; Quinto et al. 2014; Gouix et al. 2015). In general, larger habitats may be more productive and heterogeneous and contain more microhabitats than smaller habitats (Schoener 1989). Large habitats may also be more stable and resilient to disturbance allowing larger populations of species (Wright 1983). However, experimental studies on Diptera from dendrotelms show that modifying abiotic factors such as water oxygen concentration may affect community structure in ways not predicted simply by habitat size (Harlan and Paradise 2006). Moreover, more individuals (associated with more stable and productive conditions) did not lead to higher species richness in artificial tree holes (Srivastava and Lawton 1998) or in natural hollows (Schmidl et al. 2008). Hollow volume (and wood mould volume) is normally positively correlated with species richness and abundance of saproxylic beetles (Micó et al. 2015; Gouix et al. 2015), but quantity is not the only factor of importance; substrate quality is both the cause and consequence of tree hollow diversity (Jönsson et al. 2004; Reemer 2005; Micó et al. 2015). In this way, the chemical composition of cavities could provide information about the past and present diversity of certain taxa in the cavities and could also become a useful tool in functional diversity studies for the future (Micó et al. 2015).

The contribution of biotic factors in the hollow assemblage's structure and composition occurs at different levels. Because fungi constitute the trophic resource for mycetophagous species, for example, fungal composition plays a key role in determining substrate quality and the successional trajectory for the entire assemblage. In the same way, the presence of vertebrate nests provides more nutrients mainly for saprophagous guilds. However, one of the less explored biotic factors concerns the interspecific interactions including facilitation, predation and competition. Sánchez-Galván et al. (2018) found that predation and facilitation, together with habitat segregation, are major factors shaping tree hollow assemblages. The presence of ecosystem engineers such as *Cerambyx* and Cetoniinae larvae not only favours species diversity in tree hollows but also affects the structure of the assemblage, each one favouring predator and saprophagous guilds, respectively (Micó et al. 2015). Sánchez-Galván et al. (2014) also demonstrated under laboratory conditions that an enriched substrate with *Cetonia aurataeformis* (Curti, 1913) larval faeces improves syrphid larval growth rate and the fitness of adults (measured as longer wing length) of *Myathropa florea* (Linnaeus, 1758). A similar example of facilitation occurs with the leaf scraping scirtid beetles that increase the rate at which leaf litter is converted to fine particles favouring *Ochlerotatus triseriatus* (Say, 1823) (Diptera, Culicidae) populations (Daugherty and Juliano 2003).

Among interspecific interactions, competition may be especially important in tropical habitats that harbour high species diversity (Fincke 1999). In fact, intraguild predation plays an important role in organizing odonates that develop in water-filled tree holes in Panama, where the fast initial growth of some species realizes a competitive advantage (Fincke 1992, 1994, 1999). However, competition does not seem to be driving the assemblage structure in wood mould cavities (Sánchez-Galván et al. 2018).

Understanding the contribution of the biotic variables, including interspecific interactions in tree hollows, is still a challenge as it seems to be an important piece of the puzzle to comprehend this peculiar habitat.

21.7 The Future of Tree Hollow Assemblages

Tree hollows provide important habitats for a wide range of invertebrates, reptiles, amphibians, birds and mammals (Gibbons and Lindenmayer 2002; Ranius et al. 2005; Kosinski 2006). However, species dependent on tree hollows are facing decreasing habitat availability because ancient trees have declined both in forests and agricultural landscapes (Nilsson 1997; Kirby and Watkins 1998). From the wide range of tree hollow inhabitants, some are obligate cavity users and others are opportunistic or facultative users. The loss of cavities in an area will most heavily impact obligate users and variably affect facultative users (Warakai et al. 2013; Bergman et al. 2012).

Forest reduction affects all saproxylic diversity, but it affects greatly the tree species most likely to form hollows (Remm and Lohmus 2011). In addition, the number of hollows within a landscape may drastically reduce due to climate change (Hunter 2015). Moreover, forest fragmentation has been shown to preclude movement between remnant forest fragments of tree hole-breeding specialists (Ranius 2002; Khazan 2014; Khazan et al. 2015).

In addition, forestry has reduced old tree density because trees are often cut before hollows are formed (Eliasson and Nilsson 2002; Fan et al. 2004; Andersson and Östlund 2004; Lindenmayer et al. 2012) and old trees in natural woodlands are dying without regeneration. Trees in agricultural landscapes represent seminatural habitats that can act as biodiversity reservoirs (Micó et al. 2010). However, the intensification of agricultural production has resulted in the loss of many traditional orchards and the associated saproxylic biodiversity (Donald et al. 2006) due to the installation of modern cultivation systems. Hence, forest reduction and fragmentation, climatic change, forestry and the abandonment of cultural practices together result in a situation where tree hollows as keystone habitats are threatened. Because hollow trees will not persist forever, it is essential to ensure that new hollow trees are generated to maintain a given number (Ranius et al. 2009). A particular problem in addressing this goal is the long time that hollows take to form; the age at which eucalypts produce hollows is 150–250 years (Gibbons and Lindenmayer 2002), and the same occurs with the pedunculate oak (*Quercus robur* L.) which has a probability of cavity presence of 1% at less than 100 years compared to 50% at 200–300 years (Ranius et al. 2009). In Australia, the smallest arboreal marsupials and hollow-dependent birds could recolonize regrown *Eucalyptus pilularis* Smith trees after about 165 years; however, hollows suitable for larger animals would not be available for around 210 years (Wormington and Lamb 1999). The same has been shown for some flagship species of hollow insect assemblages such as *Osmoderma eremita* (Coleoptera, Cetoniinae) and *Limoniscus violaceus* (Coleoptera, Elateridae) that are dependent on big cavities with abundant and mature wood mould (Ranius and Nilsson 1997; Gouix et al. 2015). This means that there can be a significant lag time between detecting a species' population decline and arresting the lack of hollows through reducing tree mortality and increasing regeneration (Manning et al. 2013).

Fig. 21.4 Pollarded *Quercus pyrenaica* trees (Photo E. Micó)

It is necessary to preserve tree hollows to maintain the complex assemblages living in them, but in addition, we need to ensure that sufficient numbers of hollow trees are maintained continuously in the future (Ranius et al. 2009). A key question is how many hollow trees are needed to preserve diversity. Bergman et al. (2012) found that at least 0.15 ha^{-1} big and mature trees were needed to preserve the richness of those obligate cavity users in Northern Europe; however, more studies in other regions are still needed. To overcome the problem of the lack of tree hollows, nest boxes have been employed largely as a management tool to aid cavity-dependent vertebrates (Newton 1998; Warakai et al. 2013). However, there is uncertainty as to whether nest boxes can be considered an adequate functional substitute for tree holes as tree cavities and nest boxes may differ in many aspects, including microclimate (Maziarz et al. 2017). Jansson et al. (2009) suggest using special boxes that mimic tree hollows to help preserve endangered populations of hollow-dependent beetles as is commonly done with bird nest boxes. In a 10-year experiment using these wooden boxes, Carlsson et al. (2016) showed that beetle richness decreased from the fourth year as wood mould volume also decreased; however, the assemblage became increasingly dominated by specialized hollow tree species including *Osmoderma eremita* that requires old trees and mature wood mould (Ranius et al. 2009). However, as we have seen before, species interactions are important in determing assemblage structure, and it remains unknown how losses of facultative species from these artificial cavities may affect assemblage structure.

Another alternative for reaching the goal of replacing hollow-bearing trees as they are lost is to promote the formation of hollows in younger trees. Sebek et al. (2013) suggest going back to the age-old practice of pollarding (Fig. 21.4). Traditionally, pollarding has allowed harvesting of firewood from trees without killing them and has already been considered as a conservation practice for both the trees and their associated faunas (Read 1996; Sebek et al. 2012; Quinto et al. 2014). Sebek et al. (2013) demonstrated that at least in willows, pollarding increases the probability of hollow formation (e.g. in trees of 50 cm DBH, the probability of hollow occurrence was 0.75 in pollards versus 0.3 in non-pollards). However, during the last century, pollarding has been abandoned in most of Europe (Read 1996; Leppik et al. 2011).

Conservation and retention of hollowed trees has crucial importance for forest diversity maintenance worldwide; thus, actions should be urgently adopted. Creating artificial habitats and active management could help to prevent the gradual decimation of saproxylic biodiversity (Sebek et al. 2013); however, researchers, forest managers, policy makers and citizens all have a role to play in the protection and cultivation of these keystone structures.

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Chapter 22
It's the End of the Wood as We Know It: Insects in Veteris (Highly Decomposed) Wood

Michael L. Ferro

> Living trees are all alike, every decaying tree decays in its own way.
>
> —*with apologies to Tolstoy*

Abstract The final decay stage of wood, termed veteris wood, is a dynamic habitat that harbors high biodiversity and numerous species of conservation concern and is vital for keystone and economically important species. Veteris wood is characterized by chemical and structural degradation, including absence of bark, oval bole shape, and invasion by roots, and includes red rot, mudguts, and sufficiently decayed wood in living trees and veteran trees. Veteris wood may represent up to 50% of the volume of woody debris in forests and can persist from decades to centuries. Economically important and keystone species such as the black bear [*Ursus americanus* (Pallas)] and pileated woodpecker [*Dryocopus pileatus* (L.)] are directly impacted by veteris wood. Nearly every order of insect contains members dependent on veteris wood, including species of conservation concern such as *Lucanus cervus* (L) (Lucanidae) and *Osmoderma eremita* (Scopoli) (Scarabaeidae). Due to the extreme time needed for formation, veteris wood may be of particular conservation concern. Veteris wood is ideal for research because invertebrates within it can be collected immediately after sampling. Imaging techniques such as Lidar, photogrammetry, and sound tomography allow for modeling the interior and exterior aspects of woody debris, including veteran trees, and, if coupled with faunal surveys, would make veteris wood and veteran trees some of the best understood keystone habitats.

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22.1 Introduction

The study of deadwood is in its infancy, and researchers are currently staggering under the immense variety of microhabitats (decay stage, size, position, sun exposure, etc.) made possible by deadwood. The purpose of this chapter is to comment on insects found in the final decay stage of wood, an often overlooked habitat of little immediate economic value. The term “veteris,” invented and defined below, is meant to collect related things—a rotting log half buried under leaf litter, a dead limb still in the canopy, heartrot almost entirely encased in a living trunk, exposed deadwood in a living tree, and a tree hole itself—and bring them together. The following is both an overview of the collective “final decay stage of wood” (herein “veteris wood”) as it relates to insects and in part a larger argument for the next stage of saproxylic research, one that seeks to be more universal and allow for realistic comparisons across studies.

22.2 Beginnings

Much like the growth of a baby bird, the study of saproxylic environs and organisms has progressed from a generalized egg stage, with its grand potential fully recognized but not fully known, through the downy squawk of adolescence reeling about trying to understand limits and possibilities, to a full-fledged adult bound in a seeming infinity of feathers, and revealing further infinities of interactions, behavior, and song.

Early authors provided tantalizing but general descriptions of rotting logs and dead trees: Beebe’s (1925) description of diversity of insects associated with the early stages of tree decay reads like an adventure novel; Hubbard (1899) similarly described collecting insects from decaying Saguaro (*Carnegiea gigantea* (Engelm.) Britton and Rose) like a child opening Christmas presents; Morley (1935) provided a list of the myriad species and their parasites found swarming a beech snag; Adams (1915), Shelford (1913), Silvestri (1913), Wallwork (1976), and Wilson (1959) gave a general overview of log decay, listed species, and designated successional stages; Fager (1968) studied invertebrates in decaying oak wood and “synthetic logs”; Hickin (1963) highlighted insects as decay agents in structural wood; Blackman and Stage studied insect succession in American larch (1918) and Hickory (1924); Howden and Vogt (1951) did the same for standing dead pine (*Pinus virginiana* Mill.); Graham (1925) reported the effect of abiotic differences (especially temperature and moisture) on insects in logs; Savely (1939) provided a well-rounded expedition into biotic and abiotic aspects of succession in pine and oak logs; Mamaev (1961) began classifying succession and quantified insect use of logs; the descriptions of wood decay by Käärik (1974) and Swift et al. (1979) concentrated on nutrients, the fate of macromolecules, and microorganisms; Shigo and Marx (1977) and Shigo (1979) demonstrated how trees react to damage and set the stage for understanding creation and maintenance of saproxylic habitats within living trees; Hamilton (1978) forced us to reconsider the deadwood habitat beyond simple succession and place it within an evolutionary context; and finally Elton (1966) placed rotting wood within the framework of the surrounding forest, clearly demonstrated the importance of the habitat, asked more questions than he answered, and inspired a future generation of students.

After Elton (1966), researchers began to move beyond the rotting log as an independent unit (an island in the ocean) and began to recognize it as a dynamic component that creates a part of the landscape, rather than simply residing within it (the same quality as, say, a stream in the woods). Harmon et al. (1986) provided perhaps the first and last review of coarse woody debris that could encompass every aspect of the subject and still adequately reflect the extent of the literature available. Thomas (1979), Triska and Cromack (1980), Maser et al. (1979), Maser and Trappe (1984), and Maser et al. (1988), all working in the Pacific Northwest of the USA, characterized deadwood with increasing breadth and specificity and illustrated that it was a necessary component of a functioning forest. In the USA, the Forest Service expanded their conception of deadwood beyond salvage and fuel for fires to include many aspects such as ecosystem services and use by invertebrates and fungi (e.g., Bull et al. 1997; Laudenslayer et al. 2002; McMinn and Crossley 1996).

The recognition that deadwood was more than a curio, nuisance, or a wasted resource—but actually a component of a healthy forest, as important as the living trees themselves—resulted in a wave of specialized research. Long-term studies of log decomposition are underway in Oregon, USA (Harmon 1992), and Tasmania, AU (Grove and Forster 2011). Whereas earlier the plight of a rotting log occupied a few pages in a book (e.g., Adams 1915: 148–157), deadwood and saproxylic insects were given entire chapters and volumes (Dajoz 2000; Johsson and Kruys 2001; Lofroth 1998; Rose et al. 2001; Schlaghamerský 2000). Speight (1989) authored the foundational document that linked biodiversity loss to the loss of the saproxylic habitat. Immediately conservation of saproxylic organisms became a major research topic (e.g., Kirby 1992: habitat management for saproxylics; Kirby and Drake 1993, “Dead wood matters!”). Initially “general” research was conducted on the more specific topic of saproxylic invertebrates, for example, linking amount or quality of deadwood to saproxylic diversity at the stand level (see Tables 2 and 3 in Grove 2002). More specific research into the subsets of saproxylic habitats, their origin and fate, their place within the landscape, and the organisms involved followed (e.g., Grove 2002; see Ferro et al. (2012b) for a partial review). Ferro et al. (2012a) provided a review of research on downed coarse woody debris in the final stage of decay.

Presently the study of biodiversity in deadwood, and the conservation and management thereof, has matured into a fully developed and independent discipline. Harmon (2002) proposed “morticulture”—management of woody debris for future needs—and Cavalli and Mason (2003) showed the practical application of that idea in Bosco della Fontana Nature Reserve in Italy. Lonsdale (2013, and references therein) provided management advice to maintain and enhance saproxylic habitats at the level of the individual tree! A series of meetings specific to European saproxylic beetles of conservation concern began (e.g., Bowen 2003) and continues; the ninth was held in Belgium in 2016. Some flagship saproxylic species of conservation concern are particularly well studied (e.g., *Osmoderma eremita* (Scopoli) (Coleoptera: Scarabaeidae), Chiari et al. 2012, 2013a, b; Ranius et al. 2005, and references therein). For some specific topics related to saproxylic biodiversity, published literature is sufficient to warrant a review and synthesis (e.g., canopy habitat, Ulyshen 2012; a decade of "deadwoodology," Grove 2009). Book-length works illustrating the importance of deadwood and its role in particular landscapes are available (Maser et al. 1988, well ahead of its time; Cavalli and Mason 2003; Bobiec et al. 2005). Finally, Stokland et al. (2012), a text devoted entirely to biodiversity in deadwood, simultaneously serves as the capstone of the present era and as the foundation for future studies.

22.3 Definitions

> *…we expect the world to be classifiable. For most of us it requires almost a change of creed to admit that it is not…*
> —Hynes 1975

To ease communication, or reduce overwhelming complexity, we create definitions—a small set of "boxes" that, together, hold the majority of the entities within a particular system. Because of the simplification or generalization that takes place when a definition is created, it's unlikely that a single definition will work equally well in all situations.

Saproxylic Numerous definitions of saproxylic exist. Speight (1989) provided the most popular definition of saproxylic, and Alexander (2008) provided a well thought-out refinement. Both definitions take a "positive" or "resource-centric" approach, attempting to encompass organisms that require deadwood. An alternative definition could take a "negative" or "community-centric" approach: Saproxylic species—*any species that would no longer be present in a community if deadwood were no longer available, including deadwood in live trees*. Stokland and Siitonen (2012b: 249) describe a similar approach. The definition removes the awkward necessity to highlight species that indirectly use deadwood but are ultimately dependent upon it (e.g., a hyperparasite of a parasite of a beetle that eats fly larvae on the fruiting body of a fungus that consumes the decaying heart wood of a living tree). Of course any given species will still fall on a spectrum from obligate to facultative.

Wood For our purposes, a meaningful definition could be *tissue of a plant, usually part of a stem, trunk, or limb, composed of a combination of cellulose, lignin, and hemicellulose*. Some plant parts that may or may not be covered by that definition include the flowering stalk of an agave, "trunk" of a banana tree (composed of leaves), and/or the petiole of a palm leaf (rigid, similar to a limb).

Dead Occasionally there is confusion between "living," "dead," and "functional," for example, in some trees, cells may be "dead" but still functional for support and transportation of water; in birds, feathers are functional despite being "dead." Shigo (1991) divided trees into dynamic mass ("alive," requiring energy) and static mass ("dead," no longer requiring energy). Ideally "dead" plant material *lacks the ability to metabolically react to stimuli*. Exceptions may include "live" but frozen material, a fresh-cut limb which contains cells that react to stimuli but with little intensity or short duration (not dead but "dying"), and heartwood with no metabolism but containing compounds that remain active to confound insects and fungi.

Deadwood *Tissue composed of cellulose, lignin, and hemicellulose that can no longer metabolically react to stimuli*. Based on the above definitions, what answer would be given to the following question: How much deadwood is in a forest?

Multis wood *Deadwood available to saproxylic organisms*. Every year, a new tree grows over the old (core-skin hypothesis, Shigo 1991), and in many tree species, the inner portion of the tree consists of "deadwood" as defined above. Deadwood sheathed in living wood is generally not available to saproxylic organisms. Therefore the amount of (1) deadwood in a landscape and (2) deadwood available to saproxylic organisms differs greatly. This distinction has not been encountered in the literature by the author; therefore it is introduced here. While not given a specific term, the concept of "multis wood" has existed for a while, e.g., high stumps and other strategic tree wounding to make already deadwood available (see Birtele 2003). The term "multis" is Latin meaning "many," referring to the many organisms that utilize it as a resource.

Veteris wood *The final decay class of wood*. Decay stages are designated and defined in a variety of ways (see below), but all decay classifications contain a final stage. A single term (keyword) used to designate that stage facilitates online alerts and literature searches. The terms "really rotten," "highly decayed," "advanced decay," and "final decay" are restricted to English and too generalized, whereas "veteris" provides an unambiguous designation and is useful across multiple languages. The term "veteris" is taken from Latin meaning old or ancient.

The conception of veteris wood, based on decay class descriptions below, is of wood that has undergone both structural and chemical degradation. Generally, veteris wood is *not structurally sound and has undergone chemical decomposition due to weathering or mechanical and/or enzymatic action of decomposer organisms*. Cells in a wooden ax handle may be devoid of virtually all their cell contents, but as long as the wood maintains structural integrity, it would not be considered veteris. Similarly a fresh-cut log that is chipped to smaller pieces would not be considered veteris because of its "fresh" chemical composition.

Types of veteris wood may include (Fig. 22.1) all or part of logs, stumps, and roots, portions of snags and canopy wood such as limbs, heartrot within healthy trees, sufficiently decayed material within and on the side of tree hollows, and the outer covering of exposed deadwood within living trees—which may range from a few millimeters to centimeters thick but still offers protection to organisms in the

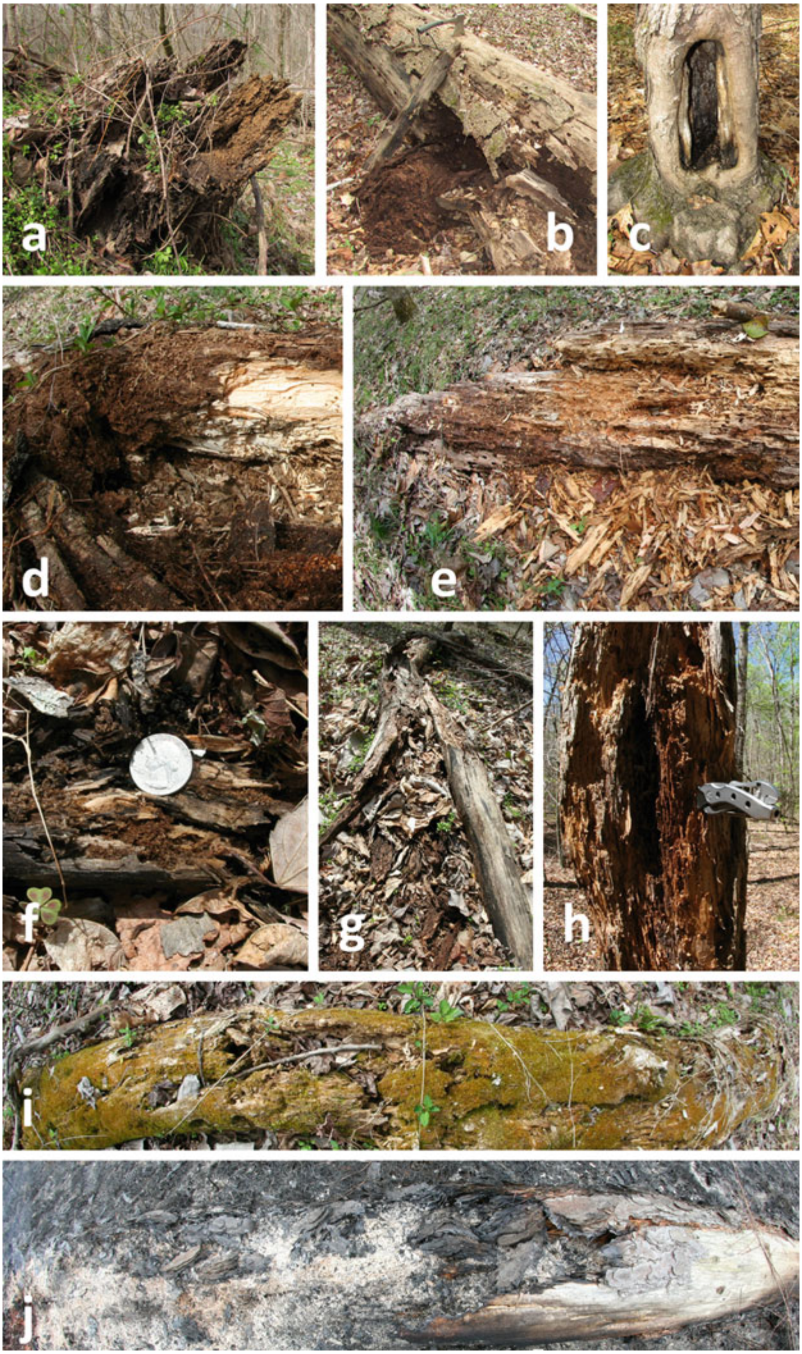


Fig. 22.1 Examples of veteris wood. (**a**) Stump; (**b**) log with a structurally sound exterior, but with interior highly decomposed, dissected to show anatomy; (**c**) tree hollow; (**d**) log with highly

less-decayed wood beneath. Organisms that rely on external fruiting bodies of fungi that cause inner heartrot may be considered veteris wood dependent, as well. Tree holes or tree hollows could be thought of as "veteris structures."

As is obvious above, veteris wood is a broad concept that includes many varieties of wood that have reached a highly decomposed state in a variety of ways. The concept of veteris wood is partially an artifact of human ideas and partially a natural grouping. It is a human-derived and meaningful concept in the same way that the term "tree" is human-derived and meaningful.

22.4 Decay Class and Veteris Wood

Decomposition of wood is divided into useful subsets through the concept of decay class (e.g., overview in Stokland and Siitonen 2012a: 126). How to measure decay class and how many decay classes exist depend on the woody species, environment, and question being asked (fuel quality, structural integrity, nutrient content, biodiversity supported, etc.; see Feller 2003); thus many valid decay classifications exist. Based on the decay classifications surveyed (Table 22.1), the criteria used to designate veteris wood include (1) structural aspects (bark absent, wood easily broken or crushed, oval bole shape, integration with the soil); (2) overgrowth by mosses, herbaceous plants, or trees; (3) invasion by roots; and (4) the presence of worms and other organisms associated with the soil.

Further refinements of decay class will be necessary as researchers strive to increase the accuracy and precision of their observations. Enrong et al. (2006) reviewed the concept and definition of coarse woody debris and recommended a three-part classification system where deadwood was classified by (1) size (coarse, fine, etc.), (2) position (standing, fallen, etc.), and (3) decay class. Pyle and Brown (1999) recognized that while any given log could be designated a particular decay class (e.g., 3 on a scale of 1–5), the log actually consisted of a mosaic of decay classes with pockets and sections of less or greater decay. A living tree with exposed deadwood would add an additional tile to the mosaic (to expand on the analogy). Grove et al. (2011), working in Tasmania, surveyed *Eucalyptus obliqua* logs across all decay stages and designated 27 types of rotten wood, but concluded that a system of five externally derived classes was sufficient to accurately describe decomposition in their study area. Yee et al. (2006), dissecting long-dead *Eucalyptus obliqua* logs,

◄

Fig. 22.1 (continued) decomposed exterior, but with structurally sound interior, dissected to show anatomy; (**e**) fragmentation of a decomposed log by woodpeckers; (**f**) veteris fine woody debris; (**g**) log with central portion completely humified; (**h**) snag with at least outer 8 cm composed of veteris wood based on knife penetration definition (García-Lopez et al. 2016); (**i**) veteris log covered in moss; (**j**) log with a portion highly decomposed by fire. All images from Sumter National Forest, Laurens Co., SC (~N 34.549°, W 81.709°), except (**h**), from Clemson Experimental Forest, Anderson Co., SC

Table 22.1 Definitions of veteris wood based on various classification systems

Class	Veteris definition	Region	Citation/notes
2	Rotten: "…the piece at the intersection is obviously punky or can be easily kicked apart"	Western NA	Brown (1974). CWD
2	Rotten: "Rotten material includes downed pieces that show rot visibly on the outside"	Rocky Mountains, NA	Brown and See (1981), in relation to fire fuel. CWD
2	Decayed: "If the outer layer could be fragmented by hand, and the branches could be pulled free from the bole, including heartrot"	Boreal NA	Sturtevant et al. (1997). CWD. Based on Brown (1974)
3	3: Combination of classes 4 and 5 from Maser et al. (1979) [Structural classes for wildlife use (vertebrates)]	Oregon, Washington, USA	Bull et al. (1997). CWD. Based on Maser et al. (1979). Used by Rose et al. (2001)
3	3: "Knife penetrates the wood without resistance, bark loose and mostly gone"	Chile (central)	García-Lopez et al. (2016). CWD. Based on Franc et al. (2007)
3	3: <60% log covered by bark; >30% log covered by nonvascular and vascular plants; >60% of cross-sectional area showing decay	Western Canada	Hammond et al. (2004). CWD, *Populus*
3	III: "More than 75% of the wood soft and rotten, can be kicked into pieces"	Chile (central)	Schlegel and Donoso (2008). CWD
3	Humification phase: wood has been converted into a red-brown friable mass, composed largely of the feces of saproxylics. Species from the soil invade	Europe, general	Speight (1989). CWD
4	4: "Knife penetrates the wood without resistance, bark loose and mostly gone"	S. Sweden (temperate)	Franc et al. (2007). CWD
4	Age class 4: "The form is amorphous, several wood pieces are still maintained, but overall the wood is more or less totally rotted"	Germany	Irmler et al. (1996). CWD. Based on Brauns (1954); Schimitschek (1953); and Szujecki (1987)
4	IV: "Wood soft and rotten, partly integrated to the forest soil (humus)"	Benin, Africa	Lachat et al. (2006). CWD
4	Earthworm: "Lumbricidae, Enchytraeidae, and other invertebrates of the fourth complex repeatedly digest the wood dust formed and can be regarded as humifiers"	Caucasus, Russia	Mamaev (1961). CWD. See also Dajoz (2000) for English summary

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
4	4: "The bark fallen off; the log a mere mass of rotten wood"	Temperate, USA	Shelford (1913). CWD
4	IV: Mean relative density <45% of initial density	Germany	Spänhoff et al. (2001). FWD, aquatic
5	Much decayed wood: "...the tree trunk decays and naturally sinks lower and lower, the woody fibers disappear, the debris becomes darker in color, the autumn leaves, twigs, and other litter of the forest gradually add layer to layer, and finally the remains of the log become blended with the humus of the forest floor"	Chicago, USA	Adams (1915). CWD
5	V: "Leaves, twigs, and bark absent; bole shape oval to flat; wood consistency soft; other wood properties, fragmented to powdery"	Chile (central)	Carmona et al. (2002). CWD. Based on Sollins (1982) and Spies et al. (1988)
5	5: Structural integrity soft; leaves, branches, bark absent; bole shape oval to flat; wood consistency fragmented, powdery; color of wood heavily faded; all of log on ground; invaded by roots throughout; knife blade penetrates all the way	General	Enrong et al. (2006). CWD. Based on Carmona et al. (2002); Maser et al. (1979); Spetich et al. (2002); Sollins (1982); and Rouvinen et al. (2002)
5	No formal definition; see p. 190	General	Harmon et al. (1986). CWD.
5	Class 5: "Logs were elliptical in cross section (indicative of advanced decay) and in many cases the wood was scattered across the soil surface"	Yucatan, Mexico	Harmon et al. (1995). CWD. Based on Harmon et al. (1986). Used by Keller et al. (2004)
5	V: Bark absent; twigs <3 cm absent; texture soft and powdery; shape oval; color of wood red brown to dark brown; all of tree on ground; invading roots in heartwood	Oregon, Washington, USA	Maser et al. (1979); Maser and Trappe (1984). CWD, Douglas fir. Used by Shifley et al. (1997); Bobiec et al. (2005)
5	V: Bark not firmly attached; wood without has fresh color; branches without small twigs; log not a solid piece; log shape may be oval; no hard chunks remaining; kicked log will not cleave into large pieces; log may crush when thudded with a foot; log is	Eastern USA	Pyle and Brown (1999). CWD. Used by Ferro et al. (2012a, b). Modified by Woldendorp et al. (2002a, b)

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
	predominantly powdery wood; log shape may be flattened		
5	5: Bark absent; no structural integrity; twigs <3 cm absent; texture of rotten portions soft, powdery when dry; color of wood red- to dark-brown; invading roots throughout; vegetation—*Tsuga* up to 200 cm dbh; shrubs, some large, moss; fungal fruiting; mycorrhizae present	Oregon, Washington, USA	Triska and Cromack (1980). CWD, Douglas fir. Used by Sollins (1982); Sollins et al. (1987); Spies et al. (1988); Hale and Pastor (1998); Hardt and Swank (1997)
5	V: Description, very decayed; leaves absent; wood punky; shape and form <oval, collapsed	Wisconsin, USA	Tyrrell and Crow (1994b). CWD
5	V, Staphylinid stage: "The bark has mostly or entirely fallen off, and the entire log may be covered with moss or herbaceous plants. Wood adjacent to the ground has deteriorated to the point of mingling with the soil"	Tropical, New Guinea	Wilson (1959). CWD
5	No longer retains original shape; wood very soft or largely disintegrated; sometimes only outline visible beneath moss, invading roots, etc.	Australia	Meggs (1996). CWD. Used by Grove et al. (2011)
5	V: Soft and powdery (when dry), often just a mound; log does not support own weight; does not hold original shape, flattened and spread out on ground; moss, herbs, fungal bodies may be present; invading roots (when present) are throughout; hollow log from termite damage may have collapsed or be a thin shell	Australia	Woldendorp et al. (2002b). CWD. Based on Sollins et al. (1987); Pyle and Brown (1999); Spetich et al. (1999)
5	5: Wood very soft, almost completely decomposed, and easily crushed between fingers, trunk considerably shrunken, mostly covered with ground floor cryptogams and/or shrubs. Spruce trunks often bearing spruce seedlings	Finland	Renvall (1995) (Knife method). CWD. Used by Kuuluvainen et al. (2001)
6,5	Yellow cedar, 6: "Bole broken at soil level." Western Hemlock, 5: "Integrated into soil"	Western NA	Hennon et al. 2002. CWD
6	DC 6: Diameter hard to measure; no bark; wood texture soft; oval	Boreal NA	

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
	cross section; needles, branches absent; ground contact, >50% sunken, >30% covered in plants, mostly covered in moss		Lee et al. (2014). CWD, white spruce. Based on Hofgaard (1993)
6 (0–5)	5: "Little visible structure remaining, the wood having mostly degraded into soft, particulate matter," exterior no longer intact	NSW, Australia	Barclay et al. (2000). CWD
8	8, Incorporation: Wood no longer recognizable by species, 20–30% soil mixed into wood, mass of mycelia, fibrous and woody root systems colonizing throughout the area	Eastern USA	Ausmus (1977). CWD. Used by Hendrix (1996)
8	Stage 8: Ten years dead and over—"Trees with sapwood reduced almost to pulp, and with only a small hard core of the heartwood remaining"	Virginia, USA	Howden and Vogt (1951). CWD, standing dead *Pinus virginiana*
8,8,5	Three systems. System A, 8: Pulverized wood, log buried. System B, 8: Completely soft without evidence of hard wood, outline indeterminable. System C, 5: Fragmented, overgrown with contours of completely decomposed log	Norway	Storaunet and Rolstad (2002). CWD, Norway spruce. Based on multiple authors

Class = total number of classifications the woody debris was separated into. Veteris definition = verbatim or paraphrased description of the final decay stage within that classification system. Notes include the type of woody debris and association with other research

designated 11 "rotten wood types," of which all would probably be considered veteris. Most practical applications of decay class designation have only been applied to down woody debris, snags (Thomas et al. 1979), and occasionally stumps; few exist for twigs (but see Mertl et al. (2009)), roots, or deadwood within living trees. However, decay in living trees has been well studied from the standpoint of trees as a renewable resource (e.g., Shigo 1979; Shortle and Dudzik 2012), but that work has not been incorporated by the larger saproxylic research community.

While a few researchers have conducted research specific to wood decay in relation to habitat (Grove et al. 2011; Pyle and Brown 1998, 1999), historically the creation, definition, and study of decay classes have been subservient to initial study questions such as fuel loads or biodiversity use. Ultimately description of types, states, classes, etc. of saproxylic habitat will probably become much more complicated than the simplistic decay classes presented here. There is no reason to believe that classification of wood decay cannot/will not become as refined as, for example, the modern soil classification system which employs a six-level hierarchy and lists 19,000 series (most refined unit) in the USA alone (USDA 1999).

22.5 Amount of Veteris Wood

Many publications provide measures of the amount of woody debris at a location or study site (see Goodburn and Lorimer 1998, Table 4 for a brilliant example). Often they provide the wood type (coarse, fine, dead limbs in standing trees, hollow trees, etc.), disposition (standing, fallen, partially submerged, etc.), state of decay (multiple classes used), site characteristics (unlogged, selectively logged, clear-cut, fire, hurricane, etc.), time since disturbance, tree species present, tree species absent, tree species studied, etc. (see references in Table 22.2). Findings are typically reported as a measure of volume, mass, or percentage, and a wide variety of units are used (board feet per acre, Mg ha^{-1}, etc.). Needless to say, a summary or meaningful comparison of amount of deadwood, much less veteris wood, across sites is difficult to compile. Feller (2003) provides a good case history for British Columbia, Canada. The "community" of publishers and researchers should develop a standard set of measurements and units that must be taken at a study site and reported in the resultant publication, whether all are necessary for the particular research or not. Similar standards already exist for reporting biodiversity data (e.g., Darwin Core, Wieczorek et al. 2012).

Table 22.2 summarizes 17 studies, ranging from 3° to 65° from the equator, in which amount of veteris wood was measured. Virtually all studies looked at coarse woody debris logs, while a few included snags or stumps. None listed estimated amount of attached deadwood (multis) within living trees (but see Nordén et al. (2004) for a rare example). The volume of veteris ranged from 0 to 54.4 m^3/ha (average 13.5 m^3/ha), and percentage of deadwood that was veteris ranged from 0 to 53.3% (average 18.2%).

The relationship between the amount of veteris and disturbance (logging, fire, etc.) is not straightforward (Table 22.2; Feller 2003). Within studies where multiple locations were compared, four studies (Table 22.2; #1, 8, 17a-reduced impact, 17b) showed an increase in veteris after selective logging (either by volume or percentage), and four showed a decrease (Table 22.2; #12, 13, 16, 17a-conventional). However, measurements at a single time may be misleading. Woody debris volume often follows a U-shaped trend after a disturbance because of carryover woody debris—debris in the present stand that originated in the previous stand (Carmona et al. 2002; Feller 2003; Maser et al. 1988). A large reduction of veteris was reported in a Newfoundland forest chronosequence study 60–70 years after disturbance (Sturtevant et al. 1997) and in hemlock-hardwood forests 200–250 years after disturbance (Table 22.2; #6). A postfire chronosequence in Quebec (Table 22.2, #5) showed a complete loss of veteris during ~55–75 years postfire; however, other decay classes were available throughout the entire 90-year period studied. These findings indicate that maintaining continuity of specific decay classes at a site is not a simple matter and may require decisions decades in advance.

Table 22.2 Amount of veteris wood reported from various locations arranged from furthest to nearest equator

#	Amount of veteris			Substrate	History of site	Forest type	Lat.	Location	Citation
	m^3/ha	Mg/ha	%						
1	8		15.6	CWD, logs	Primary	Boreal, Norway spruce dom.	65°N	Finland, eastern	Sippola et al. (2001)
1	9.4		32.3	CWD, logs	Selective logging ca. 1930–1960	Boreal, Norway spruce dom.	65°N	Finland, eastern	Sippola et al. (2001)
2	5		5.7	CWD, logs	Primary	Northern Boreal	63°N	Russia, Vodlozero NP	Siitonen et al. (2001)
3	36.9		31.5	CWD, logs	Primary	Southern Boreal	61°N	Russia, near Ural Mountains	Kuuluvainen et al. (2001)
4	10		16.9	CWD, logs	Minor—no human disturbance	Temperate Norway spruce	49°N	Poland, Tatra NP	Zielonka and Niklasson (2001)
5	20		39	CWD, logs	40 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
5	0		0	CWD, logs	65 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
5	13		25	CWD, logs	85 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
6	13		40.6	CWD, logs	Stand age <200 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	7		20	CWD, logs	Stand age 200–250 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	11		18	CWD, logs	Stand age 250–300 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	10		12.2	CWD, logs	Stand age >300 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
7	0.7			CWD, logs	Primary	Douglas fir, western hemlock	46°N	USA: Cascade Range, OR, WA	Sollins et al. (1987)
8			17	CWD, logs	Primary	Maple-oak hardwood	45°N	USA, Minnesota	Hale et al. (1999)
8			26	CWD, logs	Managed, 80–120 years old	Maple-oak hardwood	45°N	USA, Minnesota	Hale et al. (1999)

(continued)

Table 22.2 (continued)

#	Amount of veteris			Substrate	History of site	Forest type	Lat.	Location	Citation
	m^3/ha	Mg/ha	%						
9a	16.8	3.3	37.4	CWD, stump	Selective logging	Cool temperate wet forest	43°S	Australia, Tasmania	Woldendorp et al. (2002b)
9a	54.4	11.1	4.5	CWD, logs	Selective logging	Cool temperate wet forest	43°S	Australia, Tasmania	Woldendorp et al. (2002b)
10		4	10	CWD, logs	Primary and secondary	Temperate forest	42°S	Chile, Chiloe Island	Carmona et al. (2002)
11		27.7	30.7	CWD, logs and snags	Primary	Temperate rainforest *Nothofagus* dom.	39°S	Chile, Valdivian Andes	Schlegel and Donoso (2008)
11		20.1	33.7	CWD, logs and snags	Primary	Temperate rainforest mixed spp.	39°S	Chile, Valdivian Andes	Schlegel and Donoso (2008)
12	3.23		9	CWD, logs	Old growth, minor human disturbance	Oak-hickory, oak-maple	38°N	USA, Missouri	Shifley et al. (1997)
12	1.75		1	CWD, logs	Secondary, selectively logged ca. 1920	Oak-hickory, oak-maple	38°N	USA, Missouri	Shifley et al. (1997)
13	25.2		16.7	CWD, logs	Primary	S. Appalachian	35°N	USA, North and South Carolina	Hardt and Swank (1997)
13	27.4		21.8	CWD, logs	Maturing, selective logging ca. 1920	S. Appalachian	35°N	USA, North and South Carolina	Hardt and Swank (1997)
13	13.3		11.7	CWD, logs	Young, clear-cut ca. 1960	S. Appalachian	35°N	USA, North and South Carolina	Hardt and Swank (1997)
9b	10.4	2.5	10.4	CWD, logs	Selective logging	Temperate rainforest	35°S	Australia, New South Wales	Woldendorp et al. (2002b)
9b	7.1	0.3	14.1	CWD, stumps	Selective logging	Temperate rainforest	35°S	Australia, New South Wales	Woldendorp et al. (2002b)
14	3.5		2.4	CWD, logs	Primary	Mediterranean, *Cryptocarya* dom.	33°S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)

14	13.6		19.7	CWD, logs	Primary	Mediterranean, *Quillaja* dom.	33°S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)
14	59		33.9	CWD, logs	Primary	Mediterranean, *Lomatia* dom.	33°S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)
9c	4.8	1.23	25.7	CWD, logs	Minor human disturbance	Temperate	25°S	Australia, Queensland	Woldendorp et al. (2002b)
9c	0.2	0.08	53.3	CWD, stumps	Minor human disturbance	Temperate	25°S	Australia, Queensland	Woldendorp et al. (2002b)
15		2	1.7	CWD, logs and snags	Moderate hurricane and fire	Tropical dry	19°N	Mexico, Yucatan Pen.	Harmon et al. (1995)
16	8.4		27.8	All dead wood	Minor human disturbance	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
16	0		0	All dead wood	Teak Plantation, planted ~1960	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
16	0		0	All dead wood	Fuelwood plantation, planted ~1990	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
17a	11.9		10.9	CWD, DWD	Primary	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17a	12.5		8.8	CWD, DWD	Reduced impact logging	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17a	1.8		0.9	CWD, DWD	Conventional logging	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17b	22.4		20.6	CWD, DWD	Primary	Tropical dense moist	3°S	Brazil, Tapajós NF	Keller et al. (2004)
17b	31.5		20.4	CWD, DWD	Reduced impact logging	Tropical dense moist	3°S	Brazil, Tapajós NF	Keller et al. (2004)

22.6 Residence Time of Veteris Wood

While deadwood is considered to be an ephemeral habitat, described as a “sinking ship” (Jonsson 2012), or “spatiotemporally dynamic habitat” (Seibold et al. 2017), some forms of deadwood are among the most persistent habitats in a landscape and stubbornly hold their ground for generations. Angers et al. (2010) studied degradation of four species of snags in Boreal North America, each of which had a half-life of more than a decade, and some individual snags stood for half a century. Ranius et al. (2009) showed that tree hollows in European *Quercus robur* L. persist for centuries. Rotting logs in two long-term decomposition studies in Oregon, USA (Harmon 1992), and Tasmania, AU (Grove 2009), are both expected to last several centuries (some nearly a millennia; see Foster and Lang 1982). Feller (1997) used radiocarbon dating to estimate date of death and found a coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.: Pinaceae) in British Columbia that died approximately 1200 years previously. Kelly et al. (1994) developed a 1397-year-old chronology using live trees, snags, and exposed logs of *Thuja occidentalis* L. (Cupressaceae) in Ontario, Canada. Veteran trees may survive from centuries to more than a millennium, and multis wood within them may persist for centuries after tree death (Lonsdale 2013). Other than a cave, deep soil, or a piece of exposed granite, it’s hard to imagine a more stable habitat than veteris wood.

Residence time specific to decay classes is poorly studied. Typically larger wood lasts longer, and the time spent in decay classes increases as decay increases (Harmon et al. 1986: 213). Using a five-class system, Tyrell and Crow (1994a) found residence time of hemlock logs in Wisconsin and Michigan to be 2, 10, 20, 35, and ~15–100 years, respectively. In a globally extreme example, Daniels et al. (1997) studied residence time of western red cedar, *Thuja plicata* (Donn ex D. Don in Lamb.), in coastal British Columbia. In a four-class system, logs averaged 2, 47, 141, and 780 years since death for each class, respectively. Swift et al. (1979) point out that ultimately decomposed plant matter may persist for hundreds to thousands of years in the form of soil organic matter and humus. Thus the “end,” “death,” or “loss” of veteris wood is dependent on an as of yet undetermined cutoff point. Currently the “end” of a log is generally based on visual clues as no formal descriptions, such as physiochemical measurements or comparisons of soil quality or structure, could be found in the literature.

22.7 Wood Structure and Digestion

Extended overviews of this subject are found in Dajoz (2000: Chap. 14), Käärik (1974), Stokland (2012c), and Swift et al. (1979). Unless indicated, the following is taken from them. See Ulyshen (2016) for a detailed account of invertebrate influence on wood decomposition. Wood is composed of three classes of carbohydrates: cellulose, hemicellulose, and lignin. Digestion of cellulose requires the synergistic effect of three types of enzymes and is accomplished only by a few fungi, bacteria, marine organisms, and insects. Within insects there are four mechanisms for cellulose digestion: use of protozoan symbionts in the hindgut, use of bacteria in the hindgut, use of fungal cellulases originating in the food, and, rarely, creation of the full cellulose system by the insect (Martin 1991). Hemicelluloses and lignin each require specialized enzymes for digestion, and as the composition of the molecules differs greatly between conifer and broadleaf trees, so do the enzymes needed for digestion.

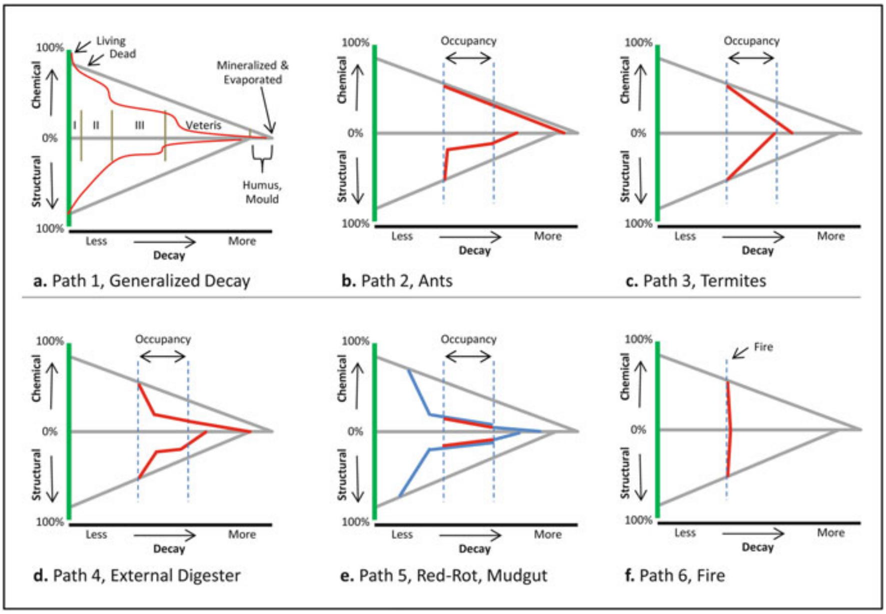
Fungal digestion of wood is often lumped into three major categories: white, brown, and soft rot. White rot is the digestion of all three components (cellulose, hemicellulose, and lignin), although the rate of digestion may not be equal for all molecules. "Brown rot" is the preferential digestion of cellulose and hemicellulose leaving lignin intact and is found principally in conifers in boreal forests, although exceptions exist. Soft rot preferentially digests cellulose and hemicellulose but occasionally lignin as well. Soft rot typically occurs in water or high-moisture situations and has been found in initial decay of oak heartwood.

When plant matter dies, it often initially undergoes "microbial conditioning" (Swift et al. 1979), a process where microorganisms, including bacteria and fungi, begin digesting the material. During this process, the material is often softened, nitrogen is fixed, secondary compounds are detoxified, etc. The conditioning creates a "detritus-buffered system" (Nalepa et al. 2001a) where arthropod detritus feeders are not exposed to the full force or variety of plant defenses. Additionally the predigestion and the presence of the microorganisms, which possess nutritive value themselves, make the substrate more favorable to arthropod consumers.

Feces are not much different from rotting organic matter, and reconsumption of feces, coprophagy, allows for additional digestion of the originally consumed material and digestion of any microflora that grew after defecation. Many cockroach species will engage in coprophagy when available, but fungus-gardening termites (Blattodea: Isoptera) and passalid beetles (Coleoptera: Passalidae) take the practice to an extreme. They use an "external rumen" technique: material is eaten, inoculated with microbes, and voided. Continued "digestion" of the material by the microbes takes place in the feces which are then reingested, and nutrients and energy are absorbed by the arthropod (Mason and Odum 1969; Nalepa et al. 2001a; Swift et al. 1979). An external rumen can be used to "burn off" excess carbon and decrease the carbon to nitrogen ratio (Eggleton and Tayasu 2001).

22.8 Hypothetical Paths to Creation of Veteris Wood

Many paths lead from wood in a living tree, through death, to loss of individuality, and complete evaporation/mineralization, but several predictable paths specific to veteris formation and/or "long-term" use can be highlighted. A conceptual model of woody debris decay is presented in Fig. 22.2a, where the structural and chemical qualities of the wood are tracked from life (green line on left, 100%) through decay



a. Path 1, Generalized Decay **b.** Path 2, Ants **c.** Path 3, Termites

d. Path 4, External Digester **e.** Path 5, Red-Rot, Mudgut **f.** Path 6, Fire

Fig. 22.2 Predictable paths to creation and use of veteris wood. Exterior gray lines represent "idealized" decay, while red lines represent "actual" decay. (**a**) Generalized decay, (**b**) excavation of a log by ants, (**c**) consumption of wood by termites, (**d**) excavation and occupation by external digesters such as Passalidae, (**e**) alterations of wood made by fungi (blue lines) and subsequent use by red-rot inhabitants such as Micromalthidae, (**f**) degradation by fire. See text for details

until complete loss (on the right, 0%). More specific aspects (e.g., lignin content, density) could be tracked on each side in a qualitative or quantitative manner but are not shown here. Use of a standardized figure similar to this would allow comparison across sites and studies. As decay occurs, the woody material passes through decay stages until it enters the veteris stage. After all structural quality is gone, the remainder of the woody debris consists of humus, wood mold, etc. The outer gray lines represent the total "decay space" of the model, while the red lines illustrate the deviation from typical decay by the proposed scenario. Path 1 (Fig. 22.2a) might be typical for many pieces of woody debris that experience biotic and abiotic processes that degrade the wood in an incremental manner and where no single taxon drives the decay.

Path 2 (Fig. 22.2b) is a hypothetical example of veteris formation by log-dwelling ants. Immediately after occupancy, removal of the material (but not consumption) for nest building results in rapid structural damage, but little chemical degradation, as illustrated by the red lines. Minimum structural integrity must be maintained while the colony is in the wood, and once that is gone, the colony must move on.

Path 3 (Fig. 22.2c) is a hypothetical example of rapid decay by termites which remove and consume wood (that may or may not be infected with fungi) which is digested in the termite body. Structural and chemical decomposition occurs nearly symmetrically. Depending on the type of termite, the log may be fully consumed while the colony resides elsewhere, or if the colony resides in the logs, an outer protective shell must remain intact for protection (see below).

Path 4 (Fig. 22.2d) is a hypothetical example of decay by taxa that initially cause a large amount of structural and chemical degradation but maintain a residency within the wood for a long period of time, during which rate of chemical and structural change is greatly reduced (e.g., Passalidae (Coleoptera), *Cryptocercus* spp. (Blattodea), etc.). These taxa remove and consume wood but reconsume partially digested wood that has been inoculated with other organisms (external rumen *sensu* Mason and Odum 1969). The outer shell of the wood must maintain a minimum of external structural integrity to remain suitable for the colony.

Path 5 (Fig. 22.2e) is a hypothetical example of a situation involving arthropods [e.g., *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae), *Prostomis atkinsoni* Waterhouse (Coleoptera: Prostomidae)] that live within veteris wood that has been specially conditioned by fungi, sometimes called brown or red rot, and that directly consume the substrate created by the fungi. An extreme version of that rot type found in Australia is called mudguts (Grove 2007). Here the majority of chemical and structural decay are initiated by the original fungi, illustrated by the blue lines, and little to no meaningful chemical and structural changes are made by the arthropod taxa within (red lines).

Path 6 (Fig. 22.2f) is fire. Both chemical and structural quality are simultaneously driven to 0%, or nearly so, in a very short amount of time. Unlike other "natural disasters," such as floods, hurricanes, and mudslides, fire is unique in that it causes chemical rather than physical changes. Fire can be thought of as a "proto-life," a metabolism without a body. Fire is a form of autocatalytic reaction (one product of fire, heat, is also a reactant); it grows, reproduces, digests organic material, and respires CO_2. Ash is fire "feces" (especially important for fungi), and scorched items can be thought of as "partially digested." Fire is a "universal omnivore" that readily digests fats, proteins, and carbohydrates including cellulose, hemicellulose, and lignin (no enzymes needed!). Fire cannot adapt or evolve, but populations of organisms can evolve in relation to fire, and saproxylic organisms are obviously in competition with fire.

Two trends are noticeable: (A) from high structural damage (Paths 2, 3) to low or no meaningful structural damage, because the previous rot had already degraded the wood (Paths 4, 5), and (B) from no consumption of the wood (Path 1) to consumption with internal digestion (Paths 3, ~4) to an increasing requirement for external pre-digesters (Paths ~4, 5).

22.9 Insects in Veteris Wood I: The Bestiary

> *Entomologists are a necessary evil!*
> —Harding and Alexander 1993

The following is a general survey of insects that are known or suspected to use veteris wood. In many cases, the reported habitat ("in logs") is too general to fully judge if a specimen was collected from veteris or less-decayed wood. Insects in many orders (Phasmatodea, Mantodea, Lepidoptera, etc.) exploit the existence of deadwood by using cryptic colors, textures, and shapes to look like bark, twigs, etc. but don't necessarily rely on the existence of deadwood per se. Additionally, as was pointed out above, no distinct boundary separates veteris wood from well-humified soil; therefore the case could be made that any number of soil-dwelling organisms that specialize on humus utilize "extreme" veteris wood. All insect orders are covered for completeness so that a sense of what is and isn't known is available.

22.9.1 Protura

Protura are a poorly known group of incredibly abundant, very small hexapods with a worldwide distribution (Pass and Szucsich 2011). About 790 species are known, with many more undescribed. They are generally found anywhere sufficiently moist organic matter is present and have been reported from tree holes, "moist woodland humus," and "moldering timber" (Copeland and Imadaté 1990; Pass and Szucsich 2011). Protura are known to feed on fungal mycorrhizae; other feeding habits are suspected but unknown. Certainly Protura will be present in veteris wood, but beyond that, all else remains a mystery.

22.9.2 Collembola

Springtails are a highly diverse group (~8000 spp.) with a worldwide distribution and are some of the most abundant soil-dwelling arthropods (Hopkin 1997; Smolis and Kadej 2014). They feed on fungal matter and decomposing debris, and some are predatory on other invertebrates (Grimaldi and Engel 2005; Hopkin 1997). Teasing apart specific habitats of Collembola has only recently begun. For example, in Poland, about 40% of Collembola are associated with deadwood, and about 5% are considered saproxylic (Skarżyński et al. 2016). Skarżyński et al. (2016), in Wigry National Park, Poland, provide a good description of the community of Collembola in deadwood. They found that most species in the forest make little distinction between forest litter and deadwood; however about 20% of the species were "saproxylic" (predominantly in deadwood), and about 20% of the specimens collected from deadwood were of those species. Species richness and number of specimens increased with decay class; veteris wood (class III) was the highest. Smolis and Kadej (2014) described a new species of saproxylic Collembola from hemlock logs in Oregon, USA, that were "very rotten, soft and moist inside." Despite searching, they could not find it in any other habitat. The presence and influence of Collembola in veteris wood is largely unknown, but studies cited above indicate that many saproxylic and veteris-dwelling Collembola are to be expected.

22.9.3 Diplura

Diplura are soil-dwelling invertebrates (800+ spp.) with a worldwide distribution (Allen 2002). They can be split into two groups, the Campodeomorpha and Japygomorpha; the former are considered herbivorous, while the latter are predatory (Grimaldi and Engel 2005). Reddell (1983) lists species that were collected in rotten wood, redwood duff, and deep humus, all of which could be considered veteris wood. As members of the soil fauna, Diplura are expected in veteris wood; whether any species are obligate is currently unknown.

22.9.4 Archaeognatha (Microcoryphia) and Zygentoma (Thysanura)

Both orders are largely soil-dwelling insects with about 350 and 370 species, respectively (Triplehorn and Johnson 2005). They are generally considered browsers or grazers of detritus, soft plant matter, and lichens (Ferguson 1990). They have been reported from deadwood and can be found in cavities within and beneath veteris wood, but that use may be restricted to shelter. As members of the soil and leaf litter fauna, both are expected in veteris wood.

Some species of Zygentoma may use deadwood more consistently. Some species of the Nicoletiidae subfamily Atelurinae are associated with ant and termite nests (Triplehorn and Johnson 2005) and may follow their hosts into veteris wood. The relic taxon *Tricholepidion gertschi* Wygodzinsky (Lepidotrichidae) is known from under decaying bark or in rotten wood of fallen Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.). At a northern California site, specimens were found under decaying bark, but absent from the soil and leaf litter, despite specific searching (Engel 2006; Wygodzinsky 1961).

22.9.5 Ephemeroptera

Mayflies are aquatic as immatures with a short-lived, nonfeeding adult phase (Grimaldi and Engel 2005). Immatures of many species scrape/graze microorganisms growing from the surface of woody resources or use it as structure (e.g., Waltz and Burian 2008). How many could be considered saproxylic in any sense is unknown. However, immatures of the African species *Povilla adusta* Navas

(Polymitarcidae) are clearly saproxylic. They are famous for burrowing into softened wood for shelter, including pilings and boats, and then emerge at night to filter feed on planktonic algae or periphyton if available (Bidwell 1979; Petr 1970, 1971). *Povilla adusta* prefer softened wood and could be considered denizens of veteris wood.

22.9.6 Odonata

Dragonflies are a worldwide taxon with predominantly aquatic immatures and active flying adults; both life stages are predatory (Corbet 1999; Grimaldi and Engel 2005). Immatures of at least 24 genera and 47 species are associated with phytotelmata (plant-based container habitats) including saproxylic/veteris habitats: water-filled bamboo, tree stumps, and tree hollows (Corbet 1999; Kitching 2000, species list). Two species in the family Megapodagrionidae are obligate tree-hole breeders and immatures of the family Pseudostigmatidae, and several other genera are only known from tree holes and may be considered obligate as more is known (Corbet 1999). While traditionally not thought of as a saproxylic habitat, water-filled tree holes have been microcosms for important ecological studies and will certainly be of conservation concern in the future (Kitching 2000).

22.9.7 Plecoptera

Stoneflies are most prevalent in flowing freshwater in the temperate zones. Immatures of many species scrape/graze microorganisms growing from the surface of woody resources or use it as structure (e.g., Stewart and Stark 2008). Omad et al. (2015) found that *Diamphipnopsis samali* Illies (Diamphipnoidae) specifically fed on wood (50% of gut content) and fungal hyphae (30%) in first-order Patagonia streams. How many other Plecoptera could be considered saproxylic in any sense is unknown.

22.9.8 Embiidina (Embioptera) (Embiodea)

Web spinners are gregarious subsocial insects that generally live within tunnels or under sheets made of silk produced by glands in the proximal tarsomere of the front legs. About 360 species are described (although Ross (1970) reports the existence of 800+ mostly undescribed species), and most are found in the tropics, although some range into the warmer temperate zones (Grimaldi and Engel 2005). They are general detritivores and grazers of lichens, etc. Many species construct galleries under or among rocks, within leaf litter, and in the crevasses of bark. At least seven species have been reported from under "bark of dead limbs and trunks"; on dead vines; on an old oak stump; "on bark of a high, dead stump"; and "in bark crevices of trees and dead stumps" (Ross 1944, 1984a, b). Whether association with deadwood among these species is consistent or happenstance is unknown. Probably some species will be recognized as saproxylic as more becomes known.

22.9.9 *Zoraptera*

Zoraptera (Fig. 22.3a) are the only order of insects that are exclusively found in deadwood (Stokland 2012a). Despite their taxonomic paucity—only 32 species are known—Zoraptera are of interest for a variety of reasons. The relationship of

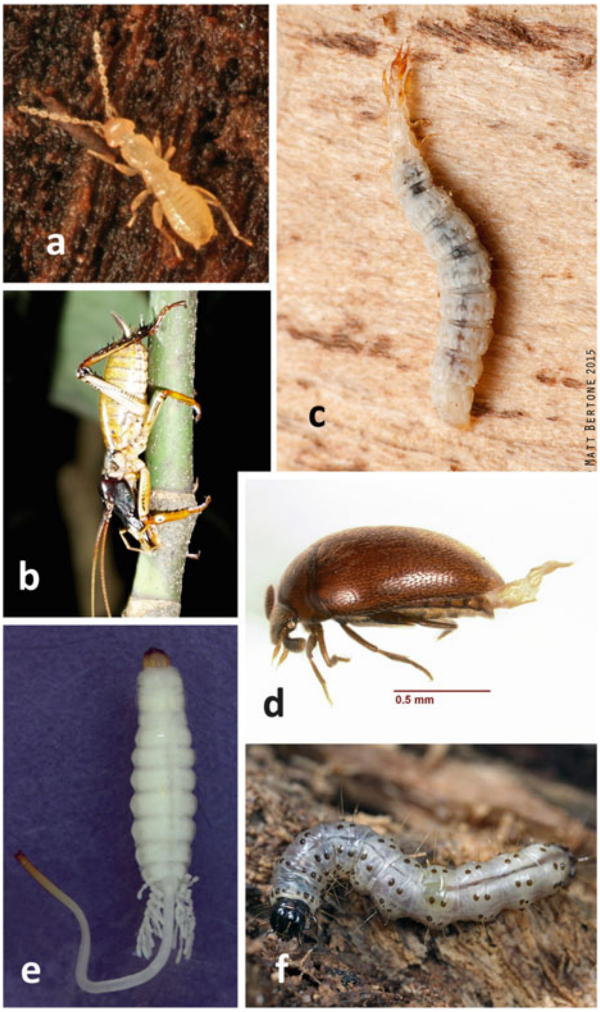


Fig. 22.3 Interesting insects in veteris wood. (**a**) *Zorotypus hubbardi* Caudell, Zoraptera: Zorotypidae, adult (photo by Art Evans); (**b**) *Hemideina thoracica* (White) Orthoptera: Anostostomatidae, adult (photo by Shelly Myers); (**c**) *Nallachius americanus* (McLachlan) Neuroptera: Dilaridae, larva (photo by Matt Bertone); (**d**) *Tohlezkus inexpectus* Vit, Coleoptera: Eucinetidae, adult; (**e**) *Axymyia furcata* McAtee, Diptera: Axymyiidae, larva (photo by M. J. Hatfield); (**f**) *Scolecocampa liburna* (Geyer), Lepidoptera: Erebidae, larva (photo by Kim Fleming)

Zoraptera to other orders has long remained a mystery, but recent studies have confidently placed it within the Polyneoptera (Grimaldi and Engel 2005), and Misof et al. (2014) placed them sister to the Dermaptera. Adult Zoraptera come in two forms: alate (eyed, winged) and apterous (blind, wingless). The alate form is the dispersal stage and tends to appear when resources are being reduced (Grimaldi and Engel 2005). Zoraptera eat fungal hyphae, nematodes, or minute arthropods and are often reported from rotten logs, termite galleries, and sawdust piles (Shetlar 1978).

Zoraptera have played a prominent role in the description and thoughts on deadwood: Silvestri (1913) introduced the term "saproxylic" in his description of the order; Wilson (1959) designated his third log decay stage (of 5) the "Zorapteran stage"; and Hamilton (1978) pointed out they were one of the numerous insects associated with deadwood that exhibit flight polymorphism.

22.9.10 Orthoptera

The crickets, grasshoppers, katydids, and relatives are represented by about 23,000 species, most of which are phytophagous, while others are detritivores or predatory (Grimaldi and Engel 2005). Orthoptera associated with veteris wood include members of the cricket family Myrmecophilidae, which are obligate inquilines of ants and may be found in deadwood as they follow their hosts (Blatchley 1920; Wetterer and Hugel 2014; Wheeler 1910). Other Orthoptera may interact with veteris wood by seeking shelter within and beneath it, and some arboreal species may insert eggs within the moist veteris wood on the outside of dead limbs, although the last part is purely speculative.

The grand saproxylic Orthoptera are the wetas or king crickets (families Anostostomatidae and Rhaphidophoridae) which are endemic to New Zealand (Field 2001). Wets represent some of the largest and most enigmatic insects alive. Many wetas occasionally use tree holes or crevices, but species in the genus *Hemideina* Walker (Fig. 22.3b) are specifically associated with tree holes where they reside during the day, presumably to avoid predation (Gibbs 2001). *Hemideina* don't excavate their own holes de novo but typically use holes previously created by larvae of *Ochrocydus huttoni* Pascoe (Coleoptera: Cerambycidae) or *Aenetus virescens* (Doubleday) (Lepidoptera: Hepialidae) (Gibbs 2001). Wetas maintain holes in live trees by nibbling the cambium at the edge of the hole to maintain an opening and can enlarge and excavate the tunnel when heartrot (veteris) exists (Field and Sandlant 2001).

22.9.11 Phasmatodea

Walking sticks or stick insects are typically cryptically colored and/or shaped herbivorous insects that reside on the plants they are consuming (Grimaldi and

Engel 2005). However some members are loosely associated with deadwood. Members of the genus *Anisomorpha* Gray will sometimes rest under loose bark or logs (fresh to veteris) possibly for protection from predators or due to a more suitable microclimate (Blatchley 1902; Conle et al. 2009; personal observation). *Eurycantha calcarata* Lucas (Phasmatidae) has also been reported to rest in rotten logs and stumps during the day (Gurney 1947b). *Dryococelus australis* (Montrouzier) (Phasmatidae), the (presumed extinct and then rediscovered) Lord Howe Island stick insect, would rest in tree holes during the day. A single tree hole might be used by multiple individuals for many generations, and the accumulation of droppings might exceed several bushels (Gurney 1947b). Hollow sections of banyan figs are currently used for rearing captive populations, and plans are under way to reestablish the species on the island (Crew 2012).

The eggs of many walking sticks have a distinct cap on the operculum called a capitulum (Clark 1976) which greatly resembles an elaiosome, a process found on plant seeds which invokes myrmecochory, dispersal by ants. Instances of ants collecting phasmid eggs and taking them back to the nest have been recorded but mostly in ground-nesting ants. Compton and Ware (1991) conducted several studies on the interaction of ants with the eggs of *Phalces brevis* (Burmeister) (Phasmatidae). Eggs with an intact capitulum were greatly preferred by ants. First instar walking sticks from eggs that hatched within a laboratory colony of *Acantholepis capensis* Mayr were ignored by the ants, and presumably the same would happen in the wild. Stanton et al. (2015) showed that ants collected and moved eggs of the walking stick *Eurycnema goliath* Audinet-Serville (Phasmatidae) specifically because of fatty acids found on the capitulum. There are more than 3000 species of walking stick known (Grimaldi and Engel 2005), and if any species have eggs that are attractive to ants that nest in rotting wood, and if the protection of the ants is important for the early development of the phasmid, then the interaction would represent an important use of veteris wood.

22.9.12 Dermaptera

Earwigs (~2000 spp.) prefer warm moist climates, and most species are detritivores/omnivores while a few are herbivores or predators (Grimaldi and Engel 2005). Dermaptera are subsocial; the female will often create a burrow and guard the eggs and newly hatched offspring. Dermaptera are often found in leaf litter and in, on, and under deadwood. Blatchley (1920) lists several species in eastern North America collected from half-buried logs and beneath bark of various types of dead trees. Some species may live entirely on or within veteris, or prefer to create natal burrows in veteris, but to what extent that occurs is currently unknown.

22.9.13 Grylloblattodea and Mantophasmatodea (Notoptera)

The ice crawlers and rock crawlers are placed in two closely related orders (Misof et al. 2014) that are occasionally combined (Notoptera). Mantophasmatodea were first described as an order during 2002 (Klass et al. 2002) and currently consist of about 15 predatory species all known from Africa (Grimaldi and Engel 2005). They have not yet been reported to interact with deadwood.

Grylloblattodea are represented by 26 species restricted to North America and Asia. North American species are known from higher elevations and are active at cold temperatures, while some Asian species occur in leaf litter and are active at "normal" temperatures (Ando 1982). North American species are famous for creeping out at night and scavenging dead insects and other debris off of snow banks. Reportedly they can be kept as "pets" in a refrigerator at 8 °C for several months (Gurney 1953, and references therein) but will become sluggish or even die from "high" temperatures (still below human body temperature). Gurney (1953) reported a specimen collected from the center of a rotten log about 2.5–3 ft (~80 cm) in diameter: "The wood was almost completely decayed and it was fairly damp in the center." A female of a Russian species was collected from a rotten tree stump (Bei-Bienko 1951; see Gurney 1953), and in Montana, several specimens were collected in rotten logs and stumps, including one collected a foot (~30 cm) above the ground in a rotten stump (Pletsch 1946). Esch et al. (2017) collected numerous *Grylloblatta campodeiformis* Walker (Grylloblattidae) from several species of dead pine in Alberta, Canada, using emergence traps. Gut examination revealed no plant matter but plenty of saproxylic arthropods.

The extent to which grylloblattids use deadwood and for what purposes are unknown, although the findings of Esch et al. (2017) clearly show some species are saproxylic. Adults and immatures are generally soft bodied and probably don't dig into sound wood. As climate change alters temperature regimes and reduces snow fields, grylloblatids will certainly become taxa of conservation concern, and knowing the full extent of their natural history will be important.

22.9.14 Mantodea

The preying/praying mantises/mantids are an order of exclusively predatory orthopteroids closely related to cockroaches, with about 2300 described species (Grimaldi and Engel 2005). Mantises are often morphologically cryptic and exhibit a variety of colors, shapes, and textures. "Bark mantids" spend most of their time on tree trunks (Prete et al. 1999) and resemble bark, lichen, etc., but there is no indication that any are found on, or exclusive to, dead trees. Certainly mantises will place their oothecae (egg cases) on or under deadwood of various sizes and decay states, but there is no indication that this isn't simply an opportunistic use of an available substrate.

22.9.15 Blattodea (Cockroaches)

Many species of cockroaches (exclusive of the termites) are associated with soil and leaf litter habitats, and many are considered to be generalist detritivores and are therefore expected to be found in, near, and around deadwood of all decay stages. Bell et al. (2007: 46) list 16 species of cockroaches that are associated with rotten wood (not including members of *Panesthia* Serville (Blaberidae) and Cryptocercidae) and provide a good summary of cockroach interaction with deadwood. Some cockroach species, which are morphologically convergent with wood boring beetles, are suspected of boring into solid wood (Bell et al. 2007: 12). Myrmecophylic and termitophilous cockroaches may accompany their hosts into deadwood. Needless to say, much more research needs to be done on non-synanthropic cockroaches, and their role in wood decay may be more extensive (especially in the tropics) than currently thought.

Two cockroach genera are of special interest when it comes to creation of veteris wood, *Panesthia* and *Cryptocercus* Scudder (Cryptocercidae). *Panesthia* are subsocial and live as multigenerational groups in a variety of rotting logs that they excavate and feed on over many years (Bell et al. 2007). Additionally they can digest cellulose independent of gut symbionts (Scrivener et al. 1989).

The cockroach genus *Cryptocercus* consists of 14 species distributed in western NA (1 sp.), eastern USA (4 spp.) (Burnside et al. 1999), eastern Russia (1 sp.) (Mamaev 1973), China (7 spp.) (Grandcolas et al. 2005; Nalepa et al. 2001b; Wang et al. 2015), and South Korea (1 sp.) (Grandcolas et al. 2001). With the exception of a brief walking dispersal stage, *Cryptocercus* spends its entire life living and feeding within decayed sections of rotted logs (Nalepa et al. 1997), and where present, *Cryptocercus* may play a critical role in log decomposition (Nalepa et al. 2017). While of minor global importance for wood decay, *Cryptocercus* are sister taxa to all "termites" (Legemdre et al. 2015) and represent an important link between "cockroaches" and "termites" in regard to lifestyle, gut biota, and sociality (see overview in Grimaldi and Engel 2005: 235). [Grandcolas (1994) and subsequent publications (see Grandcolas et al. 2001) maintain wildly differing views conceding the phylogenetic placement of *Cryptocercus* despite enormous evidence to the contrary (see Legemdre et al. 2015; Lo et al. 2000; Nalepa and Bandi 1999).]

Cryptocercus differ from most cockroaches and are similar to most termites by (1) using deadwood as an exclusive food source, (2) dependence on protozoan gut fauna for digestion of cellulose (Martin 1991), and (3) subsocial behavior (Cleveland 1934; Grimaldi and Engel 2005). *Cryptocercus* was well studied by Cleveland (1934) who described 12 genera and 25 species of flagellate protozoa in the gut fauna, which share a common ancestor with protozoa in termites (Cleveland 1934; Nalepa 1984). *Cryptocercus* have been found living in logs of numerous species including American chestnut (*Castanea dentata* (Marsh.) Borkh.), oak (*Quercus* spp.), and eastern hemlock (*Tsuga canadensis* (L.) Carrière) (Cleveland 1934).

Cryptocercus are subsocial with a basic social unit of an adult pair and ~15–20 offspring from one (rarely two) reproductive season(s) (Nalepa 1984). Individuals of *Cryptocercus punctulatus* Scudder take 6–8 years to reach maturity after which they disperse to a new log and start a family. Adults typically remain with their brood at least 3 years (Cleveland 1934; Nalepa 1984). Multiple families may live within a single log, but galleries are separated by structural boundaries (Nalepa 1984). Nymphs acquire protozoans by proctodeal feeding from adults and may continue this activity for up to a year after hatching (Nalepa 1984).

Cryptocercus exhibits a distinct "Greyian" distribution (Grimaldi and Engel 2005; Nalepa and Bandi 1999). During the Late Cretaceous and early Tertiary, vast forests covered the Northern Hemisphere. Over time those forests were diminished, but "relic temperature" refugia remained in East Asia and eastern North America, which today share numerous relic taxa (Hsü 1983). Based on divergence of endosymbionts, Nalepa et al. (1997) estimate that the split between the eastern and western North American species of *Cryptocercus* took place 25–70 million years ago. Migration from one location to the other could have taken place during the Eocene optimum 65–34 million years ago when the forest was contiguous between both locations (Nalepa and Bandi 1999). Low vagility and the requirement for dead logs imply that current populations of *Cryptocercus* are found in places that have been continually forested since the early Tertiary (approximately 60 million years) (Nalepa et al. 1997; Nalepa and Bandi 1999). The restricted ranges and requirements of *Cryptocercus* increase the likelihood that it will become a taxon of conservation concern in the future (Nalepa et al. 2017), for example, *C. clevelandi* Beyers may already be extirpated from Washington, USA (Nalepa et al. 1997).

22.9.16 Blattodea (Termites)

The role of termites in deadwood is treated by Bignell (2018; see Chap. 11). The following is presented with specific attention to veteris wood.

Termites are a branch of eusocial "cockroaches" composed of about 3000 species that first evolved in the Late Jurassic to Early Cretaceous (Grimaldi and Engel 2005; Legendre et al. 2015; Lo et al. 2000; Thorne et al. 2000). They are mostly absent from boreal regions but predominate in the tropics (Abe 1987). Termites actively alter wood themselves through excavation and consumption and, by their presence, increase wood decay when predators dig out colonies; see Redford (1987) for a list of mammals that feed on termites. Strong evidence indicates that members of the Cretaceous dinosaur family Alvarezsauridae (Saurischia) preyed on wood-nesting termites (Longrich and Currie 2009), indicating termites have been dug out of logs for the past 100 million years.

Mastotermes darwiniensis Froggatt (Mastotermitidae) is sister to all other termites and contains several ancestral cockroach-like characteristics, including a full complement of wing veins and symbiotic bacteria only otherwise found in cockroaches, and it lays eggs in an oothecae-like pod rather than singly as do other termites. *Mastotermes* is restricted to Australia but has been introduced to New Guinea. The voracity of *Mastotermes* is legion; they will eat all forms of deadwood, live trees, paper, ivory, bitumen, asbestos, creosote-soaked poles, the rubber of buried tires, and bore through lead (Grimaldi and Engel 2005; Hill 1942). Additionally they will construct short towers and tunnels tens of meters long to gain access to resources (Hill 1942). Colonies in the wild tend to be small, but in urban settings colonies (or numerous fused colonies) may reach nearly a million individuals (Grimaldi and Engel 2005; Hill 1942). No indication is given concerning the usefulness of *Mastotermes* for bioremediation of landfills, but exploration of the topic seems worthwhile.

Abe (1987) separated termite "life types" based on nest and feeding habits. Nest habits came in three varieties: one piece, nesting within a single piece of wood for the life of the colony; intermediate, living within wood but also using multiple pieces of wood; and separate, living away from the food source. For a colony to reach maturity, one-piece nesters require large pieces of long-lived wood that can provide adequate food and protection, perhaps up to 30 cm diameter or greater in the tropics (Abe 1987). One-piece nesting termites may be more heavily impacted by forest management than species with other life types.

The general evolutionary trend in termites has been to move from wood as a nest structure to soil and to move from consuming less-decayed food material (e.g., log) to more decayed material (e.g., humus) (Donovan et al. 2001; Eggleton and Tayasu 2001). Not all termites feed on deadwood, Hodotermitidae eat dead grass, and many Termitidae are humus feeding, although this might be considered "extreme" veteris wood!

22.9.17 Psocodea

Recently the orders Psocoptera and Phthiraptera have been combined into Psocodea. The bark lice, book lice, or bark flies (Psocoptera of old) are a largely overlooked order consisting of about 4400 described species. They feed by scraping encrusting lichens, algae, fungal hyphae, and spores. Many live on the bark surface, within decaying plant material, on deadwood, in insect galleries, with ants and termites, or associated with bird and mammal nests (Grimaldi and Engel 2005).

Psocoptera in relation to the saproxylic habitat are poorly studied. Deyrup and Mosley (2004) reported Psocoptera from fire-killed pine. Paviour-Smith and Elbourn (1993) collected nine species from deadwood in Wytham Woods, UK. Matthewman and Pielou (1971) collected 15 species within six families from sporophores of *Fomes fomentarius* (L.) Fr. (Polyporaceae). More research needs to be done to discover which species use, and what role they play in, saproxylic habitats, including veteris wood.

The chewing and sucking lice (~5000 spp., formally Phthiraptera) are exclusive parasites of bird and mammal hosts (Grimaldi and Engel 2005). Any louse species that is an obligate parasite on a species of bird or mammal that is an obligate cavity nester is just as saproxylic as a mite on a bark beetle. Presumably the vertebrate will get most of the attention.

22.9.18 *Thysanoptera*

Thysanoptera are an order of small insects, 0.5–10 mm long, that consist of about 5500 described species (Grimaldi and Engel 2005). Thrips are poorly studied as an order with the exception of economically important species, but even then, gaps in basic biology remain (Mound 2005). Recently eusocial gall-inhabiting thrips were discovered in Australia (Grimaldi and Engel 2005). While traditionally thought of as phytophagous, about 40% of known thrips are frugivorous (Mound 2005). In fact, Mound (2005) notes: “The English common name, thrips, is the Greek word for ‘woodworm,’ derived from observations by early naturalists that many species are found on dead branches.” Stannard (1968) reports at least 42 species of thrips from dead branches or under bark of dead trees or logs in Illinois, USA. Kettunen et al. (2005) collected 23 species of thrips from dead Aspen (*Populus tremula*) in Finland. Kobro (2001) found that the polypore-feeding thrips *Hoplothrips polysticti* (Morison) (Phlaeothripidae) was most numerous in “semi-old” forest, but markedly less numerous in younger or older forests, a rare trend. Certainly many species of saproxylic thrips exist, which of those are associated with veteris wood is unknown.

22.9.19 *Hemiptera (Including Heteroptera and “Homoptera”)*

Hemiptera represent the largest non-holometabolous order of insects (~35,000 spp.) and are characterized by possession of piercing-sucking mouthparts (Triplehorn and Johnson 2005). Few species possess morphological features that would indicate they can burrow into sound wood, but they may be able to burrow into veteris wood or utilize external features of less-decayed wood (Gossner and Damken 2018; see Chap. 9). Ulyshen et al. (2012) collected 14 species within eight families of Hemiptera emergent from less-decayed (non-veteris) wood.

The suborder Heteroptera is largely composed of predators, while a few taxa have changed to phytophagy or fungivory. The unique-headed bugs (Enicocephalomorpha) are micropredators largely associated with soil but can be found under rocks, moist detritus, and in rotten logs (Wygodzinsky and Schmidt 1991: Table 1). The group is poorly known and in need of additional study. The Aradidae are saproxylic fungivores typically associated with subcortical habitats (Deyrup and Mosley 2004); however some species are found in termite nests or exposed on dead trees or shelf fungi (Froeschner 1988). Seibold et al. (2014) found that Aradidae activity increased with increased amount of deadwood in a forest but not abundance of sporocarps in the area. Aradids may or may not be associated specifically with veteris wood, depending on the extent of decay or type of shelf fungi. The closely related morphologically reduced family Termitaphididae is fungivorous and associated with termites (Grimaldi and Engel 2005) and may enter wood with their hosts.

The extent to which Heteroptera utilize deadwood as structure is unknown. Blatchley (1926) lists at least three Reduviidae species found overwintering in oak stumps and "beneath logs, the sides of which are deeply buried in leaves and mold" [*Melanolestes picipes* (Herrich-Schaeffer), *Pygolampis pectoralis* (Say), and *Zelus longipes* (L) (as *Zelus bilobus* Say)], and one Miridae [*Fulvius imbecilis* (Say)] found beneath logs in autumn. Other associations with deadwood include *Amnestus spinifrons* (Say) (Cydnidae) taken beneath decaying wood and *Mesovelia mulsanti* White (Mesoveliidae) which "possesses an ovipositor for inserting her eggs into the stems of plants and even in the spongy wood of floating logs" (Blatchley 1926). Some *Nerthra* Kirkaldy (Gelastocoridae) burrow into rotting logs and can be carried some distance over open water (Polhemus and Polhemus 1988; Todd 1959).

The historic "Homoptera" have been divided into three suborders: Sternorrhyncha, Auchenorrhyncha, and Coleorrhyncha (Grimaldi and Engel 2005); the latter is only known from moss and leaf litter, while the other two have some members in deadwood. As with the Heteroptera, these groups probably do not burrow into sound wood and are probably limited to well-decayed wood. O'Brien (1971) reported nymphs of Achilidae, which are believed to be fungus feeding, collected from standing dead trees, "deep in a rotten log" and berlesed from "redwood duff." Holzinger and Friess (2014) reported an adult Achilidae (*Cixidia lapponica* Zetterstedt) from "deep inside a rotten pine log." Certainly more associations between Hemiptera and veteris wood are waiting to be found.

22.9.20 Neuropterida

The snakeflies (Raphidioptera), alderflies (Megaloptera), and lacewings (Neuroptera) are three closely related orders with members that are chiefly predators as both adults and immatures (Grimaldi and Engel 2005). Some ground- and tree-dwelling Neuropterida larvae will certainly use deadwood as structure or substrate while resting or pupating, but others are associated with deadwood, including veteris, as immatures. Larvae of more than 70 species of Raphidioptera are reported to be subcortical (Aspöck 2002). Larvae of the North American ant lion species *Glenurus gratus* (Say) (Myrmeleontidae) are known from dry tree holes, especially in oak trees (Miller and Stange 2006). In Illinois, USA, Adams (1915: 153) reported, "When a log reaches such a condition that it looks like brown meal, and is nearly level with the surface of the ground, it may during the summer become so dry that it affords a favorable haunt for myrmeleonid larvae; probably the ant-lion of *Myrmeleon immaculatus* DeG., a woodland species." Thus veteris wood may provide a substrate for ant lion larvae in places where the soil is unsuitable. Immature pleasing lacewings (Dillaridae) (Fig. 22.3c) are associated with deadwood. Steyskal (1944) collected 6 females and 14 males of *Nallachius americanus* (McLachlan) from a "large long-dead" standing tree, and Bowles et al. (2015) reported collection of larvae emergent from deadwood. Immatures of Berothidae are hypermetamorphic predators of termites and may be found in deadwood as they follow their prey

(Gurney 1947a). Berothid larvae kill termites by emitting a fatal gas from their anal region (Johnson and Hagan 1981).

22.9.21 *Coleoptera*

The beetles are the largest order of insects (~350,000 described species) and the best studied group of saproxylic organisms. Gimmel and Ferro (2018; see Chap. 2) provide an overview of saproxylic Coleoptera. One of the chief adaptations of the Coleoptera is the presence of hardened forewings called elytra, which protect the flight wings and allow for movement through firm substances such as dirt, wood, and crevasses. The beginning of modern beetles may be the result of some little proto-beetle utilizing deadwood resources (Grimaldi and Engle 2005).

Some beetles associated with veteris wood and structures are some of the best known saproxylic insects, such as *Osmoderma* spp. Lepeletier and Serville (Scarabaeidae) and *Lucanus* spp. Scopoli (Lucanidae) (see Conservation, below). Additionally some of the most interesting beetles are associated with veteris wood. *Micromalthus debilis* is found deep in logs with red rot and has perhaps the most unusual and elaborate life history of any insect, but its life history is not yet fully understood (Grimaldi and Engle 2005: 363; Pollock and Normark 2002). *Titanus giganteus* (L.) (Cerambycidae) adults are the world's largest beetles by length (ca. 170 mm) and weight (although "largest" anything is always debatable), and their grubs may be the largest insects known (Acorn 2006). The larvae almost certainly feed on subterranean veteris wood but have never been found!

Large beetles, beetles in veteran trees, beetles associated with early stages of decay, and pest beetles are all actively being studied. The group of saproxylic Coleoptera most likely to be overlooked are small species associated with veteris down woody debris, essentially well-rotted logs. Leaf litter has been called the "poor man's tropical rainforest" (Giller 1996), and the temptation to concentrate collection from, and research on, such a rich environment is very high. Veteris woody debris straddling the O and A soil horizons harbors few specimens per equivalent volume of immediately adjacent leaf litter (Ferro et al. 2012a). Most studies on saproxylic insects concentrate on early stages of decay for various reasons. Therefore, veteris logs represent an overlooked habitat, spurned by leaf litter collectors and ignored by saproxylic workers.

In a singular study, Ferro et al. (2012a) compared beetles in veteris down coarse woody debris (referred to as CWD5) with beetles in adjacent leaf litter at six sites in Great Smoky Mountains National Park, Tennessee, USA. More species (170) and specimens (3471) were collected from leaf litter than an equivalent volume of CWD5 (111 and 790, respectively). However, species richness wasn't significantly different between the two habitats. Of 59 species available for analysis, 8 were significantly associated with CWD5. Those included the rarely collected *Tohlezkus inexpectus* Vit (Eucinetidae) (Fig. 22.3d), previously known from only five specimens; the genus *Sonoma* Casey (Staphylinidae: Pselaphinae), recently shown to harbor numerous cryptic species (Ferro and Carlton 2010); and *Mychocerus striatus* (Sen Gupta and Crowson) (Cerylonidae), which, despite being the fourth most numerous beetle on the forest floor, was represented by only four specimens in leaf litter but 246 in CWD5. Clearly veteris wood contains many more surprises, even within the comparatively well-known Coleoptera.

22.9.22 Strepsiptera

The twisted-winged parasites are a small order of about 600 species, all of which are parasitic. At various times, the group has been placed within and/or sister to Lepidoptera, Diptera, Hymenoptera, and Coleoptera but is now generally considered to be a unique order, sister to the Coleoptera (Misof et al. 2014). Basal taxa have free-living males and females, while females of more derived taxa permanently reside within the host. Strepsiptera are known to parasitize 34 families within seven orders of insects including Zygentoma and aculeate Hymenoptera (Grimaldi and Engel 2005). Strepsiptera will be in deadwood, including veteris wood, as they follow their hosts.

22.9.23 Hymenoptera

How bees, ants, and wasps relate to deadwood has been treated in greater detail in this volume (Bogusch and Horák 2018, Chap. 7; Hilszczański 2018, Chap. 6; King et al. 2018, Chap. 8). Many Hymenoptera will use veteris wood—from paper wasps (Vespidae) which construct nests from chewed plant fibers, including the thin outer layer of veteris wood on snags, to sweat bees (Halictidae) that overwinter in rotting logs and stumps. Additionally, hymenopteran parasitoids are as dependent on veteris wood as their hosts. Creation and use of veteris wood by ants are highlighted here specifically because of the economic and ecological implications.

Ants (Formicidae) are a worldwide taxon of eusocial insects numbering more than 15,000 species (Antweb 2017) that probably evolved in the mid-Cretaceous about 120 million years ago (Grimaldi and Engel 2005). Since the availability of a durable nest (especially hollow logs and twigs) is considered to be an important factor in the evolution of eusociality (Nowak et al. 2010), ants as we know them (and perhaps termites) may be the product of the interplay between a proto-ant population and deadwood, an idea first proposed by Hamilton (1978). In boreal habitats, deadwood is preferred by many ants because it provides a warmer nesting environment than soil (Boucher et al. 2015; Higgins and Lindgren 2012). Wheeler (1910: Chaps. 12–13) offers an overview of ant nests including those within deadwood and cavities in plants. Ants contribute to creation of veteris wood through mechanical removal of wood and, by their presence, induce predators to further destroy the wood resource. Redford (1987) lists 216 mammals that have been reported to eat ants or termites, 47 of which are known to break into nests.

Twig-dwelling ants live in dead, hollow twigs found in the canopy and on the forest floor (Byrne 1994) where density can be high (e.g., 0.31 nests/m^2 on the ground) (Fernanders et al. 2012). Arboreal twig-dwelling ants are also the subject of numerous studies concerning their use as biocontrol of pests within coffee agroecosystems (Jiménez-Soto and Philpot 2015; de la Mora and Philpott 2010) including use of artificial nests (Philpott and Foster 2005). However, no measure of the alteration of the substrate (twig) by the ants, nor destruction by predators, could be found.

Carpenter ants (*Camponotus* spp. Mayr) consist of ~1000+ spp. worldwide and are predacious, and many species excavate deadwood to create nest sites (Antweb 2017; Chen et al. 2002). They have been implicated in induced wind damage of trees in urban settings (Fowler and Roberts 1982). Chen et al. (2002) found that *C. vicinus* (Mayr) prefer to nest in logs and stumps 20–30 cm in diameter in Idaho, USA, while in New Brunswick, Canada, Sanders (1964) found that only snags greater than 15 cm DBH were colonized by *Camponotus* spp. Boucher et al. (2015) looked at postfire succession of ants in deadwood. They found that ant nest abundance peaked 30 years postfire, that the presence of wood-boring beetle holes increases the likelihood of colonization, and that ant presence within a log had an impact on carbon and nitrogen dynamics, possibly speeding decay.

Wood-nesting ants are ecologically and economically important in relation to bears and woodpeckers. In a Minnesota, USA, study, Noyce et al. (1997) found that black bears [*Ursus americanus* (Pallas)] regularly dug into stumps and logs for ants. In July, while brood is high, ants consisted of 58% of bear scat volume and were found in 96% of scats. A study on foraging habits of *Ursus arctos* L. in central Sweden showed that ants accounted for up to 16% fecal volume and that bears preferred carpenter ants (which are stump and log dwelling and have less formic acid and higher fat content) over mound-building ants (Swenson et al. 1999). In that same study, ant biomass available to bears was 10 times greater than moose biomass at the same locations. The relationship between forest management, woody debris, wood-dwelling ants, and bears is in need of additional study (Swenson et al. 1999).

Woodpeckers (Piciformes: Picidae) excavate cavities for nests, regularly tear into wood (living and dead) for arthropod prey, and have been studied in relation to use of trees and wood products (McAtee 1911). Conner et al. (1976) found that woodpeckers would often create nests in sound trees with heartrot (possibly veteris)—the sound sapwood protected the nest from predators while the soft heartwood was easy to excavate. Nappi et al. (2015) found differences in foraging behavior among woodpecker species ranging from utilization of newly dead trees to preference for highly degraded snags.

The pileated woodpecker (*Dryocopus pileatus* (L.)) feeds primarily on ants (Beckwith and Bull 1985) and is considered a keystone species because abandoned nest cavities are used by secondary cavity nesters (Newell et al. 2009). A study in Oregon, USA, where ants consist of 97% of the pileated woodpecker diet, found that 61% of logs contained ant colonies, ant colonies were more common in the larger diameter logs, and ants preferred decay class 4 (out of 5) (Torgersen and Bull 1995). In Oregon, *Camponotus* spp. are important predators of the western spruce budworm (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae), an important forest pest (Torgersen and Bull 1995). Thus deadwood of the appropriate size and decay class is an important factor in management practices that promote woodpeckers (keystone species) and *Camponotus* spp. (biocontrol of western spruce budworm but also woodpecker prey).

Many of the studies cited above (and others not included) indirectly provide measures of amount and incidence of deadwood at various locations and times. Mining literature for indirect measurements of deadwood, snags, tree holes, etc. may be profitable.

22.9.24 Mecoptera

The scorpion flies, hanging flies, earwig flies, snow fleas, and allies are not yet known to be associated with deadwood in a meaningful way and may be the only order with no saproxylic members (?!). But they are a fascinating group nonetheless (Grimaldi and Engel 2005). Immatures are unknown for many species, and some immatures are found in moss, which in some cases may be predominate on, or restricted to, rotting logs in some forests. Certainly more work is needed.

22.9.25 Siphonaptera

The fleas (~2500 spp.) are exclusive parasites of bird and mammal hosts (including rodents, bats, and marsupials) (Grimaldi and Engel 2005). Any flea species that is an obligate parasite on a species of bird or mammal that is an obligate cavity nester is just as saproxylic as a mite on a longhorn beetle. Presumably the vertebrate will get most of the attention.

22.9.26 Diptera

Diptera are represented by 120,000+ species and found in virtually all terrestrial and aquatic habitats (Grimaldi and Engel 2005) and are second to the Coleoptera (and may be first when all is said and done) in number of saproxylic species. Compared to beetles, little research has been conducted on saproxylic Diptera, much less in veteris wood. How the "true flies" relate to deadwood has been treated in greater detail by Ulyshen (2018; see Chap. 5). The following section will concentrate on Diptera known from veteris wood (including tree/rot holes) and briefly outline North American saproxylic fauna.

In a magnificent study, Hövemeyer and Schauermann (2003) collected Diptera emergent from beech wood over a 10-year period in Germany. In total they collected 163 species within 37 families. They found that some species showed temporal patterns—77 species predominantly emerged from logs 8–10 years old (veteris?)—and number of individuals and species increased as the log aged. Rotheray et al. (2001) surveyed the saproxylic Diptera of Scotland resulting in the collection of 258 species in 32 families. Of 85 species reared, nine were certainly from veteris wood—heartrot or tree holes. Savely (1939) studied logs in North Carolina, USA, and recorded 10 fly species (three in veteris) from pine logs and 10 species (seven in veteris) from oak logs. Howden and Vogt (1951) collected 20 fly species (one from veteris wood), in 14 families from standing dead pine. Irmler et al. (1996) collected Sciaridae and Mycetophilidae emergent from deadwood in a forest in Germany. They found flies were more numerous in veteris wood and listed 24 species of Sciaridae and 35 species of Mycetophilidae from veteris wood. Komonen et al. (2001) collected ~14 species of flies in seven families emergent from basidiocarps of two species of old-growth forest polypore fungi. The family Tipulidae certainly has many members with larvae in veteris wood. For example, an expedition to Sumatra obtained larvae of 4 species from tree holes, 48 species from saturated decaying wood, and 11 species from decaying fleshy fungi (Alexander 1931).

Syrphidae, larvae of which are often associated with saproxylic microhabitats in live trees rather than down woody debris, have been well studied in Europe (see Speight (2011) for species-level treatment). Reemer (2005) found that saproxylic syrphids may be increasing in the Netherlands, possibly due to changes in forest management and aging forests. However, several species dependent on the actions of other insects, such as wood borers, may be in decline. Ricarte et al. (2009) surveyed syrphids in a Mediterranean forest in Spain. They collected several threatened species, and, while some species were found in holes of multiple tree species, *Callicera macquarti* Rondani has only been collected in rot holes of a single tree species. Rotheray (2013) showed that in the UK, four species of syrphids, including the red-listed *Blera fallax* (L), may reduce competition by occupying distinct depths when they co-occur within tree rot holes.

Axymyiidae is one of the more extraordinary flies associated with veteris wood. The family consists of four genera and eight species distributed in the Holarctic including Taiwan and Southern China (Sinclair 2013). In general the larvae burrow into wet rotting logs and extend a siphon to the exterior of the log; see Krogstad (1959) for a diagram of the unique larval position. Wihlm et al. (2012) illustrate morphology of all life stages for *Axymyia furcata* McAtee (Fig. 22.3e). In practice the larval habitat (at least for *A. furcata*) is very specific, and they require all of the following: moderate to dense hardwood to mixed forest, small lotic habitats (such as springs or streams) that are *not* prone to flooding, deadwood greater than 3 cm diameter, generally wood without bark or moss, and wood that is light in color, soft enough to push a pencil into it but firm enough to resist prying apart; and the larvae are generally located in a part of the log near the water surface that stays perennially wet but does not get submerged (Wihlm and Gregory 2011). A recently described species from Alaska and Washington was first collected in 1962 but, despite decades of search, is only known from two specimens, the second collected in 2012 (Sinclair 2013). Whether the specific requirements of Axymiidae will put its members in peril is yet to be seen.

At least 75 fly families worldwide are known to contain saproxylic members (Ulyshen 2018, Chap. 5), and many of these are associated with veteris wood. Members of several additional families that are ectoparasites on birds and mammals (Hippoboscidae, Nycteribiidae, Streblidae, etc.) may also qualify as saproxylic when their hosts are frequent or obligate snag or tree hole nesters. The 55 North American dipteran families known from veteris (McAlpine et al. 1981, 1987; Teskey 1976) include Acartophthalmidae, Anisopodidae, Anthomyiidae, Asilidae, Asteiidae, Aulacigastridae, Axymyiidae, Braulidae, Canthyloscelidae, Cecidomyiidae, Ceratopogonidae, Chironomidae, Chloropidae, Chyromyidae, Clusiidae, Culicidae, Cypselosomatidae, Dolichopodidae, Drosophilidae, Empididae, Heleomyzidae, Lauxaniidae, Lonchaeidae, Micropezidae, Milichiidae, Muscidae, Mycetophilidae, Mydidae, Neriidae, Odiniidae, Pachyneuridae, Pallopteridae, Periscelididae, Phoridae, Platypezidae, Psychodidae, Rhinophoridae, Richardiidae, Ropalomeridae, Sarcophagidae, Scatopsidae, Scenopinidae, Sciaridae, Stratiomyidae, Strongylophthalmyiidae, Syrphidae, Tabanidae, Tachinidae, Therevidae, Tanyderidae, Tipulidae, Trichoceridae, Ulidiidae, Xylomyidae, and Xylophagidae.

22.9.27 Trichoptera

The caddisflies consist of more than 14,500 species (Morse 2017) all of which have aquatic larvae. Caddisfly larvae can produce silk, and many use that to construct cases out of materials including sand, rocks, leaves, bark, and small chips of rotten wood. Few, if any, are associated with veteris wood, other than those which use it for case-making material. However, in North America, larvae in the genus *Heteroplectron* McLachlan (Calamoceratidae) are found in pools where plant material accumulates, and they create cases by excavating the center out of small twigs (Wiggins 1996). In Australia, several species of *Triplectides* Kolenati (Leptoceridae) are known to create or use hollow twigs as cases (St Clair 1994). How dead terrestrial plant matter affects caddisflies is interesting, or to put it another way, the tethering of twigs to Trichoptera is titillating.

22.9.28 Lepidoptera

Butterflies and moths are generally phytophagous and rarely associated with deadwood, except when using it as structure for hiding or cocoon placement. The larvae of Cossidae and Sesiidae are wood borers but require living wood as they only digest cell contents (Stokland 2012b). The caterpillar of the eastern North American species *Scolecocampa liburna* (Geyer) (Erebidae) (Fig. 22.3f) lives in and eats decaying logs and stumps of chestnut, oak, and hickory (Pogue 2012). Caterpillars, presumably of the western species *S. atriluna* Smith, have been found (with frass) living in veteris logs in the Chiricahua Mountains, Arizona (personal observation).

The economically important family Tineidae consists of about 3000 species (Grimaldi and Engel 2005) that eat a wide variety of dry organic matter including keratin, wool, fungi, grain, leather, and even mummified human corpses (Holland 1913; Katz 1997). Often the larvae construct and reside within cases made of debris held together by silk. The family Oecophoridae is also known for larvae that eat dead plant material including carpets and textiles. While noneconomic species of both families have traditionally been overlooked, species associated with saproxylic habits are gathering more attention (Jaworski 2018; see Chap. 10).

Ols et al. (2013) recorded five species of Tineidae emergent from stumps in Sweden, and Komonen et al. (2001) reared two species from polypores in Finland. Both studies each reported collecting one species of Oecophoridae. Lawrence and Powell (1969) provided biological information on 13 species of Tineidae and Oecophoridae associated with polypore fungi in western North America. They noted that larvae were often found in the bark or wood under the fungal fruiting body and suggest retaining the wood immediately around fungi when conducing emergence surveys. They found most species could be considered polyphagous, but at least one appeared to be host specific. Working in Poland, Jaworski et al. (2012, 2014, 2016) have studied the association between tineid species and polypore fungi. In total they have recorded over 20 species of saproxylic tineids from their study areas, many new to Poland, and associated moths with fungal hosts. In some cases, tineid species preferred red-listed fungal hosts and were of conservation concern themselves.

22.10 Insects in Veteris Wood II: Ecological Concerns

Veteris wood has received so little study that the following section is presented mostly as a series of questions and speculations. While analogies and extrapolations could be gleaned from the literature, a few simple studies would be much better.

22.10.1 Diversity

In general, studies have shown that diversity of saproxylic insects peaks around the stage where bark loosens from the trunk (e.g., Blackman and Stage 1924) and then drops as wood moves into the final decay stage. Ferro et al. (2012a, b) surveyed beetles in coarse woody debris across a decomposition spectrum of decay classes 1, 2, 3–4, and 5 (veteris) and found a humped diversity curve: 110, 156, 127, and 111 species, respectively. However Ulyshen and Hanula (2010) and Howden and Vogt (1951) found highest richness the first year of death, but Hammond et al.

(2004) found a gradual increase over many years (none surveyed the final decay stage).

There are several reasons to suspect that saproxylic insect diversity should *decrease* as decomposition occurs. Necessarily less material and energy are available to later successional individuals. Fewer distinct habitats are available (subcortical, heartwood, etc.) as the well-defined layers of the dead tree decompose into a more uniform heap. The mechanical protection provided by the wood decreases over time. And finally decomposition removes many secondary chemical compounds which makes the substrate available for generalists rather than specialists (see Wood Structure and Digestion above).

On the other hand, diversity may *increase* as decomposition occurs. Microbial conditioning may make the substrate more favorable to insects (e.g., adjustment of the C/N ratio). Growth of fungi may create new additional "habitats" (mudguts, etc.) or resources (fungi itself as food). Removal of secondary compounds may "homogenize" wood of different species (e.g., the characteristics of oak and maple wood converge) which acts to increase the amount of available wood across the landscape (less fresh-oak is available than all well-decayed hardwood combined). And finally less-sound wood may offer protection from parasites and predators because vibrations are dampened and tunnels collapse.

The question of diversity across successional stages is complicated by (1) how many stages are recognized; (2) the study system and scale in question (diversity within a particular dead tree, within members of a particular tree species, or across all deadwood types in the landscape); (3) poor taxonomic coverage, especially for flies which may have a different successional diversity profile than beetles (see Brauns 1954; Hövemeyer and Schauermann 2003); and (4) most importantly, lack of studies cataloging species in final decay stages of wood (veteris).

22.10.2 "Wood" and "Soil" Fauna

As was pointed out above, no quantitative (or even qualitative) definition for the "end" of deadwood exists. Presumably a "log" becomes "soil" when certain qualities of the ground where the log was match qualities of the ground where the log was not. However, the impact of deadwood on soil characteristics begins soon after it touches the soil and lasts long after the log is no longer recognizable (see Lodge et al. (2016), and references therein).

The ambiguity of deadwood disappearance also greatly affects the question of when does soil fauna replace wood fauna. Ferro et al. (2012a) found two distinct beetle communities when they compared veteris wood and the surrounding leaf litter. However, in their study, the pieces of decayed wood were still large (liter scale) and not mixed with the soil. Communities associated with dead logs that have fragmented into smaller pieces (cubic centimeter scale) and mixed with the soil have not been sampled, except, perhaps, as "soil fauna." Clearly a spectrum exists where saproxylic and soil fauna overlap and replace one another, but the character of that spectrum is unknown.

22.10.3 Big Beetles!

Some of the largest insects (by weight) are beetles with immature stages that live in veteris wood (Acorn 2006). Most of the biggest are within a few lineages in the families Lucanidae (stag beetles), Scarabaeidae (scarabs) (both in the superfamily Scarabaeoidea), and Cerambycidae (long-horned beetles) (superfamily Chrysomeloidea). Using phylogenetic reconstruction, McKenna et al. (2015) showed that Scarabaeoidea living in logs today transitioned into them from leaf litter-dwelling ancestors, and that once in logs, lineages have not transitioned out into other lifestyles. While most cerambycids today feed on damaged, dying, or (rarely) healthy plant tissue, ancestral cerambycids were probably deadwood feeders, a habit still prominent in several subfamilies including those with the largest species (Svacha and Lawrence 2014). It is speculated that consuming deadwood next to living wood (e.g., in a tree hole or veteran tree) may have led to consumption of live wood.

Why gigantism would arise in beetles associated with veteris wood is unknown. However, all things being equal, large-bodied beetles need more time, food, and protection from enemies while developing than small-bodied beetles. As Ferro et al. (2012b) pointed out, large pieces of deadwood (especially veteris) are a unique habitat. They represent large, stable, long-term resources in the presence of plenty of oxygen that are not actively metabolically defended. Perhaps giant beetles are in veteris wood simply because it is one of the few places where giant beetles could develop. Or, as vertebrates do not eat rotten wood, lack of competition may have left a size-related niche open that beetles were the first/best to fill. Despite the potential for very large quantities, deadwood is finite, and large body size may be the result of competition among individuals of the same species over resources within a log [e.g., Tanahashi and Togashi (2009) reported larval cannibalism in the stag beetle *Dorcus rectus* (Motschulsky)]. Whatever the reason, veteris wood and structures (e.g., tree holes) are an important habitat for giant beetles and important for conservation concerns.

22.11 Study of Invertebrates in Veteris Wood

Deadwood is an opaque habitat, and while chemical and fungal attributes can generally be sampled and analyzed quickly, the study of invertebrates that reside within it can be difficult. Additionally, the time encompassing complete decay of woody debris generally takes longer than research timespans, whether artificial (degree, grant) or real (career, researcher lifetime). Studies of the early stages of deadwood, from death until interest or funding runs out, are well suited for experimental manipulation and replication. However, generally that research requires a complete expanse of time (studying 1 year after death requires waiting 1 year after death), and, when invertebrate taxa are involved, additional time (months to years) is required for adult emergence. Therefore the benefit of studying early stages of deadwood is the increased control over starting circumstances and replication, but the costs are the time required to carry out the study and inability to perform extended studies.

Study of veteris wood offers the opposite costs and benefits. Invertebrates from most veteris wood can be obtained within days of sample collection if extraction with a berlese funnel or Winkler eclector is used (see Owens and Carlton (2015) for best practices; Ferro et al. (2012a) offer an example). Or if only adults are desired, samples can be placed immediately within emergence chambers after collection (see Ferro and Carlton (2011) for a review). For collection of invertebrates associated with fungi or veteris wood in living trees, including tree holes, emergence traps can be deployed. Most species that emerge and disperse will do so during the warmer months; therefore 4–6 months may be all that is required to conduct a meaningful survey/study of insects in veteris wood in living trees. However, the time required for veteris wood to form, which may take years, decades, or centuries, precludes any control over starting circumstances and replication. Therefore the benefit to study of veteris wood or veteris structures (tree holes, etc.) is the short timeframe needed to survey the substrate (~less than 1 year), but the cost is that studies tend to be more observational than experimental.

Several veteris wood types have received little or no attention and are of particular research interest. Bouget et al. (2011) found differences in saproxylic beetle assemblages based on vertical strata within a forest. Ulyshen (2011) reviewed vertical stratification of arthropods in temperate forests and saproxylic beetles in canopies (Ulyshen 2012) and came to the same conclusions. Heartrot not exposed by tree holes has received little attention, but Berry (1969) and Berry and Beaton (1972) showed that heartrot is quite prevalent in central and eastern North American forests. At the time of their study, most infection courts began at fire scars; how fire suppression has altered heartrot and other resultant saproxylic habitats is unknown. The review by Gange (2005) on sampling insects from roots makes no mention of the saproxylic insects or deadwood. In a rare study involving dead tree roots, Victorsson and Jonsell (2016) collected 47 species of beetles associated with early decay roots of Norway spruce (*Picea abies* (L.) H. Karst.), five of which were associated with roots and not aboveground stumps.

From a conservation standpoint, veteris wood warrants study and may be of as much conservation interest as large-diameter trees and woody debris. Dahlbeg and Stokland (2004) surveyed needs of all organisms (plants, animals, fungi) associated with deadwood in Sweden and found that 15% were dependent on veteris wood. Veteris structures, such as tree holes, are associated with numerous species of conservation concern (see below). Veteris wood requires time to form, and the lag between current and future resources needs to be taken seriously. While fresh deadwood can be artificially "created" within minutes (simply cut a tree; although

Komonen et al. (2014) found differences in polypore communities between natural logs and chainsaw felled logs, so be careful), we currently lack the ability to "create" veteris wood (but see pollarding and artificial habitats below). For example, *Euperipatoides rowelli* (Reid) (Onychophora: Peripatopsidae), which lives in south-eastern Australian forests, requires hollow *Eucalyptus* L'Hér. logs for shelter. Barclay et al. (2000) showed that suitability of a log was highest after 45 years of decay—nearly half a century *after* the time it took a tree to grow big enough to have a log that, after 45 years of rot, is still substantial enough to make suitable habitat. Veteris wood in one location will already be inhabited, so movement to another location (if that is even possible) to provide resources is not a reasonable option.

Thankfully the structural aspects of veteris wood allow for relatively rapid surveys of chemical properties and fungal and invertebrate inhabitants on time scales that match undergraduate to Ph.D. level research schedules. There is no reason why invertebrates in veteris wood could not be thoroughly surveyed across the globe within the next few decades, making veteris wood the best understood phase in the deadwood cycle. Because so many endangered species are associated with veteris wood, study of veteris wood and conservation will go hand in hand.

22.12 Conservation Related to Veteris Wood

> *There are no 'pests' in a natural forest.*
> —Bobiec et al. 2005

One of the natural traits of the species *Homo sapiens* L. is modification of the environment, which may occur across multiple scales, from the bending of a twig to the straightening of a river. Despite misconceptions by the public and often misleading statements by parks and conservation organizations, modern conservation efforts are not and will not be able to return most localities to the *urwald* state. Urwald is currently a term loosely meaning *primeval forest before alteration by man* (Buckland and Dinnin 1993) but could easily be expanded to encompass any region of the Earth before human alteration. The reality is most of the landscape falls on a continuum from less altered to more altered. Modern conservation efforts need to recognize humans as a part and product of the Earth and strike a balance between the needs of human-related activities with the needs of other components of nature (Stone (1972) articulates this sentiment in a legal framework). The notion that some areas will be unaltered by nature (urban) and others unaltered by man ("protected" parks) is naive.

Conservation of saproxylic species and habitat has been the focus of many studies, and a variety of proposals and strategies have been suggested. At the landscape scale, most proposals fall within two categories, morticulture, actively managing for deadwood (Cavalli and Mason 2003; Harmon 2002; Key and Ball 1993), and "benign neglect" (noninterference, letting "nature" take its course) (Müller et al. 2010). Retention of veteris wood (a hybrid of the two) during logging has been suggested by Ehnström (2001) (loggers should work to decrease fragmentation of existing logs at sites), and Hagan and Grove (1999) (down and hollow logs should be preserved during logging). Bergman et al. (2012) recommended retention of one hollow oak per 7 ha to optimize habitat for associated saproxylic beetles. At smaller scales, active management through pollarding to increase tree holes (Sebek et al. 2013) or use of seminatural areas in urban settings [e.g., golf courses; see Powell et al. (2016)] to enhance saproxylic habitat has been described. Conservation efforts will reach their pinnacle with the reintroduction of extirpated saproxylic species, similar to the concept of "Pleistocene rewilding" (Donlan et al. 2006). Reintroduction of the Lord Howe Island stick insects (see Phasmatodea above) is an important example.

Conservation of organisms associated with veteris wood has been the subject of much work and research, especially at very localized scales when considering ancient and veteran trees. Ancient trees are particularly old for their species, and veteran trees show signs of having "survived various rigors of life" including signs of decay and exposed deadwood (see Lonsdale (2013) for more complete definitions). Both are important for maintaining habitat for saproxylic species ranging from insects to rare lichens (Kirby 1992; Lonsdale 2013). Among the varieties of deadwood available in veteran trees, including tree holes, much would be considered veteris wood. Jonsell (2004) showed that a park with ancient trees harbored nearly as many red-listed saproxylic beetle species (20 spp.) as a high-value seminatural area (24 spp.) in Sweden. In a larger study across eight park sites, Jonsell (2012) found that old park trees were as valuable for maintenance of species in hollow trees and red-listed species as trees from more natural areas. In France, Parmain and Bouget (2018) compared saproxylic beetles between trees within forests and trees outside forests. They found similar alpha diversity and abundance, indicating the importance of retaining habitat trees in the landscape even if they are isolated. Sverdrup-Thygeson et al. (2010) found that hollow oaks in forests and parks were both rich in red-listed beetles but that assemblages differed between the two. Ranius et al. (2005), and references therein, showed the importance of tree hollows for the red-listed species *Osmoderma eremita* (Scopoli) (Coleoptera: Scarabaeidae). Lonsdale (2013), and references therein, offer guidance for management of veteran trees, which are considered important cultural elements across Europe. While not specific to veteran trees, Stone (1972) promoted the "unthinkable idea" that rights should be conferred to natural objects, including trees. The idea seems particularly applicable to ancient and veteran trees, especially those that may have a historic or cultural value.

However, large dead and dying trees can be a safety hazard. Lonsdale (2013) (Chap. 4) provides advice on balancing care for ancient trees and safety for people and property, and Watkins and Griffin (1993) provide advice specific to England and Wales. Carpaneto et al. (2010) found that 41% of surveyed trees in urban parks in Rome that harbored target beetle species, including red-listed species, were labeled as dangerous to citizens and needed to be cut for safety. They provide several recommendations to promote conservation and maintain safety, including leaving cut trunks and branches in the area for larvae.

The advice above highlights another stumbling block in the conservation of saproxylic habitats. Veteran trees and deadwood in general have to overcome the current fad of considering decaying logs, limbs, and stumps unaesthetic. Whitehead (1998) describes the "grafting" of a cut decaying limb onto a nearby tree to prolong the life of the "discriminating arboreal invertebrates" within but warned of the public perception that those "efforts may compromise the appearance of the landscape at large." Education (see below) may help to reverse this trend. Thankfully some instances of retaining dead trees as "features of the historic landscape" do exist; see Lonsdale (2013: 11) for examples.

The stag beetle, *Lucanus cervus* (L) (Lucanidae), is a beetle of conservation concern across Europe and represents one of the "enigmatic megafauna" (flagship species) associated with veteris wood. Harvey et al. (2011a) reported that it was declining across Europe and "absent or extinct" from 13 countries. Their survey found that larvae are generally on decayed oak stumps but have been collected from a dozen other tree species, and it may use other substrates, such as oak fence posts, provided the wood is sufficiently decayed. Several monitoring studies have been conducted: Hawes (2008) developed and tested a mark and recapture technique; Harvey et al. (2011b) tested several noninvasive monitoring techniques including road transect surveys, acoustic detection, and adult lures; and Campanaro et al. (2016) used a standard transect walk technique to detect populations within eight countries. Sprecher (2003) studied the life cycle of *L. cervus* in northern Switzerland and noted that adults will eat sap from wounded trees or ripe fruit including cherries, illustrating that adults have resource needs not just larvae. She also described habitat enhancement by creating oak stumps and mounding wood chips on the shady side of the stump. In the UK, the People's Trust for Endangered Species currently coordinates several types of monitoring for *L. cervus*, including the "Great Stag Hunt" and advocates creation of log "pyramids" and "piles" as artificial habitat for the species (PTES 2017).

The hermit beetle, *Osmoderma eremita* (Scarabaeidae), is another relatively well-studied flagship species associated with tree holes (see Ranius et al. (2005), and references therein). Creation of artificial tree holes for *Osmoderma* and other species has been attempted and is reminiscent of Fager's (1968) "synthetic logs." Green (1995) re-erected the hollow trunk of a dead tree and filled it with sawdust, guano, and a few dead animals in a successful attempt to create additional habitat for the violet click beetle (*Limoniscus violaceus* (Müller), Elateridae). A simple pilot study by Whitehead (1998) found a compost bin and a plastic bag each filled with coarse beechwood sawdust attracted saproxylic species. Birtele (2003) made artificial habitats consisting of wooden boxes filled with sawdust to study the saproxylic fauna of Bosco della Fontana Nature Reserve in Italy. In a twist, Hilszczański et al. (2014) created artificial tree cavities and seeded them with larvae of *Osmoderma barnabita* (Motschulsky) to test the efficacy of the design. They found a high survival rate and successful recolonization within the boxes.

Jansson et al. (2009) conducted a large study of artificial tree holes in Sweden. In total, 47 boxes simulating artificial tree holes, each 60 l in volume, were created. All containers were filled with oak sawdust, leaves, and one of four additional ingredients, including a dead hen to simulate a hollow used by birds. After 3 years, 105 saproxylic beetle species were recovered from the boxes representing 70% of the total species known from tree hollows in the area. Boxes with a dead hen had a higher number of beetle specimens. The substrate volume decreased by 15–30% over the 3-year period, possibly because of the "fresh" quality of the sawdust used. Probably many years of processing by fungi and invertebrates would be necessary before the substrate more fully mimicked true tree hollows. Micó et al. (2011) and Sánchez et al. (2017) studied chemical changes in wood eaten by the tree-hollow-inhabiting beetle *Cetonia aurataeformis* Curti (Scarabaeidae). They found a higher concentration of nitrogen and other changes associated with tree hollow substrates and concluded that wood processing by *C. aurataeformis* facilitated use by other saproxylic organisms. Presumably laboratory-reared beetle larvae could be used to condition fresh sawdust and convert it into veteris wood for future artificial habitats.

In the USA, few if any specific saproxylic species are of conservation concern. It is not clear if this is accurate or due to ignorance. A review of insect conservation in the USA by Bossart and Carlton (2002) did not mention any deadwood species. A recent study by Powell et al. (2016) about suitability of deadwood habitat on golf courses was interested in reducing the general degradation of the environment, not increasing habitat for a specific species or guild. Ulyshen et al. (2017) studied the North American *Lucanus elaphus* F. (Coleoptera: Lucanidae), a relative of the European red-listed *L. cervus*, but found that it is probably not immediately threatened.

22.13 Education

> *Verily, the most common things about*
> *us are those of which we know the least.*
> —W. S. Blatchley 1902

All conservation begins with education—the existence of that to be conserved must first be known. Whether the "knowledge" itself is emotional ("Save the whales!"—it doesn't really matter why) or intellectual (water pollution causes general degradation to the environment) matters little at the first step. Books for popular audiences, such as *What a Plant Knows* (Chamovitz 2013), *Bark: An Intimate Look at the World's Trees* (Pollet 2010), *Remarkable Trees of the World* (Pakenham 2003), *The Hidden Life of Trees* (Wohlleben 2016), *Oak: The Frame of Civilization* (Logan 2005), *Trees: A Complete Guide to Their Biology and Structure* (Ennos 2016), *The Secret Life of the Forest* (Ketchum 1970), and *Reading the Forested Landscape* (Wessels 1997), and innumerable field guides help to inspire (emotion) and educate (intellect) the public about plants, trees, and forests in general.

Other resources occupy a middle ground between popular and technical and are very important bridge between the two. A series of richly illustrated publications by the USDA help to explain tree wounding and decay: *A Tree Hurts Too* (Shigo 1974), *Compartmentalization of Decay in Trees* (Shigo and Marx 1977), *Tree Decay: An*

Expanded Concept (Shigo 1979), and *Wood Decay in Living and Dead Trees: A Pictorial Overview* (Shortle and Dudzik 2012). Not only do they provide a background for the processes that lead to veteran trees but also provide a template for similar publications.

Several public-friendly publications specific to the saproxylic habitat are available, including: *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington* (Thomas 1979); *The Seen and Unseen World of the Fallen Tree* (Maser and Trappe 1984); *From Forest to the Sea: A Story of Fallen Trees* (Maser et al. 1988); *Trees and Logs Important to Wildlife in the Interior Columbia River Basin* (Bull et al. 1997); and *The Afterlife of a Tree* (Bobiec et al. 2005). Additionally guides exist for maintaining and establishing saproxylic habitat from the scale of a landscape to individual trees: *Habitat Management for Invertebrates* (Kirby 1992); *Techniques for Re-Establishment of Dead Wood for Saproxylic Fauna Conservation* (Cavalli and Mason 2003); and *Ancient and Other Veteran Trees* (Lonsdale 2013, and references therein).

Educational information and materials for children and the public about the importance of deadwood and saproxylic fauna have been created. Possibly the first was Animal Inn (2003), initially created in 1985, it was an educational program with the motto “There’s life in dead trees” designed to inform the public about the importance of snags to wildlife. The program featured the character “Sally Snag” and at one time included a costume and merchandise as well as educational workbooks. It has since been suspended. The Australian Department of Environment and Water Resources created an educational program, including handouts and songs, called “Logs have life inside” about inappropriate firewood collection (AU 2002). Minari et al. (2003) undertook a 3-year project to educate the public about deadwood at Bosco della Fontana Nature Reserve in Italy (see Cavalli and Mason 2003). They specifically created distinct lessons for school-aged children, high schoolers, university students, and adults. Bobiec et al. (2005) provide several interesting educational activities in Appendices I and II of their book. They also suggest creation of an interpretive deadwood trail—“a living museum of dead wood!” (p. 192)—which is an immensely appealing idea. The Slovenian Forestry Institute’s Forest of Experiments group has created the “Handbook for Learning and Play in the Forest” (Vilhar and Rantaša 2016) (not yet available in English) which contains numerous forest-related activities for school children.

Finally, two popular “advocates” for deadwood must be mentioned. The Marvel Comics superhero Groot is a saproxylic-like character resembling a snag. Groot is an individual of the species *Flora colossus* Lee and Kirby from Planet X and has numerous plantlike superpowers, including totipotency. While Groot has appeared in several guises, he is currently best known as a member of the group Guardians of the Galaxy (https://en.wikipedia.org/wiki/Groot). Botanical gardens and forest preserves could capitalize on the popularity of the character among children—“Watch for Groot on the trail!”, “Can you find Groot?”, etc.

The Ents, a race of creatures created by J. R. R. Tolkien in his Middle Earth universe, were ancient shepherds of trees tasked with protection of the forests from overharvesting by Dwarves, an apt allegory for veteran trees today (https://en.

wikipedia.org/wiki/Ent). Much like the Ent, veteran trees are tasked with sustaining biodiversity until adequate forest resources can be reestablished. One could easily imagine an "Ent Trail" where participants travel across the country visiting multiple veteran trees, especially within the UK and Europe. Around the world, the concept to the Ent could be used to personify veteran trees for conservation purposes.

22.14 Future Research into Veteris Wood

Virtually all types of saproxylic research are currently being held back by the lack of taxonomic resolution and the inability to accurately characterize substrates in an agreed upon, repeatable manner. When researchers are willing, taxonomic resolution issues can be overcome or reduced using techniques, such as DNA barcoding, which allow unrecognizable forms (egg, immature, pupae, females, etc.) to be associated with described forms (typically an adult male) (e.g., Caterino and Tishechkin 2006). MicroCT scans of immature insects identified with DNA barcoding would allow for morphological recognition of additional imaged specimens not available for barcoding (e.g., imaged during nondestructive sampling). The same or similar techniques could be used to "define" an undescribed or unnamable species and track its presence, absence, and abundance over multiple independent studies.

Characterizing deadwood substrates will be much more difficult. Seemingly at least six measures need to be made: physical properties of the wood (volume, diameter, structural aspects, etc.), "chemical" profile (e.g., lignin content, C/N ratio, etc.), fungal profile (which species and in what proportions), water content (significant factor in determining extent of fungal activity), immediate abiotic environment (sun, shade, temperature, humidity, etc.), and landscape factors (see Franc et al. 2007). If implemented, the above approach would seek to define all existing deadwood "types." However, as has been pointed out (Stokland and Siitonen 2012b: Sect. 11.3.1), the possible number of deadwood types would exceed the actual number of saproxylic species by several orders of magnitude. However, "habitat" defined by nature and defined by humans is two different things. If the focus was reversed, and deadwood types were defined through their use by saproxylic species, then a reasonable list of a few hundred "functional" substrates could be created and still be described by the measures listed above. We already do something similar in a qualitative manner when we talk about species that are subcortical, only in the fermenting stage, or associated with veteris wood.

Above all else, detailed natural history of saproxylic organisms is needed. Increased accuracy and precision of how material is cycled and energy and genes flow at the species level must be known to protect species from extinction and connect the saproxylic habitat with the rest of nature. However, there is little fame in these endeavors.

New technology, tools, and techniques will allow study of the saproxylic habitat in extraordinary ways. The current smuggling/terrorism paradigm is driving improvements in technology in noninvasive scanning techniques, a boon for deadwood researchers. A variety of technologies are being developed and implemented: large arrays for scanning huge items such as cargo containers, handheld X-ray devices for smaller items, and nanoCT scanning with microscopic resolution. The result is that researchers can now obtain noninvasive images ranging from the interior a 4 m thick log loaded on the back of a truck to micron-scale images of the interior of a twig.

Veteran trees with multiple types of wood and cavities are very complex, and measuring internal and external features is daunting. However, Lidar ("light detection and ranging), which uses lasers to measure distances, can be used to create three-dimensional images of small to large complex forms. Omasa et al. (2008) combined on-ground and airborne Lidar scanning to create complete three-dimensional models of standing trees. Their models allowed for quantitative measurements of volume and length of any aspect of the tree. Photogrammetry is a technique that extracts geometric information from multiple two-dimensional images of a particular item and creates a three-dimensional model. Whereas Lidar can use UV light and create high-resolution scans, photogrammetry using visible light captures true-to-life colors. A combination of the two could create a high-resolution model of a veteran tree and allow for identification of lichens growing on its surface.

The internal attributes of live trees can also be imaged in a number of ways. Niemz and Mannes (2012) review techniques for nondestructive testing of wood artifacts, including sound tomography and electromagnetic radiation, which could be used on live trees. Allison and Wang (2015) provide practical examples of the use of acoustic devices to evaluate tree decay and create three-dimensional models of tree interiors. It is not inappropriate to expect that over the next few years techniques will be developed to scan and model an entire veteran tree and image artifacts within it, including adult and immature insects, that are as small as a few millimeters. Imaging techniques coupled with faunal surveys could make veteris wood and veteran trees one of the best understood keystone habitats on Earth.

22.15 Conclusion

The study of the saproxylic habitat has undergone a grand expansion, and necessarily a certain amount of specialization and atomization of research topics has occurred. With the concept of veteris wood, the relatedness of studies that have otherwise been treated as independent can be illustrated. For example, a living veteran tree may have more fauna in common with a severely decayed log than a fresh windfall. Expanding the scope of study is important too—studies by foresters on heartrot and wood stain in living trees cascade into studies on tree cavity nesters, veteran trees, and eventually mudguts.

The study of veteris wood suffers from being far removed from economic issues; few faunal elements are shared between fresh-cut timber and veteris wood. And it suffers from issues with experimental design and repeatability. Ferro et al. (2012b: 17) proposed a scheme to create "legacy" coarse woody debris where descriptions of trees (species, size measurements, etc.) were recorded immediately after death and available for researchers in the future. A century from now, a researcher standing over a faint line on the forest floor would know it originally was a 60 cm diameter red maple killed by wind during a particular week. However, as that plan would not bear fruit for several decades after initiation, it is unlikely to be implemented.

Nevertheless, the study of veteris wood benefits greatly by its association with large scarab (Scarabaeidae) and stag beetles (Lucanidae) which serve as nonthreatening mascots and flagship species for their habitat (Huang 2018; see Chap. 4). Some hoverflies (Syrphidae), Mydas flies (Mydidae), and the crane fly genus *Ctenophora* Meigen (Tipulidae), with the right ad campaign, could also become insect advocates for veteris wood conservation. Veteris research also benefits from veteran trees, which are important for biodiversity conservation and, due to their age, can serve as inspirational rallying points in a community. Finally, because veteris wood is removed from structural wood, it can be incorporated into private and public spaces like gardens and parks (a massive redwood log is on display outside the northeast corner of the Oregon Convention Center, Portland, USA). Allowing the public to participate in conservation issues and habitat enhancement is important for raising awareness of all saproxylic habitats.

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Journal titles should not be abbreviated (Ferro and Mayor 2016). The following is a key to the abbreviated journal titles given: Adv Ecol Res = Advances in Ecological Research; Agr Forest Entomol = Agricultural and Forest Entomology; Am Ent = American Entomologist; Am Nat = American Naturalist; Anim Biodiv Conserv = Animal Biodiversity and Conservation; Ann Entomol Soc Am = Annals of the Entomological Society of America; Ann Mo Bot Gard = Annals of the Missouri Botanical Garden; Annu Rep Dept Geol Nat Resour Indiana = Annual Report of the Department of Geology and Natural Resources of Indiana; Annu Rev Ecol Syst = Annual Review of Ecology and Systematics; Annu Rev Entomol = Annual Review of Entomology; Arch Hydrobiol = Archiv für Hydrobiologie; B Am Mus Nat Hist = Bulletin of the American Museum of Natural History; B Illinois St Lab Nat Hist = Bulletin of the Illinois State Laboratory of Natural History; B Mus Comp Zool = Bulletin of the Museum of Comparative Zoology; Behav Ecol Sociobiol = Behavioral Ecology and Sociobiology; Biodivers Conserv = Biodiversity and Conservation; Biol Conserv = Biological Conservation; Biol Rev = Biological Reviews; Bollett Di Zoologia Gen E Agr = Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricoltura in Portici; Br Wildl = British Wildlife: The Magazine for the Modern Naturalist; Can Entomol = The Canadian Entomologist; Can J Forest Res = Canadian Journal of Forest Research; Can J Zool = Canadian Journal of Zoology; Coleopt Bull = The Coleopterists Bulletin; Cretaceous Res = Cretaceous Research; Crop Forage Turfgrass Manage = Crop, Forage & Turfgrass Management; Curr Biol = Current Biology; Ecol Appl = Ecological Applications; Ecol Bull = Ecological Bulletins; Ecol Bull = Ecological Bulletins (Stockholm); Ecol Entomol = Ecological Entomology; Ecol Evol = Ecology and Evolution; Ecol Monogr = Ecological Monographs; Ecol Res = Ecological Research; Entomol Exp Appl = Entomologia Experimentalis et Applicata; Entomol Fennica = Entomologica Fennica; Entomol Gaze = Entomologist's Gazette; Entomol Mon Mag = Entomologist's Monthly Magazine; Entomol News = Entomological News; Entomol Obozr = Entomologicheskoe Obozrenie; Environ Entomol = Environmental

Entomology; Environ Modeling Asses = Environmental Modeling and Assessment; Environ Rev = Environmental Reviews; Eur J Soil Biol = European Journal of Soil Biology; Fla Entomol = Florida Entomologist; Folia Fac Sci Nat Un Biol = Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia; Forest Ecol Manag = Forest Ecology and Management; Forest Sci = Forest Science; Front Biol China = Frontiers of Biology in China; Glob Change Biol = Global Change Biology; Illinois Nat Hist Surv Bull = Illinois Natural History Survey Bulletin; Insect Conserv Diver = Insect Conservation and Diversity; Insect Soc = Insectes Sociaux; J Anim Ecol = Journal of Animal Ecology; J Arboric = Journal of Arboriculture; J Chem Ecol = Journal of Chemical Ecology; J Cult Herit = Journal of Cultural Heritage; J Forest = Journal of Forestry; J Insect Conserv = Journal of Insect Conservation; J Insect Physiol = Journal of Insect Physiology; J Insect Sci = Journal of Insect Science; J Kansas Entomol Soc = Journal of the Kansas Entomological Society; J N Am Benthol Soc = Journal of the North American Benthological Society; J Nat Hist = Journal of Natural History; J Torrey Bot Soc = Journal of the Torrey Botanical Society; J Veg Sci = Journal of Vegetation Science; J Wash Acad Sci = Journal of the Washington Academy of Sciences; J Zool = Journal of Zoology; J Zool Syst Evol Res = Journal of Zoological Systematics and Evolutionary Research; Linzer Biol Beitr = Linzer Biologische Beiträge; Mem Am Acad Arts Sci = Memoirs of the American Academy of Arts and Sciences; Mem Entomol Soc Can = Memoirs of the Entomological Society of Canada; Murrelet = The Murrelet; Nat Area J = Natural Areas Journal; New Sci Sci J = New Scientist and Science Journal; North J Appl For = Northern Journal of Applied Forestry; Northwest Sci = Northwest Science; Occas Pap Calif Acad Sci = Occasional Papers of the California Academy of Sciences; P Acad Nat Sci Phila = Proceedings of the Academy of Natural Sciences of Philadelphia; P Entomol Soc Wash = Proceedings of the Entomological Society of Washington; P Minn Acad Sci = Proceedings of the Minnesota Academy of Science; P Mont Acad Sci = Proceedings of the Montana Academy of Sciences; P US Natl Mus = Proceedings of the US National Museum; Pearce-Sellards Ser = The Pearce-Sellards Series; Philos T R Soc B = Philosophical Transactions of the Royal Society B; Polish J Entomol = Polish Journal of Entomology; Rec Aust Mus = Records of the Australian Museum; Rev Écol (Terre Vie) = Revue d'Ecologie (Terre et Vie); Rev Soc Entomol Argent = Revista de la Sociedad Entomológica Argentina; Scand J Forest Res = Scandinavian Journal of Forest Research; Silva Fenn = Silva Fennica; Southeast Nat = Southeastern Naturalist; Sov J Ecol+ = The Soviet Journal of Ecology; Syst Entomol = Systematic Entomology; T Am Entomol Soc = Transactions of the American Entomological Society; T Kans Acad Sci = Transactions of the Kansas Academy of Science; Tasmanian Naturalist = The Tasmanian Naturalist; Univ Calif Publ Entomol = University of California Publications in Entomology; Us Dep Ag Biol Surv Bull = US Department of Agriculture Biological Survey Bulletin; Verh Internat Verein Limnol = Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie; Wilson Bull = The Wilson Bulletin; Z Angew Entomol = Zeitschrift für Angewandte Entomologie; Z Morph U Ökol Tier = Zeitschrift für Morphologie und Ökologie der Tiere; and Zool J Linn Soc-Lond = Zoological Journal of the Linnean Society.

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Chapter 23
Utilization of Non-native Wood by Saproxylic Insects

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Abstract Whether intentionally or accidentally introduced, non-native woody plants now feature prominently in many ecosystems throughout the world. The dying and deadwood produced by these plants represent novel resources for saproxylic insects, but their suitability to these organisms remains poorly understood. We herein review existing knowledge about the utilization of non-native wood species by saproxylic insect communities and also provide several previously unpublished case studies from the USA, Germany, Portugal/Spain, and New Zealand. The first case study suggests that the relative number of beetle species utilizing non-native vs. native wood varies greatly among wood species, with some non-native species (e.g., *Albizia julibrissin*) supporting a high beetle diversity. A decomposition experiment found that termites did not readily attack three non-native wood species and did not contribute significantly to their decomposition in contrast to what has been shown for a native pine species. The second case study found two species of non-native wood to support a lower richness of beetles compared to two native wood species in Germany, with *Pseudotsuga menziesii* supporting particularly few species which formed just a small subset of the community collected from native *Picea abies*. The third case study, from Iberia, found *Eucalyptus* to support a relatively small number of insect species with generalist host preferences. The fourth

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case study provides a list of insects reported from non-native pine and *Eucalyptus* in New Zealand. Based on our literature review and these new case studies, we conclude that non-native wood species can support diverse insect assemblages but that their suitability varies greatly depending on host species as well as the host specificity of the insect(s) under consideration. Although many generalist species appear capable of using non-native woody resources, more research is needed to determine whether non-native wood species have any value in promoting the conservation of the most threatened taxa.

23.1 Introduction

Non-native woody plants are becoming increasingly common in forested landscapes around the world (Richardson and Rejmánek 2011). Many of these species have been and continue to be introduced intentionally, with motivations ranging from an inherent appreciation for novelty among horticulturalists and landowners (Buchler et al. 1981; Reichard and White 2001; Spongberg 1990); a commercial interest in specific non-timber forest products (Robb and Travis 2013); a desire to stabilize hill slopes, soils, and river banks (Wilkinson 1999) or reduce flooding (Dray et al. 2006; Kon et al. 1993); and demand for fast-growing species for use in timber production (Richardson and Rejmánek 2011). While the global forest area is declining, the area of planted forests is increasing and now covers 278 M ha or ~7% of the total global forest area. Most planted forests are of native species; however, 18–19% are plantations of primarily even-aged stands of non-native tree monocultures (Payn et al. 2015). At the same time, many non-native tree and woody shrub species, including some plantation species, have escaped cultivation and have developed self-sustaining (i.e., "naturalized") populations across large areas (Essl et al. 2010; Rejmánek 2014; Ledgard 2001). There is currently great interest in knowing how the expansion of non-native plantations and the spread of non-native woody plants may affect biodiversity and ecosystem processes (Brockerhoff et al. 2008; Gibson et al. 2011; Felton et al. 2013; Peterken 2001; Krumm and Vítková 2016).

A number of factors are thought to influence the diversity of insects utilizing non-native plants. Southwood (1961) showed a positive correlation between the diversity of insect herbivores and the cumulative abundance of a tree species over time, with the rarest and most recently introduced tree species supporting the fewest insect species. Support for this hypothesis was reported by Brändle et al. (2008) in Germany who showed the species richness of herbivorous insects feeding on non-native plant species increased with time since the host plant was introduced. It has also been shown that the diversity of insects associated with a particular host plant is generally higher for widely distributed species than for species confined to smaller geographic areas (Branco et al. 2015a). Phylogenetic relatedness between non-native and native plant species has also been found to be important in determining the diversity of insects utilizing a non-native species. In Europe, for example, Branco et al. (2015a) showed that the number of native forest insects on non-native tree species, and also the damage they caused, was higher when native congeneric trees were present. Gossner et al. (2009) conclude from their study on phytophagous insect communities on introduced and native tree species in Europe that phylogenetic conservatism is an important mechanism in explaining communities on introduced trees, but whether it outweighs other mechanisms such as geographic contingency and mass effects, i.e., immigration from locally abundant plant species, depends on the interplay of phylogenetic scale, local abundance of native tree species, and the biology and evolutionary history of the phytophage taxon.

While the hypotheses summarized above were primarily developed for green food webs (i.e., based on living plant material), it remains poorly understood how the production of dead plant material by non-native woody plants may affect brown food webs. Herbivorous insects feeding on living plant tissues exhibit a high degree of host specificity, and this holds true for insects that feed on dying and recently deadwood (Stokland et al. 2012). However, as decomposition proceeds, woody material becomes increasingly dominated by fungi, and saproxylic (i.e., dependent on dying and deadwood) insect communities are known to become less host specific (Stokland et al. 2012). This pattern suggests non-native woody plants may have a stronger influence on green food webs than brown food webs. Indeed, a recent meta-analysis found invasive plants affect the trophic structure of green and brown food webs differently with the nature of the difference varying among ecosystems (McCary et al. 2016). However, none of the studies used in that analysis focused on wood-dependent species, underscoring a shortage of studies on the utilization of non-native wood species by saproxylic insects.

A number of studies have employed passive trapping techniques (e.g., flight intercept traps) to compare saproxylic insect diversity between non-native and native tree species (Lachat et al. 2007; Gossner and Ammer 2006; Gossner 2004). While these efforts typically indicate lower diversity associated with non-native tree species (Lachat et al. 2007; Puker et al. 2014; Buse et al. 2010), there are indications that such differences can be largely determined by microclimatic conditions which vary with stand composition, stratum, and year (Gossner and Ammer 2006). Furthermore, it is difficult to disentangle the effects of wood quality from those of wood quantity when the availability of woody debris is typically lower in younger forests dominated by non-native species. In western Africa, for example, Lachat et al. (2006) found the volume of wood in natural forests to be 7- and 25-fold greater than that in two non-native plantations. The variety of woody debris also varied greatly in that study, with a particular shortage of highly decomposed wood and standing dead trees in the non-native plantations. Another complicating factor within managed forests is the effects of silvicultural practices, e.g., pruning and thinning and the final harvesting that create large pulses of deadwood within the forest systems with little natural mortality in between. To isolate the effects of wood quality from those of wood quantity and variety, this paper focuses on studies in which insects were collected directly from woody substrates either by hand or by using emergence devices. We provide an overview of the published literature (Table 23.1) as well as several unpublished case studies from our own research. This chapter is divided into two parts to distinguish between naturalized non-native

Table 23.1 Chronology of studies comparing saproxylic insect communities between locally native and non-native tree species

Country	Non-native species	Native species	Decay class	Main findings	Citation
Benin	*Tectona grandis* and *Senna siamea*	*Afzelia africana*, *Anogeissus leiocarpus*, *Ceiba pentandra*, *Dialium guineense*, *Diospyros mespiliformis*, *Mimusops andongensis*, and *Zanthoxylum zanthoxyloides*	I–IV	Higher rarefied species richness in wood from natural forests compared to wood from non-native plantations. Community composition also varied considerably between native and non-native wood species.	Lachat et al. (2006)
Brazil	*Eucalyptus urophylla*, *Melia azedarach*, *Pinus elliottii*	*Lophantera lactescens* Ducke, *Inga marginata* Willd	I–II	*E. urophylla* and *M. azedarach* were, respectively, the most (100%) and least (17%) readily attacked by termites.	Trevisan et al. (2008)
France	*Picea sitchensis*, *Pinus strobus*, *Abies grandis*, *Pseudotsuga menziesii*, *Thuja plicata*	*Picea abies*, *Pinus sylvestris*, *Abies alba*	I	No significant difference in bark beetle species richness between native and non-native wood species but community composition varied considerably.	Bertheau et al. (2009)
New Zealand	*Pinus radiata*	*Schefflera digitata*, *Melicytus ramiflorus*, *Aristotelia serrata*	II	Greater beetle abundance and richness associated with *P. radiata* than with native wood species	Sky (2011)
Germany	*Pseudotsuga menziesii*	*Acer* sp., *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Populus* sp., *Prunus avium*, *Quercus* sp., and *Tilia* sp.	I–II	Few beetle species associated with *P. menziesii*	Müller et al. (2015), Gossner et al. (2016)

Italy	*Robinia pseudoacacia*	*Populus alba* and *Quercus robur*	II	No difference in beetle richness or composition among tree species	Della Rocca et al. (2016)
Poland	*Quercus rubra*	*Quercus robur* and *Quercus petraea*	Mature trees	No evidence of *Cerambyx cerdo* associated with *Q. rubra*	Oleksa and Klejdysz (2017)
Chile	*Pinus radiata*	*Nothofagus* spp.	I–IV	Beetle richness and abundance lower in *Pinus* vs. *Nothofagus*	Fierro et al. (2017)
USA	*Ligustrum sinense*, *Melia azedarach*, *Albizia julibrissin*	*Fraxinus pennsylvanica*, *Quercus phellos*, *Liquidambar styraciflua*	I–II	Beetle richness and composition differed among the six wood species. The non-native species *A. julibrissin* and *L. sinense* yielded the second highest and lowest beetle richness, respectively.	Current chapter, case study 1
Germany	*Pseudotsuga menziesii*, *Quercus rubra*	*Picea abies*, *Quercus robur*	I	Beetle abundance, richness, and diversity lower in *P. menziesii* than all other species	Current chapter, case study 2

Only studies that collected insects directly from the wood are included here woody plants (e.g., invasive species) (Part I) and those that have been planted intentionally (e.g., non-native plantations) (Part II).

23.2 Part I: Invasive Non-native Species

Richardson and Rejmánek (2011) compiled a global list of 622 species of invasive non-native trees and shrubs. They found Australia to have the highest number of species (183) followed by Southern Africa (170), North America (163), the Pacific Islands (147), and New Zealand (107). The top reasons they cited for these introduction were horticulture (62%) followed by forestry (13%), food production (10%), and agroforestry (7%). While many naturalized plant species occur at low densities and go largely unnoticed, others form thick monocultures, with the potential to completely displace native forest ecosystems (Fig. 23.1b). Although generally unwanted and perceived to have mostly negative effects (Peltzer et al. 2015), invasive non-native species can sometimes provide important services, e.g., by allowing forests to recolonize abandoned agricultural areas (Lugo 2004) and contributing to forest ecosystem services such as erosion control, flood mitigation, and pollination (Branco et al. 2015b). The degree to which the deadwood produced by invasive non-native woody plant species is utilized by saproxylic insects remains mostly unknown, but several recent studies suggest this may depend on the species of tree as well as the insect(s) under consideration. Della Rocca et al. (2016) reported no difference in the species richness or composition of beetle communities associated with wood from an invasive non-native tree species (*Robinia pseudoacacia* L.) and that from two native tree species (*Populus alba* L. and *Quercus robur* L.) in Italy. By contrast, Oleksa and Klejdysz (2017) found that *Cerambyx cerdo* L., a threatened cerambycid beetle strictly associated with mature oaks (especially *Q. robur*) in Europe, did not utilize the non-native *Q. rubra* in Poland. Although the absence of *C. cerdo* from *Q. rubra* may have been due in part to the smaller size of *Q. rubra* compared to the native oaks examined in that study, these findings suggest non-native oaks may provide little benefit to this threatened beetle in Europe. Because host specificity is one characteristic common to many threatened insect taxa, species of greatest conservation concern may be less accepting of non-native wood species than less vulnerable species. Taken together, these findings suggest non-native woody plants can provide suitable resources for many saproxylic insects although this may be less true for species specific to one or several host species. In the following case study, we present the results from an effort undertaken in the southeastern USA to compare saproxylic insect activity among several non-native and native woody plant species.

Fig. 23.1 Examples of forests dominated by non-native woody plants: (**a**) Douglas-fir plantation in Germany (M. Gossner); (**b**) invasive Chinese privet in Georgia, USA (M. Ulyshen); (**c**) *Eucalyptus* plantation in southern Brazil (G. Overbeck); (**d**) *Pinus radiata* plantation in New Zealand (M. Ulyshen); (**e**) invasive camphor tree in Mississippi, USA (M. Ulyshen)

23.2.1 *Case Study I: Utilization of Non-native Wood Species by Beetles and Termites in the Southeastern USA—Implications for Conservation and Insect-Mediated Decomposition*

The trade of tree species between North America, Europe, and Asia has a long history (Spongberg 1990), and the lasting effects of these exchanges are evident today throughout the USA. Of the 163 species of invasive non-native trees and shrubs reported from North America by Richardson and Rejmánek (2011), at least 20 are rapidly invading the forests of the southeastern USA (Miller 2003; Miller et al. 2010). We selected three non-native woody plant species for use in this study: *Ligustrum sinense* Lour. (Chinese privet), *Albizia julibrissin* Durazz. (mimosa), and *Melia azedarach* L. (chinaberry). We also selected three native species: *Fraxinus pennsylvanica* Marsh. (green ash), *Quercus phellos* L. (willow oak), and *Liquidambar styraciflua* L. (sweetgum). These species were selected primarily on the basis of their abundance and availability in the area although green ash was chosen because it belongs to the same family (Oleaceae) as Chinese privet. All three of the non-native species originated in Asia and were introduced into the USA for ornamental purposes in the eighteenth or nineteenth centuries. Chinese privet is an evergreen shrub that forms dense thickets that prevent native plant regeneration (Fig. 23.1b). Mimosa (a legume) and chinaberry both grow commonly in disturbed or open conditions throughout the southeastern USA but, unlike Chinese privet, rarely form dense monocultures. This two-part study sought to (1) compare saproxylic beetle communities among the three non-native and three native wood species mentioned above and (2) quantify termite feeding activity in the three non-native wood species and the contributions of these insects to decomposition.

23.2.1.1 Methods

Beetle Community Analysis

Forty sections measuring 0.5 m in length and 14.0 ± 0.3 (range 7.6–27.2) cm in diameter were cut from the three non-native and three native woody plant species listed above (i.e., 240 sections in total) from trees felled for this purpose in forests near Athens, Georgia, USA, in May 2011. Ten sections from each tree species were placed at each of four hardwood-dominated floodplain forests within the upper Oconee river watershed in northeastern Georgia [i.e., Scull Shoals Experimental Forest (33°46′17.04″N 83°16′59.46″W), Watson Springs (33°41′59.26″N 83°17′43.18″W), Sandy Creek Nature Center (33°58′53.17″N 83°22′56.40″W), and the State Botanical Gardens of Georgia (33°54′2.93″N 83°23′16.46″W)]. Half of these sections were collected after 3 months in August 2011, whereas the rest were collected after 1 year in early June 2012. The collected sections were placed in rearing bags (Ulyshen and Hanula 2009) to collect all emerging insects over a period of 6 months. For each collection period (i.e., 3 months and 1 year), beetles from the five logs belonging to each species were pooled for each of the four sites. All captured beetles were either identified to species or assigned to morphospecies except for several excluded groups for which such designations were not possible given limits of time and expertise. Excluded groups were the family Ciidae, some Ptiliidae, the staphylinid subfamilies Aleocharinae and Pselaphinae, and male ambrosia beetles belonging to the genus *Xyleborus*. Altogether these excluded groups accounted for about 8% of all beetles captured.

We used sample-based rarefaction in EstimateS (Colwell 2013) to compare the number of species collected among the different wood species. Because there were large differences in abundance among wood species, we replotted the curves against an x-axis of individual abundance, as recommended by Gotelli and Colwell (2011). To compare the beetle communities collected from the six wood species, we performed nonmetric multidimensional scaling, PERMANOVA, two-way cluster analysis, and indicator species analysis using PC-ORD (McCune and Mefford 2011). For each sampling period and beetle species captured, we standardized abundance by wood volume. This was done by dividing the total wood volume (calculated from the length and diameter of each wood section) sampled for each tree species at each location by the largest volume of wood sampled for each sampling period. Beetle abundances were then divided by these values. We pooled standardized abundance across the two sampling periods to construct our main data matrix. Species present in less than three samples (i.e., the 24 combinations of tree species and site) were excluded, resulting in a final matrix consisting of 59 species. Abundance values were relativized by species maxima, and the Bray-Curtis distance measure was used in all analysis. For the two-way cluster analysis, we used the group average linkage method.

Termite Activity and Contributions to Wood Decomposition

Twenty logs 0.5 m in length were cut from forests growing near Athens (Georgia, USA) from each of the three non-native tree species mentioned above (i.e., Chinese privet, chinaberry, and mimosa) in June 2012. The trees were felled for this purpose in forests growing near Athens, Georgia. The logs were transported back to the laboratory in Mississippi. Image pro plus (Media Cybernetics, Inc., Rockville, MD) was used to calculate the original area of one end of each log (not including bark) using photographs taken of the cut ends. Half of the logs (ten of each species) were individually sealed within stainless steel mesh (0.38 mm openings) bags (“protected”), whereas the other logs were left “unprotected.” The same mesh bag design was used to successfully exclude termites and most beetle species in a previous study (Ulyshen 2014). At one site on the Noxubee Wildlife Refuge (northern Mississippi), a 5 m × 6 m grid was established (five line transects (rows), each containing six plots). Each of these 30 plots received a caged and an uncaged log from the same species (separated by about 0.5 m). Logs were collected in January 2015 after 31 months in the field. Following the methods described in Ulyshen (2014), two 3–4 cm-thick disks were cut from the end of the log that had been photographed at the beginning of the study. The thickness of the interior disk was measured at four equidistant points, and the mean thickness and the original surface area of the log, as measured from the initial photographs, were used to calculate the initial wood volume of the disk. Cut disks were photographed before oven drying them at 102 °C for 24 h. Following Ulyshen et al. (2016), a 20 × 20 grid was superimposed over the images and the percentage of cells with visible damage from termites was determined. After measuring the final dry weights of the disks, those with visible termite activity were burned to extract and subsequently quantify the mass of termite-imported soil. The soil weight was subtracted from the final dry disk weights following Ulyshen and Wagner (2013). Specific gravity was measured by dividing final dry wood weight (without soil) by initial wood volume (as defined above). Effect sizes (Hedges' d) and their 95% confidence intervals were calculated from these specific gravity measurements (unprotected-protected). A negative effect size suggests insects sped up wood loss (resulting in lower specific gravity) relative to the protected treatment, and the effect is considered significant when confidence intervals do not include zero. Finally, we calculated the decay rate constants for the three tree species based on their initial and final specific gravities using the single exponential model. Initial specific gravity was based on disks collected from the trees when they were initially felled (0.44, 0.57, and 0.50 for mimosa, privet, and chinaberry, respectively). Only unprotected logs were included in these calculations.

23.2.1.2 Results

Beetle Community Analysis

Overall, 2810 beetles representing 127 species or morphospecies were collected in this study. The highest total numbers of species/individuals came from sweetgum (69/1001), followed by mimosa (55/712), willow oak (55/665), chinaberry (43/242), green ash (32/98), and Chinese privet (27/92) (Fig. 23.2). Nonmetric

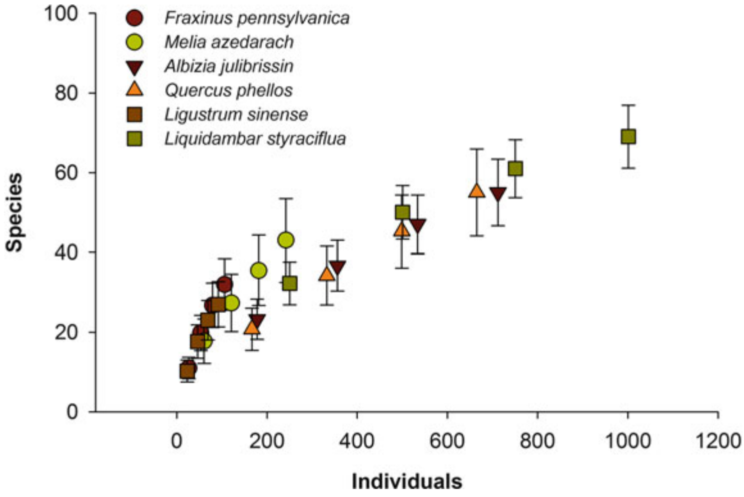


Fig. 23.2 Sample-based rarefaction from case study 1

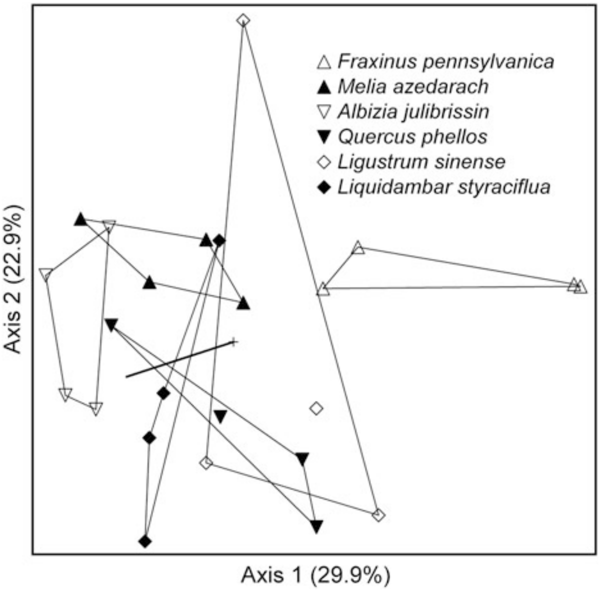
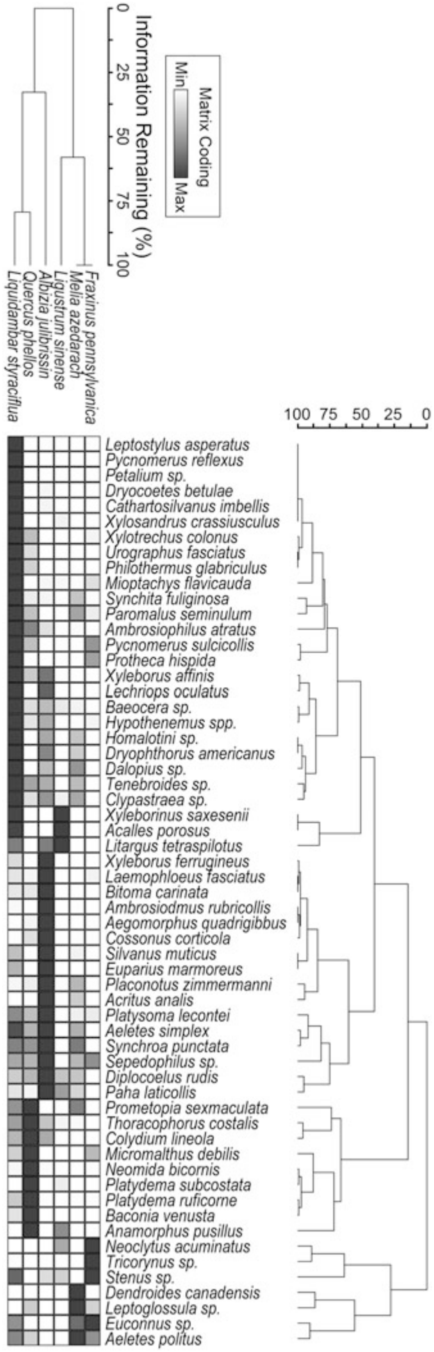


Fig. 23.3 NMS ordination of beetle assemblages among the six tree species for case study 1. Each symbol represents a separate set of logs from which insects were collected and the different symbols represent different species.

multidimensional scaling yielded a three-dimensional solution with a stress of 16.6. The ordination is depicted in two dimensions in Fig. 23.3, using the axes with the highest R^2 values (0.30 and 0.23 for axes 1 and 2, respectively). The ordination shows considerable separation in community composition among many of the tree species, and the superimposed joint plot shows the strength and direction of correlation with total beetle richness. All but 4 of the 15 pairwise comparisons between tree species were statistically significant based on PERMANOVA. These were green ash vs. Chinese privet ($p = 0.06$), chinaberry vs. willow oak ($p = 0.05$), mimosa vs. willow oak ($p = 0.05$), and willow oak vs. Chinese privet ($p = 0.06$). Two-way cluster analysis yielded two clusters for wood species, one consisting of green ash, chinaberry, and Chinese privet and the other consisting of the other three species (Fig. 23.4). Finally, based on indicator species analysis, one beetle species was significantly associated with green ash [*Tricorynus* sp. (Indicator Value (IV) = 75; $p = 0.01$)], one with chinaberry [*Dendroides canadensis* LeConte (Pyrochroidae) (IV = 75; $p = 0.01$)], five with mimosa [*Placonotus zimmermanni* (LeConte) (Laemophloeidae) (IV = 57.2; $p < 0.01$); *Platysoma leconti* Marseul (Histeridae) (IV = 45.8; $p = 0.04$); *Silvanus muticus* Sharp (Silvanidae) (IV = 52.9; $p = 0.03$); *Cossonus corticola* Say (Curculionidae) (IV = 80.3; $p < 0.01$); *Aegomorphus quadrigibbus* (Say) (Cerambycidae) (IV = 94.9; $p < 0.001$)], two with willow oak [*Platydema ruficorne* (Stürm) (Tenebrionidae) (IV = 75.5; $p < 0.01$); *Platydema subcostata* Laporte and Brulle (Tenebrionidae) (IV = 68.6; $p = 0.01$)], and five with sweetgum [*Leptostylus asperatus* (Haldeman) (Cerambycidae) (IV = 96.7; $p < 0.001$); *Xylosandrus crassiusculus* (Motschulsky) (Curculionidae) (IV = 70.5; $p = 0.01$); *Urographus fasciatus* (DeGeer) (Cerambycidae) (IV = 63.3; $p = 0.04$);

Fig. 23.4 Two-way cluster analysis of the six tree species and beetle species captured from at least three of the samples in case study 1



Pycnomerus reflexus (Say) (Zopheridae) (IV = 75; $p = 0.01$); *Petalium* sp. (Ptinidae) (IV = 100; $p < 0.001$)].

Termite Activity and Contributions to Wood Decomposition

Based on the percentage of grid cells with visible damage, Chinese privet experienced the highest level of termite activity (6.13% ± 1.27), followed by mimosa (3.48% ± 2.22) and chinaberry (2.17% ± 1.63). Effect size (unprotected-protected) was not statistically significant for Chinese privet [0.20 (−0.68 to 1.08)], mimosa [−0.23 (−1.11 to 0.65)], or chinaberry [0.03 (−0.84 to 0.91)], indicating that termites and other insects did not significantly accelerate decomposition of these species. The decay rate constant (k) for unprotected logs was 0.27, 0.10, and 0.12 for Chinese privet, mimosa, and chinaberry, respectively, corresponding to half-lives of 2.6, 6.9, and 5.8 years.

23.2.1.3 Discussion

Beetle abundance, richness, and composition varied greatly among the six wood species, with no consistent differences between non-native and native wood species. For example, the non-native mimosa yielded the second highest number of individuals and species, whereas Chinese privet, another non-native wood species, yielded the fewest. These findings are consistent with previous research from Europe where some non-native tree species (e.g., *R. pseudoacacia* in Italy) support diverse beetle assemblages (Della Rocca et al. 2016), whereas others (e.g., *Pseudotsuga menziesii* (Mirbel) Franco in Germany) are utilized by few species (Gossner et al. 2016) (Table 23.1). There is clearly a need for further research to better understand the extent to which various non-native wood species are utilized by saproxylic insect assemblages and how this might be influenced by the composition of the native plant community. As all 14 significant indicator beetle species are generalists known from a wide range of host species in our area, these findings are not remarkable. The fact that nearly half of them were more strongly associated with non-native wood species than with native wood species, however, reinforces the message that non-native trees can provide highly suitable resources for some species.

In our decomposition experiment, all three non-native wood species experienced low levels of termite activity after 31 months. This contrasts greatly with the much higher levels of termite activity observed after just 24 months in a previous study involving native loblolly pine (*Pinus taeda*). In that study, which used the same methods and took place in the same general area, an average of 42% and 25% termite damage was reported from *P. taeda* logs placed in unflooded and seasonally flooded forests, respectively (Ulyshen et al. 2016). The relatively low levels of termite activity observed in the three non-native wood species likely explain why we detected no significant effect of termites on wood decomposition in the current study, whereas Ulyshen (2014) found termites (among other insects) to significantly accelerate loblolly pine decomposition [Hedges *d* and 95% CIs: −0.74 (−1.39 to −0.10)] after 31 months in the same study area. Termites are known to strongly prefer certain types of wood over others, feeding less readily on the densest woods or on those containing high concentrations of extractives (Bultman and Southwell 1976). Results from other studies comparing how readily termites attack native and non-native wood species are mixed, suggesting that attack rate depends more on the properties of wood species than wood origin. In a comparison of three non-native and two native wood species in Brazil, for example, Trevisan et al. (2008) found non-native *Eucalyptus* and non-native chinaberry to be the most and least readily attacked, respectively (100 vs. 17%). This latter finding is consistent with our finding that chinaberry is highly resistant to termites.

While our results suggest insects may contribute less to the decomposition of non-native wood species than native wood species, this needs to be tested on a larger number of tree species before any broad conclusions can be reached. It also remains uncertain whether rates of fungal-driven decomposition vary between non-native and native wood species, but our results suggest the responses of fungi may differ from those of termites. Despite experiencing less termite activity than loblolly pine, for example, Chinese privet decomposed 25% faster (i.e., the decay rate for loblolly logs unprotected from insects for 31 months was 0.21). A recent meta-analysis found no difference in how quickly leaves and roots of non-native vs. native plant species decompose (Jo et al. 2016), suggesting that a species' place of origin is less important than interspecific differences in chemistry and perhaps other properties in determining decomposition rates.

23.3 Part II: Non-native Plantations

Planted forests, including even-aged single species stands, make up a growing proportion of the world forest cover, especially in the southern hemisphere, and commonly consist of fast-growing non-native genera like *Pinus*, *Eucalyptus*, and *Acacia* (Wingfield et al. 2015; Payn et al. 2015). Although forest cover is increasing throughout Europe, plantations of non-native trees are driving this pattern in many places (e.g., *Picea sitchensis* (Bong.) Carr. in Ireland and *Eucalyptus* in Spain) (Anonymous 2017). The non-native range of *Eucalyptus* is now particularly widespread and growing, with Asia currently having the largest coverage, followed by South America, Africa, Europe, and North America (Wingfield et al. 2015; Payn et al. 2015). The extent to which individual species have naturalized and subsequently spread beyond stand boundaries varies greatly and is influenced by a number of traits, e.g., seed size (Buckley et al. 2005). Some non-native tree species show relatively little potential for invasion (including many species of *Eucalyptus*; see Richardson (1998)), whereas others have escaped cultivation and pose a serious threat to native ecosystems (Richardson et al. 2011; Ledgard 2001). An analysis by Essl et al. (2010) suggests that conifer species used in commercial forestry have a significantly higher probability of becoming invasive than those planted for other purposes. Non-native monocultures are often planted in areas with a history of forest cover, but this is not always the case. Major afforestation efforts in China, for instance, are motivated in part by a desire to reduce flooding and erosion and sometimes include areas where forests never grew (Kon et al. 1993). Although generally thought to be bad for biodiversity, non-native plantations can provide important habitats for a wide range of native organisms [including threatened species (Pawson et al. 2010)] and can be particularly beneficial when established on degraded lands rather than displacing native ecosystems (Bremer and Farley 2010; Pawson et al. 2008; Lugo 2004). In their review of this topic, Bremer and Farley (2010) concluded that although non-native plantation forests support fewer specialist species than natural ecosystems, they should not be completely dismissed as "green deserts" by conservation biologists.

23.3.1 Case Study 2: Saproxylic Beetles Utilizing Crown Deadwood of Living Native and Introduced Trees in Germany

Central Europe is characterized by a comparatively low diversity of native tree species due to postglacial dispersal limitations (Normand et al. 2011). To increase available tree species in forestry, fast-growing native tree species, in particular Norway spruce *Picea abies* ((L.) H. Karst.), have been extensively planted outside their natural distributional ranges (Schelhaas et al. 2003). Such stands experienced large-scale losses following wind throws and bark beetle outbreaks, which are expected to further increase due to climate change (Pawson et al. 2013). This fostered the discussion on expanding the use of fast-growing non-native tree species, which may better adapt to future climatic conditions, in production forestry to reduce the risk of future stand losses (Bolte et al. 2009).

Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) introduced from western North America and red oak (*Quercus rubra* L.) introduced from the eastern North America are among the economically most important tree species in Central Europe (Nyssen et al. 2016). The ecological consequences of their introduction are, however, still debated (Schmid et al. 2014; Vor et al. 2016; Gossner 2004, 2016). Studies on the consequences for saproxylic insects are still rare and mostly consist of passively sampling adult individuals (Gossner and Ammer 2006; Gossner 2004) although some have involved experimental rearing from wood/log sections (Gossner et al. 2016). Here we test whether crown deadwood from introduced Douglas-fir and red oak can provide habitat for saproxylic beetles that is comparable to native Norway spruce (outside the natural range) and pedunculate oak (*Quercus robur* L.). Crown deadwood is known to contribute substantially to the volume of deadwood in forests, in particular for oak trees (Ammer et al. 2008), and it provides habitat for a specific saproxylic insect community (Bouget et al. 2011; Ulyshen and Hanula 2009).

23.3.1.1 Methods

The study was conducted in two forest stands in southern Bavaria, Germany. All study sites were located in a landscape called “Schotterriedel” which features soils of high nutrient content that promote rapid tree growth. European beech (*Fagus sylvatica* L.) would naturally dominate these landscapes (“Collin and High Montane Beech Forests”; Walentowski et al. 2006), but today Norway spruce (*P. abies*) is the tree species with the highest proportion in the surrounding forests. Annual precipitation reaches 750–800 mm and mean annual temperature is 7–8 °C.

Conifers were studied in a mature mixed Douglas-fir–spruce forest (mean age 94, 84–104) of 6.8 ha near Edelstetten (10°25′15″ E, 48°17′10″ N; 550 m a.s.l.). The forest was dominated by spruce (69%), followed by Douglas-fir (29%). Additionally, single pedunculate oak (*Quercus robur* L.), European beech (*F. sylvatica*), and Scots pine (*Pinus sylvestris* L.) trees occurred. Oaks were studied in a mixed pedunculate oak—European beech stand (mean age 119, 85–148) of 4.8 ha near Ettenbeuren (10°23′52″ E, 48°22′25″ N; 520–535 m a.s.l.). European beech (65%) dominated, followed by pedunculate oak (30%) and hornbeam (*Carpinus betulus* L.) (4%). Groups of red oak (*Q. rubra*) were admixed, and additional single trees of birch (*Betula pendula*), larch (*Larix decidua*), and spruce (*P. abies*) occurred.

Deadwood branches were harvested with a handsaw in crowns of three mature trees of each Douglas-fir (*P. menziesii*), Norway spruce (*P. abies*), pedunculate oak (*Quercus robur* L.), and red oak (*Q. rubra*) in the first week of March 2001 (Fig. 23.5a). The heights of the harvested branches were between 15 and 28 m in oaks and 20 and 35 m in conifers. Branches were carefully lowered to the ground using ropes (Fig. 23.5b) and stored in plastic bags, separated by tree species, individual tree, and diameter class. As the diameters of branches varied between species, being lower in conifers than oaks, we distinguished between two diameter classes in conifers (≤3 cm and >3 cm, with 1–2 replicates of each per tree and a total of 10 samples per tree species) and four in oaks (<5 cm, 5–6 cm, 6–7 cm and >7 cm, with one replicate of each per tree and a total of 12 samples per tree species). The deadwood amount per bag was standardized to 6280 cm^2 surface area (total: 276,320 cm^2). Only branches of comparable decay stage were selected (wood still hard and with complete bark coverage). Samples were transported to Freising and transferred into a transparent plastic (1 mm thick) tube that was covered by a gauze at the top and attached to a funnel with a sampling jar, containing 1.5% copper-sulfate solution in summer and ethylene glycol in winter to avoid freezing, at the bottom (Fig. 23.5c). The gauze facilitated air circulation to prevent mold growth. Tubes were hung on a scaffold in front of the Technical University of Munich in Freising. The incubation under field conditions occurred from March 2001 to February 2002. Afterward the samples were transferred into plastic barrels (Fig. 23.5d) and further incubated at room temperature (20 °C). Sampling jars were emptied in 2-week intervals until October 2001 and then monthly thereafter until October 2002.

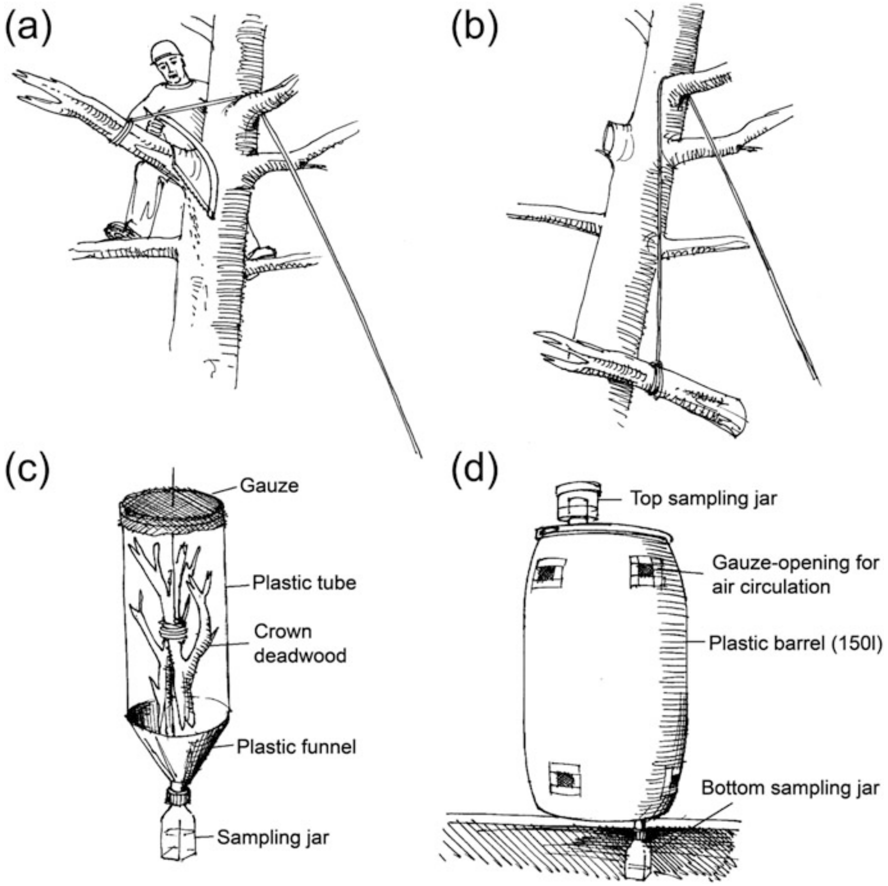


Fig. 23.5 Sampling an incubation of crown deadwood from case study 2. (**a**) Dead branches of early decay stages were harvested in tree crowns of mature trees with a hand saw. (**b**) Branches were carefully lowered and stored in plastic bags, separated by tree species, tree, and diameter class. (**c**) For the first year, deadwood branches were incubated in plastic tubes under field conditions. (**d**) The branches were transferred to plastic barrels and incubated at room temperature after 1 year in spring

23.3.1.2 Data Analyses

All data were analyzed in R version 3.3.1 (R Core Team 2016). To obtain estimates of saproxylic beetle diversity for the four different tree species, we used a framework published recently (Chao et al. 2014). This “diversity accumulation curve” framework extends methods for rarefaction and extrapolation of species richness (species accumulation curve; Colwell et al. 2012). We estimated species diversity curves for Hill numbers based on sample size and sample coverage. Coverage is defined as the proportion of the total number of individuals in an assemblage that belong to species represented in the sample (Chao et al. 2014). The reference sample size for sample size-based estimates was the number of samples taken from a particular tree species. At $q = 0$ (0D), rare and abundant species are weighted equally (species richness); at $q = 1$ (1D), species are weighted in proportion to their frequency in the sampled community; and at $q = 2$ (2D), abundant species receive more weight relative to their frequency. Diversity of beetles emerging from the four different tree species was compared for Chao's BSS (Chao et al. 2014), that is, the higher value of the minimum doubled reference sample size and the maximum reference sample size among tree species, and Chao's BSC (Chao et al. 2014), that is, the higher value of the minimum coverage for doubled reference sample size and the maximum reference coverage among tree species. Significant differences in diversity between tree species were judged by nonoverlapping confidence intervals (Schenker and Gentleman 2001).

To visualize differences in the compositions of saproxylic beetle communities among tree species, we used nonmetric multidimensional scaling (NMDS) plots produced with the metaMDS function in R package vegan (Oksanen et al. 2016) with a maximum of 20 random starts and two dimensions. PERMANOVAs on Bray-Curtis matrices with 9999 permutations (function adonis in vegan) were run to test the effect of tree species on community composition.

To identify indicator species, the approach by Dufrêne and Legendre (1997) was applied. We used the enhancement of the method described by De Caceres and Legendre (2009) and De Caceres et al. (2010) which is provided by the R package "indicspecies." We used the multilevel pattern analysis (function multipatt) that allows tests of association between species patterns and combinations of site groupings. We tested the null hypothesis that the preference of a particular beetle species for one of the tree species or a combination of tree species is due to chance only, using 9999 permutations to calculate p values for each combination. Indicator values (IndVal.g), ranging from 0 (no association) to 1 (complete association) are identical to the values returned by the original function of Dufrêne and Legendre (1997).

23.3.1.3 Results

In total, 557 individuals of 56 saproxylic beetles emerged from the harvested branches. Most specimens and species emerged from native pedunculate oak (197/24), followed by native spruce (184/22), introduced red oak (119/18), and introduced Douglas-fir (57/10). Of these species, 32% were singletons and 30% doubletons. *Ennearthron cornutum* (Gyllenhal, 1827) (Ciidae: 176, all tree species), *Pityophthorus pityographus* (Ratzeburg, 1837) (Curculionidae, Scolytinae: 130, only Norway spruce), and *Dasytes caeruleus* (De Geer, 1774) (Dasytidae: 98, all tree species) reached highest abundance.

The estimated mean sample coverage at Chao's BSS of 20 samples (double minimum reference sample size) was highest in red oak (0.868), followed by Douglas-fir (0.809), Norway spruce (0.755), and pedunculate oak (0.732). Saproxylic beetle diversity was lower on Douglas-fir than on all other tree species for $q = 1$ and $q = 2$ (nonoverlapping confidence intervals in Fig. 23.6). When

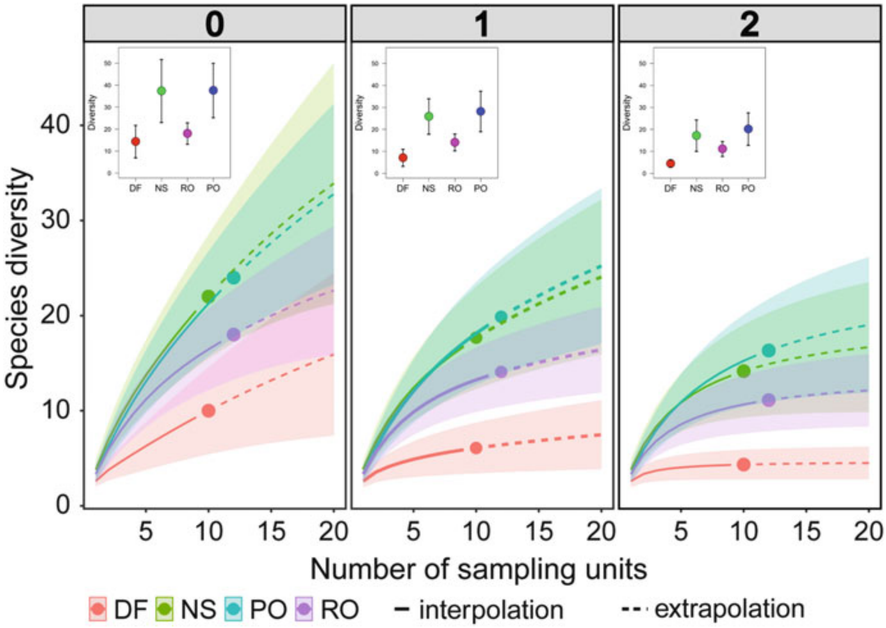


Fig. 23.6 Rarefaction and extrapolation of saproxylic beetle γ-diversity emerging from dead canopy branches harvested from tree crowns of mature Douglas-fir (DF, $n = 10$ branches from three trees), Norway spruce (NS, $n = 10/3$), pedunculate oak (PO, $N = 12/3$), and red oak (RO, $n = 12/3$), case study 2. The deadwood amount sampled per branch was standardized to 6280 cm^2 surface area. Panels show diversity quantified for Hill numbers 0, 1, and 2 (rarefaction = solid line, extrapolation = dashed line) based on frequencies of species occurrences. All curves include 95% confidence intervals obtained by bootstrapping based on 200 replications. The insets show estimated diversity at equal Chao's Base Sample Coverage of 0.788

correcting for differences in sample coverage by using Chao's BSC (0.788), the diversity on both introduced tree species was significantly lower at $q = 0$. Douglas-fir showed lower diversity also for $q = 1$ and $q = 2$, being even lower than that of introduced red oak at $q = 2$ (see insets of Fig. 23.6).

Conifers and oaks showed distinct communities (Fig. 23.7). While the communities of native and introduced oaks differed, the saproxylic community present on Douglas-fir was only a subset of the community observed on Norway spruce. A PERMANOVA showed significant differences between tree species ($F_{3,18} = 2.626$, $p < 0.001$, $R^2 = 0.304$), but this could have been influenced by the considerable difference in multivariate spread among tree species.

Six of the 56 sampled beetle species were significant indicators of particular tree species. Four species were indicators of a single tree species (two for pedunculate oak, two for red oak), one species was indicative of both Douglas-fir and Norway spruce, and one species was a significant indicator taxa for Douglas-fir, Norway spruce, and red oak. Except for *Conopalpus testaceus* (Olivier, 1790) (Melandryidae) on pedunculate oak, all indicator species seem to be host generalists

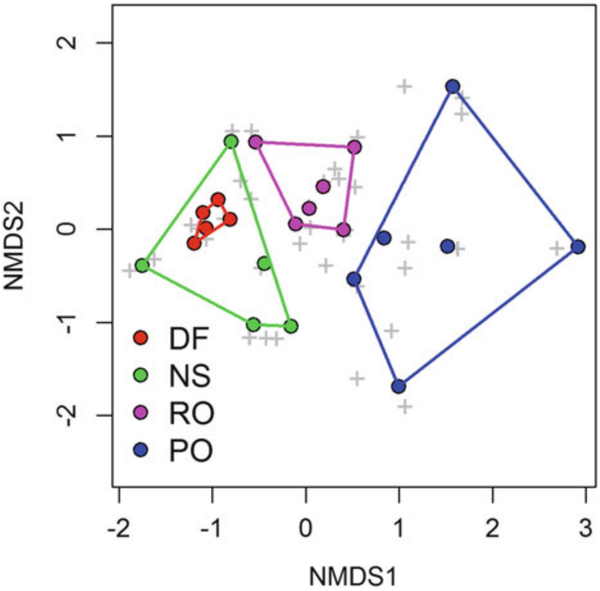


Fig. 23.7 Nonmetric multidimensional scaling (NMDS) plot (stress value = 0.118) showing the composition of saproxylic beetles emerging from deadwood branches harvested in the tree canopy of Douglas-fir (DF), Norway spruce (NS), pedunculate oak (PO), and red oak (RO), case study 2. In each tree species two branches per diameter class and tree were pooled due to low sample size. Gray crosses show the beetle species position in the two-dimensional ordination space

(Table 23.2). Overall, on non-native trees, only host generalists were observed, except two individuals of *Anobium costatum* Aragona, 1830 (Ptinidae), for which *Fagus* is described as preferential host, on red oak, and one individual of the ash specialist *Hylesinus fraxini* (Panzer, 1799) (Curculionidae, Scolytinae) on Douglas-fir (also one individual on spruce).

23.3.1.4 Discussion

This case study clearly shows that crown deadwood of introduced Douglas-fir and red oak is less suitable for native saproxylic beetle species than native spruce and pedunculate oak. The lower diversity on these two introduced tree species is partly supported by flight interception trap studies in the canopy (Gossner and Ammer 2006; Gossner 2004). Significant differences based on these passive samplings were, however, only observed in particular years or in particular stand types (pure stands in red oak/pedunculate oak and beech-dominated stands in Douglas-fir/Norway spruce). Results of the present study come from mixed native/introduced conifer and oak stands. Whether stand- and year-specific effects observed by passive sampling reflect a sampling bias needs to be clarified in future studies. For Douglas-fir, a recent large-scale study in which saproxylic beetles were reared from experimentally exposed deadwood shows that the significantly lower diversity of beetles developing in the introduced tree is independent of region and forest management (Gossner et al. 2016). This supports the idea that Douglas-fir provides a less suitable habitat for native saproxylic species.

Table 23.2 Beetle species that were found to be indicator species for one tree species or a combination of them in case study 2

Tree species	Beetle family	Beetle species	*N*	IndVal	P.value	Feeding guild	Habitat	Body size	Tree species
PO	Scraptiidae	*Anaspis thoracica* (L.)	4(4)	0.707	0.0409	xz	Deadwood with bark	2.75	*Betula*, *Fagus*, *Carpinus*, *Quercus*, *Ulmus*, *Tilia*, *Corylus*
PO	Melandryidae	*Conopalpus testaceus* (Olivier)	5(5)	0.707	0.0375	xm	Deadwood with bark	6.00	*Fagus*, *Quercus*
RO	Cerambycidae	*Mesosa nebulosi* (Fabricius)	8(8)	0.816	0.0044	x	Deadwood with bark	12.0	*Carpinus*, *Acer*, *Quercus*, *Fagus*, *Tilia*, *Ulmus*, *Alnus*, *Castanea*, *Salix*, *Populus*
RO	Staphylinidae	*Anomognathus cuspidatus* (Erichson)	4(4)	0.707	0.0383	z	Deadwood with bark	1.65	*Quercus*, *Fagus*, *Acer*, *Aesculus*, *Populus*, *Salix*, *Betula*, rarely *Picea*, *Pinus*
DF +NS	Melyridae	*Dasytes plumbeus* (Muller)	16 (16)	0.949	<0.001	z	Deadwood with bark	4.05	Broadleaved trees
DF +NS +RO	Melyridae	*Dasytes caeruleus* (De Geer)	98 (91)	0.905	0.0282	z	Deadwood with bark	5.50	*Fagus*

The number of individuals (N) sampled in total and on the indicator tree species (in brackets) is shown. Additional information on feeding guild (x = xylophagous, z = zoophagous, m = myetophagous), mean body size, and tree host genera based on Koch (1989–1992) and Palm (1959) is given

While communities on red oak were located between pedunculate oak and conifers in an ordination diagram, communities on Douglas-fir seems to be similar among samples and located within the ordination space spanned by Norway spruce samples (Fig. 23.7). Hence, Douglas-fir seems to provide habitat for only a subset of mainly generalist species that are not restricted to native conifers. In contrast, the saproxylic community associated with the introduced red oak seems to be a mixture of species that colonize native oak and native conifers. This suggests that with the exception of a few individuals of more specialized species, polyphagous species just expanded their host range, but specialists showed no major host shifts, which would imply a major change in ecology.

Our results provide evidence that non-native tree species alter saproxylic beetle communities with unknown consequences for wood decomposition. A recent study from Germany, however, indicates that wood decomposition in non-native Douglas-fir is lower compared to native tree species (Kahl et al. 2017). Future studies are needed in evaluating the degree to which current plantations of non-native tree species affect rare and threatened saproxylic species as well as potential pest species and their antagonists. Moreover, comprehensive studies on the consequences of observed saproxylic community alterations for ecosystem processes such as wood decomposition and pest control are of great interest. This will be a great step forward toward an evidence-based process for evaluating the establishment of non-native tree species in Europe in light of nature conservation and forest management.

23.3.2 *Case Study 3: Saproxylic Insects Utilizing Eucalyptus in Western Iberian Peninsula*

23.3.2.1 Background

Plantations with *Eucalyptus* trees, mostly *Eucalyptus globulus* Labill. introduced from Australia, currently cover large areas in the western Iberian Peninsula, including Portugal and northwestern Spain. *Eucalyptus* plantations in Iberia first appeared in Portugal in the 1850s and began to be widely planted and economically important since the 1940s. From 1995 to 2010, the total land area covered in *Eucalyptus* plantations in Portugal increased by 13% (ICNF 2013). At present there are over 810,000 ha of *Eucalyptus* plantation forests in Portugal, accounting for about 33% of the forest surface (ICNF 2013). Similarly, there are 760,000 ha of *Eucalyptus* in Spain, the vast majority in Galicia, causing controversy and social concern as *Eucalyptus* plantations are perceived to have negative ecological effects particularly on biodiversity (Veiras and Soto 2011) and are also thought to increase wildfire risk (Anonymous 2017). Nevertheless, the high productivity of the *Eucalyptus* forests and the high industrial return, mainly for pulp production, renders this forest use highly compensatory when compared to native pines or hardwoods.

For more than 150 years, *Eucalyptus* forests in the Iberia region were characterized by their extremely high health status. This situation changed with the increased arrival of *Eucalyptus* pests from their region of origin, including two Australian longhorn beetles of the genus *Phoracantha* (*semipunctata* and *recurva*) (Hurley et al. 2016). On the other hand, native insect pests are not usually a menace for *Eucalyptus* plantations in the region, which is in great part explained by the absence of congeneric tree species in the European flora that could harbor potential common pests (Branco et al. 2015a). Nevertheless, in a study conducted by Lombardero and Fernández (1997), in Galicia, the authors found occasional attacks to living trees from native xylomycetophagous insects (Table 23.3). Three species of ambrosia beetles were reported: *Xyleborinus saxesenii* (Ratzeburg), *Xyleborus dispar* Fabr. (Col: Scolytinae), and *Platypus cylindrus* Fabr. (Col: Platypodinae).

The *Eucalyptus* trees colonized by the three ambrosia beetles were always found to be under stress from forest fires, pathogenic fungi, or application of herbicides (Lombardero and Fernández 1997). The most frequent species, *X. saxesenii*, was recorded from 11 different host species (mostly broadleaf) native to the study area, Galicia in Spain (Table 23.3). *Xyleborus dispar* was rarer on *Eucalyptus* and only found in highly decaying trees or logs, so this species was not considered as representing a menace to living trees. Finally, *P. cylindrus* was found in one unique site in decaying trees affected by pathogenic fungi (Table 23.3). In the Iberian Peninsula, *P. cylindrus* has been mostly associated with cork oak, *Quercus suber* L. (Sousa and Inácio 2005).

Coppice forestry is the main form of silviculture used in Iberian *Eucalyptus* plantations. Cuttings allow repeated harvest of poles at about 10-year intervals, usually until a third or fourth rotation. Stems are regenerated from shoots formed at the stumps of the living tree. In a study conducted in Portugal, Cabral (1983) surveyed the saproxylic insects associated with the decay of stumps, in the years after cutting. The author studied five regions with stands presenting similar age structure to list the presence/absence of saproxylic insects (Table 23.4). Additionally, to obtain the succession of saproxylic insects following stump age, five stands over 40 years old, with plots covering all rotations after the first cutting, i.e., second, third, and fourth rotation, were sampled. Trees were selected from cuts completed at

Table 23.3 List of xylomycetophagous associated with *Eucalyptus* trees under biotic or abiotic stress in Galicia (adapted from Lombardero and Fernández 1997) from case study 3

Species	Host stress factor	Number of sites	Native known local host plants[a]
Xyleborinus saxesenii	Fire, pathogenic fungi, herbicide	6	*Alnus glutinosa*, *Castanea sativa*, *Juglans regia*, *Prunus avium*, *Prunus persica*, *Quercus robur*, *Quercus pyrenaica*, *Salix cinerea*, *Sambucus nigra*, *Ulmus glabra*
Xyleborus dispar	Fire, pathogenic fungi	3	*Alnus glutinosa*, *Castanea sativa*, *Fagus sylvatica*, *Populus nigra*, *Prunus persica*, *Quercus robur*
Platypus cylindrus	Pathogenic fungi	1	*Quercus suber*

[a] Data on local native host species retrieved from Lombardero (1995)

Table 23.4 List of saproxylic insects sampled from *Eucalyptus* at five sites in Portugal, Serra do Caramulo, Mata do Escaroupim, Região do Oeste, Odemira, and Tapada da Ajuda in Lisbon from case study 3

Species	Abundance	Number of sites (out of 5)	Native known host species
Reticulitermes lucifugus Rossi (Blattodea: Kalotermitidae)	+++	5	*Castanea sativa*, *Celtis australis*, *Cercis siliquastrum*, *Fraxinus angustifolia*, *Olea europaea*, *Pinus pinaster*, *Pinus pinea*, *Populus* sp., *Quercus suber*, *Quercus* sp.
Kalotermes flavicollis Fabr. (Blattodea: Kalotermitidae)	+	2	*Amygdalus communis*, *Castanea sativa*, *Celtis australis*, *Ceratonia siliqua*, *Cercis siliquastrum*, *Fraxinus angustifolia*, *Olea europaea*, *Pinus pinaster*, *Pinus pinea*, *Populus* sp., *Quercus* spp., *Prunus* sp., *Pittosporum undulatum*, *Rhamnus alaternus*, *Tilia* spp., *Ulmus* spp.
Esperia sulphurella Fabr. (Lep., Oecophoridae)	+++	5	_
Esperia oliviella Fabr. (Lep., Oecophoridae)	++	3	_
Dorcus parallelipedus L. (Col., Lucanidae)	+	2	*Quercus* spp., *Pinus pinaster*, Broadleaves
Ampedus sanguineus L. (Col., Elateridae)	+++	4	_
Misolampus gibbulus Herbst. (Col., Tenebrionidae)	+++	4	_
Nalassus tenebrioides Germ. (Col., Tenebrionidae)	++	3	_
Coelometopus clypeatus Germ. (Col., Tenebrionidae)	+	1	_
Corymbia fontenayi (Muls.) (Col., Cerambycidae)	+++	4	Broadleaves and conifers
Trichius fasciatus L. (Col., Cetonidae)	+	1	_
Valgus hemipterus L. (Col., Tenebrionidae)	+	2	_

different times. Average volume per stump within this study varied from about 0.07 m^3 on second rotation to more than 0.5 m^3 on fourth rotation.

The main saproxylic insect species found on the sampled sites were a termite *Reticulitermes lucifugus* Rossi (Blattodea: Kalotermitidae); two moth species of the genus *Esperia*, family Oecophoridae; a click beetle *Ampedus sanguineus* L. (Col.,

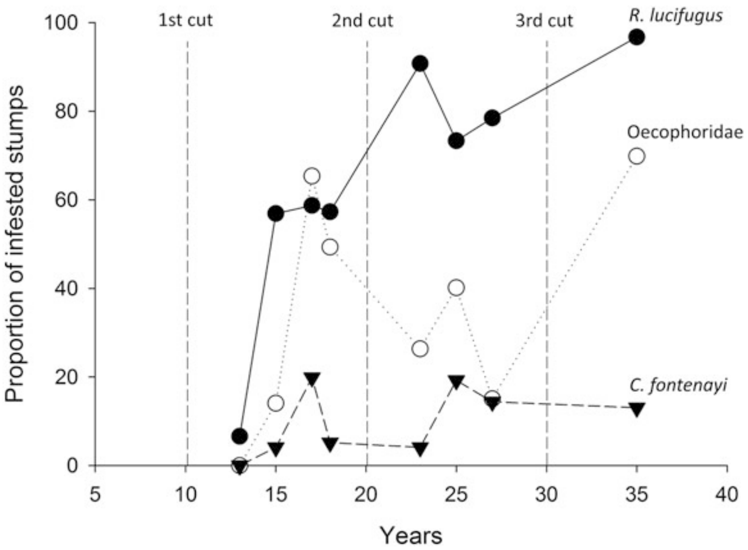


Fig. 23.8 Proportion of infested stumps by three main saproxylic insects, the termite *Reticulitermes lucifugus*, two moth species of the genus *Esperia*, family Oecophoridae, and the longhorn beetle *Corymbia fontenayi* Muls. Oeste, Portugal. Adapted from Cabral (1983), from case study 3

Elateridae); a longhorn beetle *Corymbia fontenayi* Muls. (Col., Cerambycidae); and *Misolampus gibbulus* Herbst. (Col., Tenebrionidae). The termite was the most frequent insect; it appeared after the first cut and reached almost 100% by the fourth rotation (Fig. 23.8). Its occurrence is quite conspicuous and easy to identify due to the presence of the colonies with nymphs and the stratified appearance of the consumed wood. The two species of *Esperia* share the same habitats and frequently coexist on the same stand. The larvae were found to first feed under the bark of the stumps and later penetrate the xylem. Both species have a 1-year life cycle, but with separate emergence times: February–March for *E. sulphurella* Fab. and April until July for *E. oliviella* Fabr. (Cabral 1983). Early instars of *A. sanguineus* apparently feed on wood, producing small round galleries in the wood, but later become predatory. The longhorn beetle *C. fontenayi* was quite common; it was present in all sampled sites (Table 23.4) and found on *Eucalyptus* stumps from the second to fourth rotation (Fig. 23.8). Its frequency was nevertheless low, usually between 10 and 20%. The beetle larvae consume wood of different sizes. The tenebrionids occurred only in highly decomposed wood.

23.3.2.2 Discussion

Although *Eucalyptus* is known to support diverse assemblages of saproxylic insects within the native range of the genus (Grove and Forster 2011a, b; Lawson and

DeBuse 2016), very little is known about the value of dying and dead *Eucalyptus* wood to saproxylic insects outside of Australia. A number of scolytine, platypodine, and cerambycid beetle species are viewed as potential pests of *Eucalyptus* in South America (Monteiro and Garlet 2016; Dorval et al. 2007), however, and at least one effort has been made to understand the value of *Eucalyptus* woody debris to other saproxylic insects, including termites (Trevisan et al. 2008). The studies summarized in this case study indicate that *Eucalyptus* can be utilized by some insect species, but many of them are known to have broad host ranges or are associated with wood at advanced stages of decomposition. There is a strong need for more research aimed at describing the diversity and succession of insects associated with *Eucalyptus* wood given the widespread and growing non-native range of the genus throughout many parts of the world. A recent study from Chile suggests that *Eucalyptus* plantations may create conditions unfavorable for saproxylic insects beyond the influence of wood characteristics. Fierro et al. (2017) found that non-native pine wood present in *Eucalyptus* plantations supported a lower density and richness of saproxylic beetles than similar woody debris in pine plantations nearby. The researchers suggested the toxic properties of *Eucalyptus* leaf litter and the relatively dry conditions of *Eucalyptus* stands may have negatively impacted saproxylic insect diversity.

23.3.3 Case Study 4: Native Saproxylic Species Colonizing Non-native Tree Species in New Zealand

New Zealand is an unusual country in that there is an almost complete separation of production forestry from the public conservation estate of native forests. Small areas of private native forest are managed for sustainable timber production (MPI 2013); however, the vast majority of wood products in New Zealand are produced from 1.7 million ha of even-aged, single species, plantation forests, predominantly *Pinus radiata* D. Don (90%) (FOA and MPI 2016). *Eucalyptus* spp. is also widely planted in New Zealand, covering approximately 23,300 ha (FOA and MPI 2016). These managed forest stands also provide habitat for diverse communities of plants (Brockerhoff et al. 2003), birds (Seaton et al. 2010), and invertebrates (including many saproxylic taxa) (Pawson et al. 2008, 2011), including threatened species (Brockerhoff et al. 2005; Pawson et al. 2010).

To protect plantations, New Zealand has strict quarantine regulations; however, some species continue to cross the border and establish in the native and productive ecosystems. New Zealand has operated a forest health surveillance scheme since the 1950s (Bulman 2008). Although the focus of the program has changed over the years, it has and continues to maintain a strong emphasis on identifying new incursions of non-native species. Observations of forest insects and pathogens from trees throughout New Zealand have been collated into the New Zealand Forest Health Database (FHDB). The FHDB comprises 213,563 records of both native and non-native tree pests and diseases and their hosts. Unfortunately survey methodologies have changed significantly over the decades, and it is not possible to quantify survey effort from the data available. As such a quantitative analysis is not possible. However, the FHDB provides a unique opportunity to assess the use of non-native tree species by both native and non-native saproxylic species. Here we compare the numbers of non-native and native saproxylic species that have colonized *P. radiata* or a *Eucalyptus* sp., and we also summarize the number of hosts colonized by each species.

23.3.3.1 Methods

To evaluate the use of non-native *P. radiata* and *Eucalyptus* hosts by saproxylic species, we summarize the records of insects from the termite families Kalotermitidae, Rhinotermitidae, and Termopsidae, the hymenopteran family Siricidae, the hemipteran family Aradidae, and the beetle families Anthribidae, Belidae, Bostrichidae, Bothrideridae, Brentidae, Buprestidae, Carabidae (Rhysodinae), Cerambycidae, Ciidae, Colydiidae, Corylophidae, Cryptophagidae, Cucujidae, Curculionidae, Latridiidae, Lucanidae, Lymexylidae, Mycetophagidae, Prostomidae, Ptinidae, Salpingidae, Silvanidae, Tenebrionidae, Ulodidae, and Zopheridae. Data was filtered to ensure that only observations where the species was associated with the host tree were included. This meant excluding those observations tagged with "agent not associated with disorder and/or host."

23.3.3.2 Results

A total of 55 saproxylic species are recorded in the FHDB as being associated with *P. radiata* (Table 23.5). Of these, 14 species were non-native and 41 were native. The average number of host trees (native and non-native) colonized by an individual non-native saproxylic beetle species that colonized *P. radiata* was 6.3 (±3.2 95% CI) vs. 9.8 (±6.8 95% CI) for the average individual native beetle species. The most common families of saproxylic beetles that colonized *P. radiata* were Curculionidae (19 species) and Cerambycidae (18 species). The highest diversity of non-native beetles was from the family Curculionidae, whereas Cerambycidae was the most diverse native family.

A total of 14 species of saproxylic beetles were recorded in the FHDB from *Eucalyptus* spp. (Table 23.6). Although many more species of beetles utilize *Eucalyptus* in New Zealand, most are foliar feeders. Of those saproxylic species recorded, four were non-native with the remaining ten native. The average number of hosts (all species, including *Eucalyptus* spp.) for non-native species was 5.4 (4.1 ± 95% CI), and for native species was 31.4 (27.0 ± 95% CI). The dominant group of saproxylic species recorded on *Eucalyptus* were wood borers from the family Cerambycidae.

Table 23.5 Observations of saproxylic beetle species recorded on *P. radiata* as part of forest health surveillance monitoring from case study 4

Beetle species	Family	Biostatus	Number of records from *P. radiata*	Total number of records all hosts	Year of first record	Number of hosts
Araecerus palmaris (Pascoe)	Anthribidae	Non-native	1	6	2001	4
Euciodes suturalis Pascoe	Anthribidae	Non-native	2	2	2016	1
Arhopalus ferus (Mulsant)	Cerambycidae	Non-native	110	162	1983	20
Bethelium signiferum (Newman)	Cerambycidae	Non-native	1	28	1979	10
Hylastes ater (Paykull)	Curculionidae	Non-native	49	54	1979	4
Hylurgus ligniperda (Fabricius)	Curculionidae	Non-native	30	35	2003	4
Rhinocyllus conicus (Frolich)	Curculionidae	Non-native	1	7	2001	5
Stenoscelis hylastoides Wollaston	Curculionidae	Non-native	1	6	2016	5
Kalotermes banksiae Hill	Kalotermitidae	Non-native	1	1	2001	1
Sirex noctilio Fabricius	Siricidae	Non-native	36	39	1983	3
Amarygmus tristis Blackburn	Tenebrionidae	Non-native	6	7	1979	2
Phymatus hetaera (Sharp)	Anthribidae	Native	9	9	1979	1
Phymatus phymatodes (Redtenbacher)	Anthribidae	Native	6	6	2003	1
Lasiorhynchus barbicornis (Fabricius)	Brentidae	Native	1	2	2001	2
Agapanthida pulchella White	Cerambycidae	Native	1	2	2001	2

(continued)

Table 23.5 (continued)

Beetle species	Family	Biostatus	Number of records from *P. radiata*	Total number of records all hosts	Year of first record	Number of hosts
Blosyropus spinosus Redtenbacher	Cerambycidae	Native	1	2	Unknown	2
Coptomma variegatum (Fabricius)	Cerambycidae	Native	7	12	1979	6
Eburilla sericea (White)	Cerambycidae	Native	1	14	1990	7
Hexatricha pulverulenta (Westwood)	Cerambycidae	Native	60	88	2001	15
Hybolasius vegetus Broun	Cerambycidae	Native	2	6	2003	5
Leptachrous strigipennis (Westwood)	Cerambycidae	Native	5	10	2001	4
Ochrocydus huttoni Pascoe	Cerambycidae	Native	1	11	1984	6
Oemona hirta (Fabricius)	Cerambycidae	Native	5	215	1983	132
Prionoplus reticularis White	Cerambycidae	Native	77	134	2016	20
Ptinosoma ptinoides (Bates)	Cerambycidae	Native	1	1	2008	1
Somatidia antarctica (White)	Cerambycidae	Native	6	6	2016	1
Somatidia grandis Broun	Cerambycidae	Native	1	1	2012	1
Xylotoles griseus (Fabricius)	Cerambycidae	Native	4	40	1979	19
Xylotoles laetus White	Cerambycidae	Native	9	25	1983	14
Zorion minutum (Fabricius)	Cerambycidae	Native	3	38	1979	22
Euophryum confine (Broun)	Curculionidae	Native	2	3	2006	2
Hoplocneme hookeri White	Curculionidae	Native	2	2	2001	1

(continued)

Table 23.5 (continued)

Beetle species	Family	Biostatus	Number of records from *P. radiata*	Total number of records all hosts	Year of first record	Number of hosts
Mitrastethus baridioides Redtenbacher	Curculionidae	Native	44	73	2000	11
Pachycotes peregrinus (Chapuis)	Curculionidae	Native	13	25	2013	5
Pentarthrum zealandicum Wollaston	Curculionidae	Native	2	6	2003	4
Phrynixus terreus Pascoe	Curculionidae	Native	3	4	1963	2
Platypus apicalis White	Curculionidae	Native	13	24	1983	4
Psepholax macleayi (Schonherr)	Curculionidae	Native	5	8	2006	4
Psepholax sulcatus White	Curculionidae	Native	6	14	2005	6
Rhopalomerus tenuirostris Blanchard	Curculionidae	Native	1	2	1972	2
Scolopterus aequus Broun	Curculionidae	Native	1	3	2006	3
Torostoma apicale Broun	Curculionidae	Native	24	42	1963	7
Xenocnema spinipes Wollaston	Curculionidae	Native	19	25	2001	3
Kalotermes brouni Froggatt	Kalotermitidae	Native	11	109	1979	61
Salpingus bilunatus Pascoe	Salpingidae	Native	2	2	2006	1
Brontopriscus pleuralis (Sharp)	Silvanidae	Native	4	5	2010	2
Artystona rugiceps Bates	Tenebrionidae	Native	4	5	2002	2
Tanychilus metallicus White	Tenebrionidae	Native	1	1	2002	1

(continued)

Table 23.5 (continued)

Beetle species	Family	Biostatus	Number of records from *P. radiata*	Total number of records all hosts	Year of first record	Number of hosts
Uloma tenebrionoides (White)	Tenebrionidae	Native	15	17	1997	3
Stolotermes inopinus (Gay)	Termopsidae	Native	4	5	2009	2
Stolotermes ruficeps Brauer	Termopsidae	Native	70	103	1993	19
Syrphetodes marginatus Pascoe	Ulodidae	Native	1	1	2013	1
Pristoderus antarcticus (White)	Zopheridae	Native	4	4	2014	1

23.3.3.3 Discussion

Based on the available records, more native saproxylic species are recorded as utilizing *P. radiata* than *Eucalyptus* spp. in New Zealand. One possible explanation for this is the fact that *P. radiata* covers a much larger land area than *Eucalyptus*. Or alternatively, it could reflect greater relatedness between *P. radiata* and conifers native to New Zealand, i.e., Podocarpaceae. Irrespective of host type (*P. radiata* and *Eucalyptus* spp.), individual non-native beetle species were recorded from fewer species of host trees than native beetle species (Tables 23.5 and 23.6). This suggests that colonizing non-native species could be more host specific than the native insects which utilize a wider range of both non-native and native tree species. This suggests that native species are less host specific than the exotic species that have colonized although this is tentative given that the FHDB does not provide exhaustive information on associations. Interestingly this effect was much stronger for *Eucalyptus* spp. where seven of the ten native species were known from more than ten hosts. It was a feature of *Eucalyptus* records that highly polyphagous native species were represented by few observations that indicate that *Eucalyptus* is likely to be a marginal host for such species. Few species of termites have been recorded in association with *P. radiata* or *Eucalyptus* spp. in New Zealand. This reflects the low diversity of native termites in New Zealand (Bain and Jenkin 1983) and the strict import controls on commodities that have the potential to be infested by termites.

Table 23.6 Observations of saproxylic beetle species recorded on *Eucalyptus* spp. as part of forest health surveillance monitoring from case study 4

Beetle species	Family	Biostatus	Number of records from *Eucalyptus* spp.	Total number of records all hosts	Date of first record	Number of hosts
Callidiopis scutellaris (Fabricius)	Cerambycidae	Non-native	28	34	1985	13
Phoracantha semipunctata (Fabricius)	Cerambycidae	Non-native	1	1	2004	1
Tessaromma undatum Newman	Cerambycidae	Non-native	18	20	2000	6
Porotermes adamsoni (Froggatt)	Termopsidae	Non-native	1	3	1993	2
Ctenoneurus hochstetteri (Mayr)	Aradidae	Native	1	1	1985	1
Coptomma lineatum (Fabricius)	Cerambycidae	Native	3	43	1983	15
Eburida picta (Bates)	Cerambycidae	Native	1	1	2014	1
Hexatricha pulverulenta (Westwood)	Cerambycidae	Native	1	88	1984	15
Oemona hirta (Fabricius)	Cerambycidae	Native	6	215	1983	132
Prionoplus reticularis White	Cerambycidae	Native	1	134	1979	20
Xylotoles laetus White	Cerambycidae	Native	1	25	2000	14
Psepholax sulcatus White	Curculionidae	Native	1	14	1983	6
Kalotermes brouni Froggatt	Kalotermitidae	Native	4	109	1979	61
Stolotermes ruficeps Brauer	Termopsidae	Native	3	103	1993	19

23.4 Conclusions and Future Directions

Based on the information currently available, the diversity of saproxylic insects associated with decomposing wood varies considerably among tree species, and this is true for both native and non-native taxa. Many non-native wood species appear to provide highly suitable material for saproxylic insect communities and may offer a way to increase the availability of deadwood in some forests. In Italy, for example, Della Roca et al. (2016) found no difference in saproxylic beetle species richness and composition among the non-native invasive *R. pseudoacacia* and two native wood species. Based on these results, the researchers suggested felling *R. pseudoacacia* trees for the dual purpose of controlling this invasive species and increasing the amount of deadwood available to saproxylic organisms. However, while non-native woody material may provide suitable habitat for many generalist species, it remains almost entirely unknown whether these novel resources will be of any value to specialist species, including threatened taxa of greatest conservation concern. In one of the only published studies to explore this question, Oleksa and Klejdysz (2017) found no evidence that *Cerambyx cerdo*, a threatened specialist of old oaks in Europe, can utilize *Q. rubra*, a non-native species from North America. Similarly, Della Rocca et al. (2017) found that *R. pseudoacacia* did not impact the occurrence of *Lucanus cervus* (L.) in Europe as long as it covered less than 70% of the landscape and stressed the importance of preserving native trees in invaded landscapes. Although the four case studies presented herein report many examples of native saproxylic insects utilizing non-native wood species, it is important to note that all of these insect species are known generalists with healthy populations within the regions studied. There is currently little evidence that non-native wood species will provide much benefit to the most threatened members of the saproxylic insect fauna.

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Chapter 24
The Role of Urban Environments for Saproxylic Insects

Jakub Horák

Abstract The value of urban environments to saproxylic insect conservation remains largely unstudied but is known to vary depending on the number and density of trees as well as their age, distribution, and species composition. Perhaps the most important factor influencing the distribution of saproxylics in urban areas is the degree of isolation among suitable habitats. Solitary trees form one of the primary urban habitats for beetles and other saproxylic insects, especially those that possess cavities and other characteristics common to veteran trees. Linear woody vegetation corridors, such as avenues or vegetation along riverbanks, also form important habitats. Small groups of trees, like those in city parks, can also provide valuable resources for urban saproxylics, as can small forested areas, like those that also exist in parks, zoos, or other green spaces. Of the utmost importance are larger urban forests, but much depends on the management intensity of these areas. Urban areas are defined by high human population densities, and this creates challenges for the long-term survival of saproxylic insects and complicates efforts to study and conserve these insects in public areas. Efforts to protect the oldest trees, such as pollarding which can make them less hazardous, as well as the protection or creation of downed woody debris, can make urban environments more friendly to a wide range of saproxylic insects, including some of the most threatened species.

24.1 Introduction

Urban environments cover a growing proportion of the world's land area. Already about half of the world's human population lives in cities, and most of the projected population growth over the next 30 years is expected to be concentrated in emerging mega-cities in the developing world (Cohen 2006; Clapson and Hutchison 2010). Trees are an important component of areas inhabited or utilized by people, with

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benefits ranging from alleviating stress, lowering crime, improving air quality, and supporting a wide variety of other organisms (e.g., Melichar and Kaprová 2013). Indeed, there is increasing interest in urban forestry, and the biodiversity value of these areas is a growing concern (Grimm et al. 2008; Seto et al. 2012). The biodiversity of saproxylic insects present in urban and residential areas will, of course, be dictated by the availability of suitable habitats, as well as the spatial and temporal continuity of these resources. Overall, it can be expected that urban areas will support fewer species and smaller populations of saproxylic insects than natural areas. In Chile, García-López et al. (2016) collected fewer species and individuals of saproxylic beetles in urban/agricultural areas compared to a nearby nature reserve. In some cases, however, areas inhabited or heavily utilized by people can provide more suitable habitats than natural areas. A good example of this concerns are veteran trees growing around manor houses (Jonsell 2004, 2012). There is much to be gained from better recognizing the potential of urban, residential, and recreational areas to support saproxylic insect communities. Decisions about how best to manage dying and deadwood made by city managers, as well as by individual property owners, will collectively determine the quality of urban landscapes for saproxylic insects.

In this chapter, I review the availability of habitats suitable for saproxylic beetles in urban landscapes, with a focus on examples from the Czech Republic. I document examples of saproxylic insects inhabiting these environments, consider ways to manage habitats for these insects, and discuss challenges to conservation in areas with a lot of human activity.

24.2 Availability of Resources for Saproxylic Insects in Urban Areas

Tree age, density, and species composition are three of the most important determinants of habitat suitability for saproxylic insects in urban areas. Tree age ranges from recently planted saplings that provide few saproxylic resources to centuries-old veteran trees that host diverse assemblages of saproxylic insects. Tree density ranges from solitary trees to large urban forests, with tree rows or patches falling in between these two extremes. At the smallest scale, solitary trees that fulfill the criteria for veteran trees [i.e., large diameter, old, and with a high diversity of microhabitats (Horák 2017)] provide excellent and long-term habitats for many saproxylic insects. Moreover, many of these trees are sun-exposed, which is a key factor for saproxylic activity and development (Lindhe et al. 2005; Vodka et al. 2009; Horák and Rébl 2013). Solitary veteran trees can be found in a wide variety of settings including city squares, market places, on college campuses and next to both historic buildings and memorials (Figs. 24.1 and 24.2). These are often parts of downtown areas, but we can also find them in former rural environments which were incorporated into the city during its past growth. Jonsell (2004) reported veteran trees, growing in an old

Fig. 24.1 (Upper left) Dead solitary *Tilia cordata* Mill. in the castle of Pardubice courtyard (Czech Republic) was formerly used by the jewel beetle *Lamprodila rutilans* (Fabricius). Unfortunately the tree was felled in 2016. This tree was only a few hundred meters from the castle avenue (upper right) that is inhabited by the hermit beetle (*Osmoderma barnabita* Motschulsky). Suitable hollows inside the trees were originated by pollarding in the past. One of the present important management activities regarding saproxylic insects is to keep the temporal continuity of the avenue using plantings of new saplings, unfortunately they are not pollarded. (Lower left) River bank of Labe in Pardubice (Czech Republic) dominated by the pedunculate oak (*Quercus robur* L.) that has high potential to be a suitable habitat for saproxylic insects. Majority of trees are protected by law as monumental trees. (Lower right) Another kind of pollarding of old trees in Hrob (Czech Republic)—Horse chestnut (*Aesculus hippocastanum* L.) trees in front and White willow (*Salix alba* L.) trees at the back

Swedish park, which supported nearly as many red-listed beetle species as were found in a seminatural forest. More recently, Jonsell (2012) compared saproxylic beetle assemblages associated with veteran trees growing near old manor houses to those growing in open woodlands or in younger regrowth stands. Fewer species overall were captured from trees near the manor houses than from those in the woodlands, but the number of hollow-dependent or red-listed species did not differ between the two habitats. Thus old park trees are as valuable to insect diversity as those in more natural settings.

Tree rows in urban areas mainly occur as avenues or alleys (Fig. 24.1) lining residential streets and can be very close to or inside downtown areas. Prominent examples of this type of vegetation from Europe include Unter den Linden in Berlin, Germany, and the avenues that lead to the Arc de Triomphe in Paris, France. In

Fig. 24.2 (Left) Veteran trees (*Cinnamomum camphora* (L.) Presl in foreground and several *Ficus microcarpa* L. in background, all about 150 years old) in Shamian, Guangzhou China. (Right) *C. camphora* L. tree (~130 years old) with hollow exposed from the removal of a branch, Guangzhou China (photos by Wendy Chen)

North America, examples include the Freeway Park in Seattle and New York City's High Line. Older rows of trees, often including veteran trees, appear on riverbanks (Fig. 24.1) and at fishpond dams (e.g., Třeboň, Czech Republic). Tree rows are often planted as windbreaks in towns, often surrounding football (soccer) grounds. Rows of trees are sometimes preserved as wilderness areas (Rink 2009), e.g., along city railways as greenways or greenbelts. Deadwood is sometimes present in these environments not only in the form of veteran trees but also in the form of dead trees, snags, high stumps, and all forms of downed woody debris. Long tree rows may function as corridors, facilitating the movement of saproxylic insects within urban landscapes.

Groups of trees also form important saproxylic habitats (Fig. 24.1). These often occur in urban parks, on school and university campuses, in playground areas, and also around city hospitals. Urban residential gardens with old fruit trees or orchards can provide valuable habitats for saproxylic insects, and groups of trees can also be found in military training areas inside cities (Fig. 24.3). Notable examples of groups of trees can be found in Prague Palace's Royal Garden, New York's Central Park, or Natal City Park in Brazil.

Small forests (Fig. 24.3) can also occur in urban areas. When these are commercial forests, the probability of veteran trees being present is low, but such areas may have greater overall amounts of standing and lying deadwood due to limited public access. Small stands can exist in places like cemeteries, arboreta, zoos, and botanical gardens. Other examples include wilderness areas established in green spaces or on restored brownfields as well as forests growing in areas formerly covered by oxbow lakes. The most valuable habitats to saproxylic insects are of course large urban

Fig. 24.3 (Left) Former *poplar* avenue in military training area in Pardubice (Czech Republic) is now part of wilderness area and suitable habitat for *Cucujus cinnaberinus*. (Right) This forest, in the place of former oxbow lake, in Pardubice (Czech Republic) was a place of colony of homeless people

forests, as indicated for saproxylic tenebrionid beetles in Italy (Fattorini and Galassi 2016), although the quality of these forests for saproxylics depends greatly on how the landscape is managed. Urban forests managed mainly for timber products would have a lower probability for an abundance of veteran trees, which are often mainly distributed along forest roads. The degree to which property managers value deadwood as a resource for wildlife will largely determine the availability of habitat for saproxylic insects. It is probable that urban forests may contain less coarse woody debris if managers prioritize open forest conditions. Potentially highly suitable places for saproxylic insects are urban nature reserves and sometimes also urban forests that are managed for recreational activities although this again will depend largely on local management decisions.

Tree species composition is another important consideration with respect to the suitability of urban areas for saproxylic insects. Nonnative tree species are often planted in urban areas, and, although the value of exotic wood species to saproxylic insects remains uncertain, native tree species generally provide better habitat (Ulyshen et al. 2018; see Chap. 23). Finally, it is also important to recognize the value of non-woody resources for many species of saproxylic insects. As adults, many saproxylic insect species are flower-visiting (floricoulous). Examples of this among beetles include rose chafers (Cetoniinae), cerambycids (Cerambycidae), burprestids (Buprestidae), and others. Many saproxylic hymenopterans and dipterans are also dependent on or benefit from flowers (Bogusch and Horák 2018; see Chap. 7). Wood-nesting bees of course collect pollen or nectar for their larvae and parasitic hymenopterans, like braconid (Braconidae) or chalcid (Chalcididae) wasps, are known to benefit greatly from floral resources. Thus, areas with flowers like urban gardens, unmown roadsides, or highway medians also help support the persistence of saproxylic insects in urban areas.

24.3 Variation in Habitat Quality Across Space and Time

The establishment of residential areas on land previously covered in forest or other natural habitats is happening all over the world. In many cases the land is completely cleared before building commences although there is a growing interest in eco-friendly developments. Depending on the decisions made at this early stage, the creation of a new development can range from the complete destruction of saproxylic habitat to the fragmentation of that habitat. In general, young neighborhoods commonly have fewer and younger trees than older neighborhoods, so the quality of saproxylic habitat can be expected to increase over time as the trees and neighborhoods mature. Few studies have considered this pattern, especially as it relates to saproxylic insects.

Even on small plots of land, property owners can play an important role in creating habitats for saproxylic insects. For example, fallen limbs or logs can be piled up for use by wildlife, and a stump left undisturbed can provide important resources for many years. In the UK, *Lucanus cervus* (L.) has been shown to utilize stumps in private gardens, and in the Czech Republic, *Cucujus cinnaberinus* (Scopoli) was found in fuel wood stock.

24.4 Examples of Threatened Species in Urban Environments

There are many examples of threatened beetles occurring in urban and residential areas throughout the world. Two of them have been studied intensively in Europe, the stag beetle (*Lucanus cervus*) and the hermit beetle (*Osmoderma eremita*(Scop.)).

*24.4.1 The Stag Beetle (*Lucanus cervus*)*

Lucanus cervus has become threatened across Europe due to the loss of habitat. However, this beetle appears to be quite adaptable and capable of using a wide variety of resources depending on what is locally available. Intriguingly, Harvey et al. (2011) found *L. cervus* to be largely concentrated in urban areas in the UK whereas it is primarily a woodland species in Europe. As summarized by Hawes (2008), over 75% of *L. cervus* sightings in the UK came from urban areas, and 93% of those came from residential gardens. Examples of resources used by *L. cervus* in gardens include log piles, the stumps of felled trees, fence posts, compost heaps, and even the roots of trees after the entire aboveground portion was removed (Hawes 2008; Fremlin 2009; Harvey et al. 2011). It was also found that urban areas provide support for *Lucanus cervus* in Belgium (Thomaes et al. 2008) and there is a sustainable population of the species on Petřín, the largely forested hill in the center of Prague (Horák and Chobot 2011).

*24.4.2 The Hermit Beetle (*Osmoderma eremita*)*

Another well-studied and threatened beetle species known to exist within human-dominated landscapes is *O. eremita*. This species breeds in tree hollows and thus requires very old trees. Suitable trees can be found in many urban and residential habitats and include the veteran trees growing around old houses or along roads (Jonsell 2004, 2012; Kadej et al. 2016). Although *O. eremita* is known to use hollow trees in these areas, Kadej et al. (2016) found that the probability of *O. eremita* occurrence decreased with increasing distance from forested habitats in Poland. A major challenge facing the conservation of this species in areas with a lot of human activity centers around concerns for public safety as the trees used by *O. eremita* are old and often potentially hazardous (Carpaneto et al. 2010).

24.4.3 Other Examples

The threatened great capricorn beetle (*Cerambyx cerdo* L. L.) is also known to occur in urban environments. There is a population of the species in an old oak at the Homolka fishpond dam in Prague, for example (JH, personal observation). Another threatened species known to occur in urban areas in Europe is *Cucujus cinnaberinus* which can commonly be found in dead poplars in Pardubice, Czech Republic (Fig. 24.3) (JH, personal observation).

24.5 Challenges to Conserving Saproxylic Insects in Human-Dominated Areas

Urban areas are potentially hostile environments for saproxylic insects (e.g., Carpaneto et al. 2010). Due to public safety concerns posed by old and declining trees, the trees providing the best habitats for saproxylic insects are often cut down long before they would have died naturally (Fig. 24.4). If these trees are somehow protected, however, they can provide critical and long-lasting resources for many generations of saproxylic insects. According to Carpaneto et al. (2010) in Italy, there may be greater habitat availability for saproxylic beetles associated with tree hollows, such as *O. eremita*, in urban parks compared with the surrounding countryside due to the presence of veteran trees. Unmanaged urban forests can be similarly beneficial to saproxylic insect communities, as demonstrated by the high number of

Fig. 24.4 Urban areas are not always suitable places for saproxylic insects. Healthy big *poplar* trees were cut due to the establishment of a new playground in Pardubice City park (Czech Republic); their stumps were pulverized

threatened saproxylic beetle species, including flightless species, like in Ostrava, Czech Republic (Horák 2011).

As urban forests exist in close proximity to humans, there is also a higher probability that downed deadwood will be removed by citizens for firewood, and urban forests are sometimes used by homeless people for fuel and shelter (Fig. 24.3). Deadwood habitats are also sometimes artificially set on fire—e.g., old hollow trees or loggeries (i.e., piles of deadwood created to benefit wildlife) (JH, personal observation). Flower resources are at risk from regular mowing, especially in close vicinity to buildings or on road margins.

Researchers in urban habitats must also be prepared for an increased risk of vandalism. Placing traps higher above the ground may help but will not necessarily prevent this problem. Another solution is to place the traps in private places with the consent of the owners. The use of woody resources for building fires and other purposes by human populations greatly complicates long-term research efforts in public areas. One of the possibilities for research involves citizen science, such as making direct observations of flower-visiting saproxylics.

24.6 Conservation Strategies in Urban Areas

Public education campaigns can help raise awareness about saproxylic insects and the importance of preserving their habitats. In many cases, communities already value old trees for their cultural value and for establishing a sense of place. There may be limited awareness about the rarity of these trees or their importance in providing habitats for other organisms. Similarly, Chen (2015) found that people's willingness to pay for the conservation of urban veteran trees in southern China was largely motivated by the trees' perceived recreational value. Education campaigns may help to overcome resistance among those who find dying trees, stumps, and dead woody debris to be unsightly and/or dangerous. Moreover, urban and residential areas are ideal for citizen science projects as it has been shown for several species of saproxylic beetles in Europe (Zapponi et al. 2017).

The public safety concern surrounding veteran trees is a major challenge to conservation efforts, especially for species dependent on tree hollows (Carpaneto et al. 2010). In Sweden, as elsewhere in Europe (Fig. 24.1), many veteran trees have a long history of being pollarded, and Jonsell (2012) suggested that it is important to continue pollarding to prevent the breakage of trees as shoots grow. Pollarding has the additional benefit of promoting the formation of tree cavities (Sebek et al. 2013). This management activity has been used for a long time and has been mentioned in classical literature, like in the Stendhal's novel *Le Rouge et le Noir*, in reference to urban areas. Jonsell (2012) also stressed the importance of replacing trees as they are removed to ensure the continuity of habitat availability into the future. In addition to protecting saproxylic habitats associated with standing or fallen trees, efforts can also be made to create piles of woody debris for the benefit of insects and other organisms. Loggeries are places where woody debris can be piled to provide habitats for saproxylic insects. Jonsell (2012) suggested that such "tree-graveyards" could be placed in remote areas that would be out of public view. On the other hand, these piles of woody material offer a chance to educate the public about saproxylic organisms and can be incorporated into displays or habitats for zoo animals (Fig. 24.5). In Europe, loggeries are sometimes supplied with wooden statues of saproxylic flagship beetles like the stag beetle (*L. cervus*) or the hermit beetles (*Osmoderma* spp.). Private homeowners can do the same thing in their gardens, and these efforts have been shown to promote the conservation of at-risk species

Fig. 24.5 (Left) Pieces of deadwood arranged to mimic a natural habitat for the Asian black bear (*Ursus thibetanus*) in Konopiště castle (Czech Republic). (Right) A piece of deadwood used as a bench in Častolovice (Czech Republic) castle park

such as *L. cervus* in Europe (Fremlin 2009) and provide habitats for a wide range of other invertebrates (Gaston et al. 2005).

Another way to provide habitats for saproxylic insects is to create supplementary or complementary shelters or nesting places for them. One promising development is the use of nest boxes for both beetles and bees. Wooden nest boxes can be placed in urban areas to provide for cavity-nesting bee genera such as *Osmia* (Bogusch and Horák 2018; see Chap. 7). Another possibility is to provide artificial shelters for species that are rather facultative—like some ground beetles (Carabidae). For example, if there is no decayed woody debris left (e.g., as a bench; Fig. 24.5) for them to use for overwintering, the creation of places that mimic these habitats—like a pile of stones—would be very important. Some species (like rose chafers) also use artificially made places with plant residues—like compost heaps, fuel wood stocks, or sawdust dumps (e.g., Horák 2016a).

24.7 Conclusions

Urban spaces are still rather neglected with respect to their potential importance to saproxylic insects. There are many advantages of studying the conservation value of these environments, though, including their accessibility and familiarity to professional and citizen scientists alike. Patches of ecosystem types are quite fragmented within cities (Horák 2016b), thus providing special opportunities to study the effect of anthropogenic disturbance on saproxylic insects. Scientists can model, and test, urban saproxylic responses on many spatial scales, ranging from single trees to large forest islands. There is also the possibility to study the fragmentation of forest attributes. Moreover, as the environment in cities is highly variable, they provide an excellent chance to study the temporal and spatial changes in resource availability as well as abiotic conditions.

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Part IV
Methodological Advancements

Chapter 25
Molecular Tools for Assessing Saproxylic Insect Diversity

Ryan C. Garrick and Christophe Bouget

Abstract Little is known about the amount and spatial distribution of diversity within and among deadwood-dependent insect species and saproxylic communities as a whole. Molecular approaches offer a solution to these knowledge gaps, even in cases where species and genera are not yet formally described. Indeed, molecular data are broadly connectable among otherwise unrelated studies and directly complement the invaluable work of expert taxonomists. Here we provide an overview of the applications of molecular tools for assessing saproxylic insect diversity. To do this, we use an organizational framework based on the hierarchy of biological units, beginning with diversity at the intraspecific level, followed by species-level diversity within genera, and then close with community-level diversity. Within each of these sections, we consider the types of genetic data that have typically been used and provide an overview of research questions and findings from the primary literature.

25.1 Introduction

Deadwood-dependent (saproxylic) insects are an ecological community that exhibits considerable diversity across different levels of biological organization, from populations to species and beyond. This group also encompasses an array of life history traits relating to metamorphosis, reproduction, dispersal, longevity, and feeding. Furthermore, saproxylic insects are ecosystem service providers that contribute to the decomposition of fallen trees and thus play roles in maintaining healthy, productive forests (Ulyshen 2013, 2014, 2016; Ulyshen and Wagner

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2013). While these beneficial services extend to commercial forests and unmanaged forests, saproxylic insects are an overlooked component of biodiversity (Speight 1989; Siitonen 2001; Yee et al. 2001; Grove 2002a; Garrick et al. 2006) such that their needs are usually not explicitly integrated into natural resource management or conservation plans.

Although some saproxylic insects are capable of long-distance colonization (Ranius et al. 2011), as a group they typically have poor dispersal abilities (e.g., due to winglessness and/or rapid desiccation as a consequence of adaptations to life in a rotting log; Schmuki et al. 2006a, b; Garrick et al. 2012). Accordingly, this group can be particularly sensitive to human activities that cause forest fragmentation or prevent the natural occurrence of fallen trees (Schiegg 2000; Bouget et al. 2014; Seibold et al. 2015). Indeed, a disproportionately large number of threatened or endangered arthropods depend on deadwood (Jonsson and Kruys 2001). This has led some to suggest that saproxylic insects may be an early warning indicator for assessing forest health (Langor et al. 2006). However, a critical first step is to document the amount and spatial distributions of diversity in this poorly known group.

Two major challenges to documenting the diversity of saproxylic insects exist. First, many species and genera are unnamed, and there are too few trained experts to accomplish the task of describing them in the near future (i.e., the taxonomic impediment; New 1999). The sheer diversity of tropical saproxylic insects makes them taxonomically challenging in their own right (Grove and Stork 2000). Second, due to morphological conservatism of some groups or convergent adaptations (e.g., dorsoventrally flattened bodies, reduction or loss of eyes and pigment), many named species may actually be a complex of several cryptic species. This has been demonstrated repeatedly by molecular analyses of deadwood invertebrates (e.g., Trewick 2000; Walker et al. 2009; Oliveira et al. 2011). Consequently, for saproxylic insects, traditional biodiversity metrics based on morphologically identifiable named species, such as richness and turnover (i.e., alpha and beta diversity, respectively), will likely be downwardly biased. Indeed, the magnitude of this downward bias, and the extent to which it varies across a landscape, represents a knowledge gap in itself. Furthermore, traditional biodiversity metrics do not contribute information that can be used to protect unnamed species.

Molecular tools provide a pragmatic solution to the taxonomic impediment, to the design of large-scale monitoring schemes, and to the existence of cryptic species. For instance, distinct lineages can be defined on the basis of DNA sequence similarity, and given that the underlying data can be connected across distantly related groups, additional information on evolutionary relationships can be obtained. In addition to providing opportunities for less biased measures of local biodiversity in saproxylic insects, DNA sequence data also enable preliminary classification of specimens to named species [e.g., via mitochondrial DNA (mtDNA) barcoding approaches; Hebert et al. 2003]. Furthermore, molecular approaches can reveal specimens with divergent sequences that should become the subjects of focused morphological examination by expert taxonomists (Hebert and Gregory 2005; Hajibabaei et al. 2007).

Below, we give an overview of past and potential future applications of molecular tools for assessing saproxylic insect diversity. To do this, we use an organizational framework based on the hierarchy of biological units, beginning with diversity at the intraspecific level, followed by species-level diversity within genera, and then closing with community-level diversity. Whereas the former two categories benefit from a solid body of existing literature that specifically focuses on saproxylic insects, the latter category does not. Accordingly our treatment of community-level diversity draws from related literature (e.g., studies on saproxylic fungi) in order to look to the future of insect studies, and we propose a general research pipeline that may facilitate progress and/or stimulate debate. Finally, we briefly consider emerging directions in the use of molecular data to address questions about diversity and function in saproxylic invertebrates.

25.2 Specimen Sampling and Preservation

For the purpose of DNA extraction, tissue samples from saproxylic insects have been obtained in several ways. A common collection method has been carefully breaking open logs (e.g., using a small axe) and then visually inspecting the woody material for target taxa (e.g., Schmuki et al. 2006b; Leschen et al. 2008; Garrick 2017; Ulyshen et al. 2017). Occasionally, this approach has been augmented by using a Berlese funnel or Winkler sack to further process crumpled debris (Marske et al. 2009, 2011). Some studies have employed nonlethal sampling (e.g., only taking a clipping from a middle leg; Oleksa et al. 2013; Drag and Cizek 2015; Drag et al. 2015), which may have minimal impacts on survivorship and reproduction (Suzuki et al. 2012; Oi et al. 2013). More often, however, lethal sampling of whole specimens has been conducted, presumably because this enables morphological and other data to be collected, as well as vouchering of reference material.

As an alternative to dismantling rotting logs by hand, for some saproxylic beetles, pheromone-baited flight intercept traps or window traps have been used to sample specimens for molecular work (e.g., Svensson et al. 2009; Oleksa et al. 2013, 2015; Zauli et al. 2016; Harvey et al. 2017; Ulyshen et al. 2017). Although this approach avoids destroying deadwood microhabitats and may improve sampling efficiency when working on rare species, depending on the research question at hand, there are some issues that warrant consideration. For example, samples will be sex-biased if the pheromone is attractive only to males (e.g., Oleksa et al. 2015). Furthermore, depending on the speed of response and the duration of exposure, sampled individuals may travel relatively long distances before arriving at the trap, which would compromise the accuracy of geographic coordinates associated with trapped specimens. Finally, aside from pheromone traps being applicable only to flight-capable saproxylic insects, the timing of their deployment must generally coincide with reproductive phenology, which may be poorly known or geographically variable.

When planning for subsequent DNA analyses, ethanol has most often been used to preserve sampled specimens. However, in the context of trap-based collections, evaporation might decrease the preservation property of ethanol under field conditions. In these cases, ethylene or propylene glycol might be an alternative. To obtain optimally preserved insects, Gossner et al. (2016) suggested using ethylene glycol instead of Renner solution (ethanol and glycerine) or copper sulfate, since the former solution had preserved samples better in a variety of microclimatic situations (also see Dillon et al. 1996). Propylene glycol might be used as a less toxic alternative (Höfer et al. 2015). Also, Pokluda et al. (2014) recommended using a solution of laboratory chemicals (i.e., 2% sodium dodecyl sulfate and 100 mM disodium ethylenediaminetetraacetate) as a cheap, stable, and easily transportable alternative to ethanol. However, its attracting effect has not been tested, and so potential biases in sampling for community-level studies remain unknown.

Once specimens have been collected and preserved, DNA extractions may be performed using nondestructive methods so as to preserve morphological characters. Protocols that yield sufficient amounts of genomic DNA from a broad range of terrestrial arthropods, and for which the specimens remain suitable for imaging and as vouchers, have been developed (e.g., Rowley et al. 2007; Castalanelli et al. 2010). Alternatively, if specimens are relatively large, destructive sampling of one or a few legs taken from the same side of the body should also retain morphological information.

25.3 Intraspecific Diversity

25.3.1 Genetic Data Types

Certain characteristics of different types of molecular markers influence the temporal and spatial scales over which they are most informative (Garrick et al. 2010). For example, the lag time between when a lineage divergence event actually occurred and when it registers a genetic signature can be affected by the mutation rate of different genomic regions, as well as the resolution of the assay itself (e.g., ability to distinguish heterozygotes from homozygotes or to identify mutations that are silent rather than only those that are expressed; Avise 2004; Allendorf et al. 2013). Molecular markers also differ in their level of selective constraint and the extent to which they can be connected across unrelated studies (Caterino et al. 2000; Sunnucks 2000). To date, population-level studies of saproxylic insects have employed several different types of molecular markers. Direct sequencing of mtDNA—particularly the cytochrome oxidase I (COI) gene region—has been one of the most common approaches (Table 25.1). Mitochondrial sequence data can be readily generated for diverse insect taxa due to the availability of broadly useful polymerase chain reaction (PCR) primers (e.g., Folmer et al. 1994; Simon et al. 1994). Furthermore, mtDNA sequences are phylogenetically informative. One shortcoming, however, is that the entire mitochondrial genome is effectively a single locus, and so when mtDNA data are used alone, there is little scope for cross-validation of inferences (Edwards and Beerli 2000). Nuclear microsatellite markers

Table 25.1 Summary of genetic data types, and number of individuals sampled and screened for genetic variation, in population-level studies of saproxylic insects

Region/taxon	Common name	IUCN status	Continent or country	Genetic data type and no. of loci (no. of individuals)						References
				Mt. seq.	Indel	Microsat.	Allozyme	AFLP	RAPD	
Northern Hemisphere										
Blattodea										
Cryptocercus punctulatus	Wood roach	–	E. USA	1 (95)	–	–	–	–	–	Garrick et al. (2017)
Reticulitermes flavipes	Subterranean termite	–	E. USA and W. Europe	1 (215)	–	12 (170)	–	–	–	Perdereau et al. (2013)
Reticulitermes grassei	Subterranean termite	–	SW. France	1 (52)	–	6 (512)	–	–	–	Bankhead-Dronnet et al. (2015)
Zootermopsis angusticollis	Damp-wood termite	–	W. USA	–	–	9 (963)	–	–	–	Booth et al. (2012)
Zootermopsis nevadensis	Damp-wood termite	–	W. USA	–	–	12 (468–972)	–	–	–	Aldrich and Kambhampati (2007)
Coleoptera										
Bolitophagus cornutus[a]	Fungus beetle	–	E. USA	–	–	–	5 (?)	–	–	Whitlock (1992)
Bolitophagus reticulatus[a]	Fungus beetle	–	N. Europe	–	–	–	8 (163)	–	5 (149)	Jonsson et al. (2003)
Cerambyx cerdo	Great capricorn beetle	VU	E. Europe	1 (82)	–	9 (79)	–	–	–	Drag and Cizek (2015)
Cucujus cinnaberinus	Flat bark beetle	NT	N. and E. Europe	–	–	10 (71)	–	–	–	Røed et al. (2014)
Diaperis boleti[a]	Fungus beetle	–	E. Europe	–	–	–	–	81 (136)	–	Oleksa (2014)

(continued)

Table 25.1 (continued)

Region/taxon	Common name	IUCN status	Continent or country	Genetic data type and no. of loci (no. of individuals)						References
				Mt. seq.	Indel	Microsat.	Allozyme	AFLP	RAPD	
Elater ferrugineus	Red click beetle	[b]	E. Europe	–	–	–	–	105 (247)	–	Oleksa et al. (2015)
Oplocephala haemorrhoidalis[a]	Fungus beetle	[b]	N. Europe	–	–	–	10 (83)	–	26 (101)	Jonsson et al. (2003)
Osmoderma barnabita	Hermit beetle	NT	E. Europe	–	–	–	–	91 (99)	–	Oleksa et al. (2013)
Protaetia marmorata	Marbled rose chafer	–	E. Europe	–	–	–	–	89 (136)	–	Oleksa et al. (2013)
Pytho abieticola	Beetle	–	N. and E. Europe, China	1 (39)	–	–	–	–	–	Painter et al. (2007)
Pytho depressus	Beetle	–	N. and E. Europe, China	1 (97)	–	–	–	–	–	Painter et al. (2007)
Pytho kolwensis	Beetle	–	N. and E. Europe, China	1 (145)	–	–	–	–	–	Painter et al. (2007)
Rosalia alpina	*Rosalia* longhorn beetle	VU	Europe	1 (164)	–	8 (695)	–	–	–	Drag et al. (2015)
Diptera										
Blera fallax	Pine hoverfly	[b]	N. Europe	–	–	12 (72)	–	–	–	Rotheray et al. (2012b)

Southern Hemisphere										
Blattodea										
Mastotermes darwiniensis	Giant northern termite	–	N. Australia	–	–	6 (1591)	–	–	–	Goodisman and Crozier (2002)
Microhodotermes viator	Southern harvester termite	–	W. South Africa	–	–	7(369)	–	–	–	Muna and O'Ryan (2016)
Coleoptera										
Agyrtodes labralis[a]	Fungus beetle	–	S. New Zealand	1 (187)	–	–	–	–	–	Marske et al. (2009)
Adelium calosomoides	Beetle	–	SE. Australia	–	2 (963)	–	5 (963)	–	–	Schmuki et al. (2006b)
Apasis puncticeps	Beetle	–	SE. Australia	–	3 (678)	–	5 (678)	–	–	Schmuki et al. (2006b)
Brachynopus scutellaris[a]	Rove beetle	–	New Zealand	1 (113)	–	–	–	–	–	Leschen et al. (2008)
Epistranus lawsoni[a]	Fungus beetle	–	New Zealand	1 (168)	–	–	–	–	–	Marske et al. (2011)
Pristoderus bakewelli[a]	Fungus beetle	–	New Zealand	1 (88)	–	–	–	–	–	Marske et al. (2011)

Literature searches were conducted using functions in Scopus, an abstract and citation database for peer-reviewed literature. If several papers for a given species were identified, only the paper with most extensive geographic sampling was included in this survey. Conservation status is based on the International Union for Conservation of Nature (IUCN) Red List v.2017-1, with abbreviations of categories as follows: near threatened (NT), vulnerable (VU), or not assessed (–). Other abbreviations are mitochondrial DNA sequence (Mt. seq.), nuclear loci with insertion-deletion mutations (Indel), nuclear microsatellite loci (Microsat.), amplified fragment length polymorphism (AFLP) loci, and randomly amplified polymorphic DNA (RAPD) loci

Continent or country abbreviations are as follows: northern (N.), eastern (E.), southern (S.), western (W.), southeastern (SE.), and southwestern (SW.)

[a] Lives in and/or feeds on fruiting bodies of fungi associated with rotting wood

[b] Characterized as threatened or endangered by author(s)

have also been widely used in intraspecific studies (Table 25.1). These fast-evolving noncoding regions yield information on diploid genotypes of individuals, which are reshuffled each generation in sexually reproducing species (Sunnucks 2000; Garrick et al. 2010). Accordingly, microsatellites can be informative over short timescales and fine spatial scales. However, since microsatellite loci are usually screened using species-specific PCR primers, an initial labor-intensive development and validation phase is required (e.g., Vargo 2000; Goodisman et al. 2001; Aldrich and Kambhampati 2004; Dronnet et al. 2004 Runciman et al. 2006; Rotheray et al. 2012a; Drag et al. 2013a, b; Røed et al. 2014; Yaguchi et al. 2017).

Compared to mtDNA sequencing and nuclear microsatellite genotyping of saproxylic insects, allozyme (i.e., protein electrophoresis) assays have been less frequently used (Table 25.1). Although these markers provide information on diploid genotypes of individuals and have the benefit of being attainable for diverse insect taxa, allozyme loci typically exhibit low polymorphism and thus provide poor resolution. Also, technical issues such as the need for fresh tissue stored on ice limit the utility of these markers. Two other types of molecular data that have been applied in population-level studies of saproxylic insects are amplified fragment length polymorphism and randomly amplified polymorphic DNA loci. In both cases, numerous anonymous loci, presumably with a genome-wide distribution, are simultaneously amplified via PCR to provide individual-based DNA profiles. While these profiles can be analyzed on the basis of shared versus non-shared bands following separation by size on an electrophoretic gel, the inability to distinguish heterozygotes from homozygotes and the potential for the lack of homology among fragments of the same size can complicate interpretation (Sunnucks 2000). Finally, screening of nuclear insertion-deletion mutations has also occasionally been used (Table 25.1; also see Runciman et al. 2006; Schmuki et al. 2006a). As with microsatellites, these markers can be informative over fine spatial scales but also often require extensive development of and testing of PCR primers. High-throughput screening of single nucleotide polymorphisms—an emerging data type that makes use of next-generation sequencing platforms—has not yet been applied to saproxylic insect population genetics. However, Dillard (2017) successfully used single nucleotide polymorphisms for paternity analysis of the wood-feeding horned passalus beetle, *Odontotaenius disjunctus* (Illiger). Thus, issues relating to the lack of resolution may soon be overcome by new approaches.

25.3.2 Overview of Research Questions and Findings

Although the goals of intraspecific assessments of diversity in saproxylic insects have been broad, a number of recurring themes are apparent. For example, population-level studies of eusocial insects such as termites have often used genetic data to understand colony structure. Specifically, investigations have focused on demarcating colony boundaries, distinguishing between simple and extended family colonies (i.e., a single pair of unrelated alate-derived reproductives versus many full-sib neotenic reproductives), characterizing the relationship between geographic distance and relatedness, and partitioning of genetic variation across different spatial scales (e.g., individuals, colonies, forest regions; Goodisman and Crozier 2002; Aldrich and Kambhampati 2007; Booth et al. 2012; Perdereau et al. 2013; Bankhead-Dronnet et al. 2015; Muna and O'Ryan 2016). Conversely, population-level studies of threatened or endangered saproxylic insects have typically focused on quantifying levels of genetic diversity and estimating the effective number of breeding individuals within local populations. Conservation-oriented studies have also assessed evidence for inbreeding and/or past bottlenecks and determined the magnitude of gene flow limitation among populations—often in the context of habitat fragmentation or other potential dispersal barriers (Jonsson et al. 2003; Rotheray et al. 2012b; Oleksa et al. 2013, 2015; Røed et al. 2014; Drag and Cizek 2015; Drag et al. 2015). Additionally, researchers have used landscape genetic analyses to understand the permeability of different habitat types to dispersal of individuals (Schmuki et al. 2006b; Oleksa et al. 2015). Finally, some studies of saproxylic insects have focused on reconstructing historical events that generated high intraspecific genetic diversity, such as climatically driven lineage splitting followed by long-term isolation of populations in separate refuges (Painter et al. 2007; Leschen et al. 2008; Marske et al. 2009, 2011; Drag et al. 2015; Garrick et al. 2017).

Literature survey data (Table 25.2) showed that most population-level studies of saproxylic insects have been conducted over relatively large spatial scales (i.e., >200 km between the most distant sites). Considering that dispersal abilities of these organisms are often presumed to be very limited (e.g., Ranius and Hedin 2001), it is not surprising that marked genetic structure has repeatedly been detected. Interestingly, the manner in which the basic units used for analyses are defined seems to impact the number of different populations that are reported to exist within a given species. In general, compared to objective criteria that consider only natural genetic groups that are detected via clustering analyses, the use of more subjective criteria (e.g., number of collection sites) tends to result in more populations being recognized (Table 25.2). Whether this discrepancy represents insensitivity in the clustering analyses and/or upward bias in the investigator-reliant approach remains unclear. However, in the interest of promoting standardized methods that facilitate comparisons among studies, routine reporting of the number of natural genetic clusters would be beneficial.

Estimated levels of within-population diversity and between-population differentiation can be strongly impacted by genetic data type (Avise 2004). Our literature survey showed that studies that used allozyme loci and/or anonymous genetic markers such as amplified fragment length polymorphisms (Jonsson et al. 2003; Schmuki et al. 2006b; Oleksa et al. 2013, 2015; Oleksa 2014; Table 25.1) reported the lowest values of expected heterozygosity and the fixation index F_{ST}, respectively (Table 25.2). However, within genetic data type classes, comparisons across studies are possible, such that basic trends should be identifiable. For mtDNA sequence datasets, levels of within-population diversity were moderate to high, with values of haplotypic diversity (i.e., the probability that two randomly chosen sequences are

Table 25.2 Summary of spatial scale of sampling, population genetic structure, and levels of genetic diversity and differentiation, in population-level studies of saproxylic insects

Region/taxon	Sampling scale (km)	No. of different populations			Intrapopulation diversity		Inter-population differentiation		References
		Defined a priori	Defined a posteriori						
			Mt. seq.	Other data types	Mt. seq. (Hd)	Other data types (He)	Mt. seq. (F_{ST})	Other data types (F_{ST})	
Northern Hemisphere									
Blattodea									
Cryptocercus punctulatus	880	–	5	–	NR	–	NR	–	Garrick et al. (2017)
Reticulitermes flavipes	>1000	–	2	4 or 7	NR	Very high (0.71)	NR	NR	Perdereau et al. (2013)
Reticulitermes grassei	440	–	1	2 or 3	NR	NR	NR	Moderate (0.14)	Bankhead-Dronnet et al. (2015)
Zootermopsis angusticollis	150	–	–	3	–	Moderate (0.31)	–	Very high (0.43)	Booth et al. (2012)
Zootermopsis nevadensis	320	2[b]	–	–	–	High (0.44)	–	NR	Aldrich and Kambhampati (2007)
Coleoptera									
Bolitophagus cornutus[a]	5	2	–	–	–	–	–	–	Whitlock (1992)
Bolitophagus reticulatus[a]	>1000	10	–	–	–	Very low (0.08)	–	Very low (0.04)	Jonsson et al. (2003)
Cerambyx cerdo	175	–	1	2	Moderate (0.37)	Very high (0.57)	Low (0.08)	Low (0.06)	Drag and Cizek (2015)
Cucujus cinnaberinus	>1000	2	–	–	–	High (0.48)	–	NR	Røed et al. (2014)
Diaperis boleti[a]	230	15	–	–	–	Moderate (0.35)	–	Very low (0.03)	Oleksa (2014)

Elater ferrugineus	18	10	–	–	–	Moderate (0.29)	–	Low (0.07)	Oleksa et al. (2015)
Oplocephala haemorrhoidalis[a]	>1000	6	–	–	–	Very low (0.07)	–	Moderate (0.12–0.27)	Jonsson et al. (2003)
Osmoderma barnabita	200	7	–	–	–	Low (0.21)	–	Moderate (0.11)	Oleksa et al. (2013)
Protaetia marmorata	200	11	–	–	–	Moderate (0.29)	–	Very low (0.03)	Oleksa et al. (2013)
Pytho abieticola	>1000	–	2	–	Very high (0.92)	–	High (0.61)	–	Painter et al. (2007)
Pytho depressus	>1000	–	2	–	Very high (0.92)	–	Moderate (0.42)	–	Painter et al. (2007)
Pytho kolwensis	>1000	–	2	–	High (0.58)	–	Moderate (0.49)	–	Painter et al. (2007)
Rosalia alpina	>1000	–	1 or 2	2	Moderate (0.38)	High (0.45)	Low (0.12)	Moderate (0.12)	Drag et al. (2015)
Diptera									
Blera fallax	>1000	–	–	2	–	Moderate (0.4)	–	(Moderate (0.13)	Rotheray et al. (2012b)
Southern Hemisphere									
Blattodea									
Mastotermes darwiniensis	>1000	20	–	–	–	NR	–	NR	Goodisman and Crozier (2002)
Microhodotermes viator	80	4	–	–	–	Moderate (0.42)	–	Moderate (0.20)	Muna and O'Ryan (2016)
Coleoptera									
Agyrtodes labralis[a]	780	–	6 or 7	–	NR	–	NR		Marske et al. (2009)

(continued)

Table 25.2 (continued)

		No. of different populations							
			Defined a posteriori		Intrapopulation diversity		Inter-population differentiation		
Region/taxon	Sampling scale (km)	Defined a priori	Mt. seq.	Other data types	Mt. seq. (Hd)	Other data types (He)	Mt. seq. (F_{ST})	Other data types (F_{ST})	References
Adelium calosomoides	10	NR	–	–	–	NR	–	NR	Schmuki et al. (2006b)
Apasis puncticeps	10	NR	–	–	–	NR	–	NR	Schmuki et al. (2006b)
Brachynopus scutellaris[a]	730	–	4	–	NR	–	NR	–	Leschen et al. (2008)
Epistranus lawsoni[a]	>1000	–	4	–	NR	–	NR	–	Marske et al. (2011)
Pristoderus bakewelli[a]	>1000	–	6	–	NR	–	NR	–	Marske et al. (2011)

The literature search and papers cited follows Table 25.1. Sampling scale is the maximum distance between a pair collection sites. Populations identified a priori are those that were defined by collection sites alone (or via other subjective grouping schemes). Conversely, populations identified a posteriori each form natural groups within the empirical genetic datasets (e.g., clades on a phylogenetic tree or panmictic genotypic clusters). Inferences based on mtDNA sequences (Mt. seq.) are distinguished from those based on any of the other genetic data types listed in Table 25.1. Standardized measures of intrapopulation diversity are haplotypic diversity (Hd; the probability that two randomly chosen sequences are different) and expected heterozygosity (He; the proportion of individuals that will be heterozygous at a locus assuming Hardy-Weinberg equilibrium); if these were calculated from multiple populations and loci, the mean value is reported. Across surveyed studies, the most commonly used metric of inter-population differentiation was F_{ST} (a measure of allele frequency differences). "NR" indicates data were not reported

[a] Lives in and/or feeds on fruiting bodies of fungi associated with rotting wood

[b] Classified as different subspecies

different) ranging from 0.37 to 0.92 when averaged across each population in a given study. Surprisingly, however, mtDNA-based population differentiation was generally moderate to low. Microsatellite data also tended to show moderate to very high diversity within populations, but unlike mtDNA, population differentiation was seldom low (Table 25.2). This may reflect inherent differences in the spatial scale of resolution among marker types. Although only two studies in our survey employed both mtDNA and microsatellite data and reported the standard diversity statistics that we tracked (i.e., Drag and Cizek 2015; Drag et al. 2015; Table 25.1), both showed reasonable consistency between data types in terms of inferences about levels of diversity and differentiation (Table 25.2).

25.4 Genus-Level Diversity and Integrative Taxonomy

25.4.1 Genetic Data Types

Genus-level studies of saproxylic insects have mostly used mtDNA sequence data, but the gene region(s) targeted varies by taxonomic group. Generally speaking, whereas termite studies have tended to focus on the 16S ribosomal RNA gene, beetle studies have almost exclusively used the COI gene (Table 25.3). Notably, for some beetle groups, nuclear DNA regions have been sequenced in conjunction with mtDNA. In these cases, protein-coding regions (e.g., *wingless*) or non-coding regions (e.g., internal transcribed spacer) have been used (Table 25.3). In most cases, however, authors have reported that nuclear DNA sequence datasets were less informative than corresponding mtDNA datasets, owing to fewer variable nucleotide positions in multi-sequence alignment. In addition to direct sequencing, some genus-level studies have evaluated the utility of cost- and time-efficient assays for screening known DNA sequence variants. These approaches have included restriction fragment length polymorphism (RFLP) assays, as well as modifications of PCR primers so that successful amplification occurs only for a given species (e.g., species-specific and multiplex PCR methods; Table 25.3).

25.4.2 Overview of Research Questions and Findings

Goals of genus-level applications of molecular data to saproxylic insects fall into three major categories: phylogenetic relationships across the tree of life, rapid species identification, and reassessment of existing taxonomy (Timmermans et al. 2010). Mitochondrial DNA barcode sequences have been effective for reconstructing some phylogenetic relationships (Timmermans and Vogler 2012). However, COI is not a universally appropriate gene for estimating relationships for every taxon. For example, rapid radiations present a challenge because incomplete lineage sorting is prevalent, whereas high levels of homoplasy (i.e., repeated

Table 25.3 Summary of molecular approaches, taxon sampling, and goals/findings of genus-level studies of saproxylic insects

Region/taxon	Common name	Continent or country	Molecular assay	Gene region(s)	No. of focal taxa	Goal	Major conclusion	References
Blattodea								
Cryptocercus spp.	Wood roaches	USA	Sequencing	mtDNA 12S and 16S rRNA	1	Assess taxonomy	At least two spp. in the USA (one new)	Kambhampati et al. (1996)
		E. USA	Sequencing	mtDNA 12S and 16S rRNA	1	Assess taxonomy	Four spp. in E. USA (three newly named)	Burnside et al. (1999)
Reticulitermes spp.	Subterranean termites	S. USA	Sequencing	mtDNA COII	3	Spp. identification	At least one cryptic sp. likely to exist	Jenkins et al. (2000)
		C. USA	Sequencing	mtDNA 16S rRNA	4	Spp. distributions	Spp. patchily distributed in Texas	Austin et al. (2004)
		S. and C. USA	Sequencing	mtDNA D-loop	3	Spp. identification	Assay accurate for at least one sp.	Foster et al. (2004)
		Americas and Europe	Sequencing	mtDNA 16S rRNA	2	Assess taxonomy	Two named spp. synonymized	Austin et al. (2005)
		W. USA	Sequencing	mtDNA COII	2	Assess taxonomy	Several cryptic spp. likely to exist	Copren et al. (2005)
		C. USA	Sequencing	mtDNA 16S rRNA	4	Spp. distributions	Known range extended for one sp.	Austin et al. (2006)
		E. USA	Sequencing	mtDNA 16S rRNA	6	Assess taxonomy	Recently described sp. validated	Austin et al. (2007)
		E. USA	Sequencing	mtDNA 16S rRNA	3	Spp. identification	Assay accurate for at least two spp.	King et al. (2007)
		E. USA	Sequencing	mtDNA COI and COII	5	Assess taxonomy	1 new sp. described and named	Lim and Forschler (2012)
		E. USA	PCR-RFLP	mtDNA COII	5	Spp. identification	Assay is efficient and accurate	Garrick et al. (2015)

Coptotermes spp.	Subterranean termites	Global	Sp.-specific PCR	mtDNA 16S rRNA	12	Spp. identification	Assay is efficient and accurate	Szalanski et al. (2004)
		Global	Multiplex PCR	mtDNA 16S rRNA	8[a]	Spp. identification	Assay is efficient and accurate	Janowiecki and Szalanski (2015)
		Americas	Sequencing	mtDNA 16S rRNA	6	Assess taxonomy	Three named spp. synonymized	Scheffrahn et al. (2015)
Coleoptera								
Glischrochilus spp.	Sap beetles	N. Europe	Sequencing	mtDNA COI	3	Assess taxonomy	One new sp. described and named	Clayhills et al. (2016)
Lucanus spp.	Giant stag beetles	Europe and Asia	Sequencing	mtDNA COI and nDNA Wg	16	Assess taxonomy	Sp.-level rank valid for threatened sp.	Lin et al. (2011)
		Europe and Asia	Sequencing	mtDNA COI	6	Spp. identification	Assay has mixed success	Cox et al. (2013)
		Italy	Sequencing	mtDNA COI and nDNA Wg	2	Spp. identification	COI assay has fairly good success	Solano et al. (2016)
Osmoderma spp.	European hermit beetles	Europe	Sequencing	mtDNA COI	5	Assess taxonomy	Sp.-level rank valid for named taxa	Audisio et al. (2009)
		N. and E. Europe	Sequencing	mtDNA COI	2	Spp. identification	Confirmed specimen assignments	Svensson et al. (2009)
		N. Europe	Sequencing	mtDNA COI	5	Spp. identification	Finland samples assigned to sp.	Landvik et al. (2013)
		Italy	Sequencing	mtDNA COI	2	Assess taxonomy	Sp.-level rank valid for named taxa	Zauli et al. (2016)
Morimus spp.	Longhorn beetles	Europe and Asia	Sequencing	mtDNA COI and nDNA ITS	5	Assess taxonomy	Five named spp. probably synonyms	Solano et al. (2013)

The literature search excluded strictly phylogenetic studies (i.e., those focused on resolving relationships among named species and estimating divergence dates). Note that this table only presents data from representative exemplars, as that some groups (e.g., pest species such as termites) have been extensively studied using molecular data for decades. Abbreviations are as follows: polymerase chain reaction (PCR); mitochondrial DNA (mtDNA); ribosomal RNA (rRNA); nuclear DNA (nDNA); and species (sp. = singular, spp. = plural)

Continent or country abbreviations are as follows: northern (N.), eastern (E.), southern (S.), western (W.), and central (C.)

[a] Relates to congeneric taxa only

mutations at same site, leading to saturation) become problematic for deeper-level relationships. Accordingly, for research focused on resolving phylogenetic relationships at the genus-level or higher and estimating divergence times among lineages, multiple independent loci are often needed.

The published research associated with rapid species identification can be divided into molecular toolset development versus application, where the latter includes investigations that seek to better understand species' geographic distributions (Table 25.3). Interestingly, whereas assays such as PCR-RFLP, species-specific PCR, and multiplex PCR have shown high accuracy, direct sequencing has had mixed success (Table 25.3). However, rather than indicating weaknesses of the latter data type, this probably reflects differences in suitability of the chosen DNA region or taxonomic complexity of the group at hand. Indeed, whereas PCR-RFLP, species-specific PCR, and multiplex PCR are limited by the fact that as-yet unknown variants can complicate interpretation and/or reduce accuracy, direct sequencing coupled with phylogenetic analyses is well-suited to handling newly discovered genetic variants. Indeed, for saproxylic beetles in particular, COI barcodes have shown low rates of species misidentification (Hendrich et al. 2015; Jordal and Kambestad 2014; Pentinsaari et al. 2014; Rougerie et al. 2015a).

In the context of taxonomic reassessments, molecular data have provided several valuable insights. For example, they have clarified situations where two or more named species were suspected to be synonyms (e.g., *Reticulitermes flavipes* (Kollar) and *R. santonensis* Feytaud termites; Table 25.3). Similarly, DNA sequence data also suggested that two European longhorn beetle species, *Anastrangalia dubia* (Scopoli) and *A. reyi* (Heyden), are probably synonyms (Hendrich et al. 2015; Rougerie et al. 2015a). However, among German beetles, almost 3% of specimens DNA barcoded by Hendrich et al. (2015) have low interspecific distances, yet they do not appear to reflect cases of synonymy. Other explanations for such patterns can include introgression through past or ongoing hybridization or recent divergence. Indeed, Jordal and Kambestad (2014) attributed inconsistencies between mtDNA barcodes and morphology-based identification of bark beetles to past hybridization between *Pityophthorus micrographus* L. and *P. pityographus* Ratzeburg. Furthermore, in a study of western Palaearctic stag beetles (Cox et al. 2013), COI could discriminate several named *Lucanus* species and *L. cervus* L. subspecies, but not all could discriminated. Here, haplotype sharing among taxa was suspected to be due to recurrent hybridization events or incomplete lineage sorting. Where mtDNA barcodes and existing taxonomy are discordant, large numbers of individuals from each putative group are usually needed to identify the underlying causes, yet this requirement can be a limiting factor when working with rare or difficult to sample organisms such as saproxylic insects.

In contrast to low interspecific divergences, in some studies, a single named taxon has been shown to exhibit very high levels of genetic diversity (e.g., *Cryptocercus punctulatus* Scudder wood roaches and *Osmoderma eremita* (Scopoli) hermit beetles), leading to the formal description and naming of new species (Table 25.3). Despite a long history of intensive taxonomic research, Pentinsaari et al. (2014) and Hendrich et al. (2015) reported that almost 6% of the North European beetle species and 7% of the Bavarian beetle species, respectively, contained two or more distinct barcode clusters. Even among the well-known bark beetle species, Jordal and Kambestad (2014) detected the occurrence of a cryptic species of *Dryocoetes*, on the basis of inconsistencies between mtDNA barcodes and morphological identifications. Similarly, Pentinsaari et al. (2014) used geometric morphometrics in combination with host plant characters to propose the existence of two species of beetles nested within one named taxon, *Agrilus viridis* L. However, here the findings based on mtDNA barcodes were more complex, owing to suspected past hybridization events.

Outcomes of taxonomic reassessments of saproxylic insects can have important legislative ramifications, such as when the species-level status of a threatened or endangered species is brought into question (Lin et al. 2009). That said, explicit statements about which species concept is being applied, and criteria used to assess whether empirical data support species-level designation, are critical elements of such studies. At present, the most popular approach involves the use of sequence divergence threshold values (Meier et al. 2006). However, evidence for the existence of a "barcoding gap" (i.e., substantially higher sequence divergence among species cf. within species) should be considered in the context of sampling density, given that diagnosability of related species may diminish as additional specimens are added to the sequence dataset. Also, while DNA taxonomy may be seen as a practice of its own, some researchers suggest that its most valuable role lies in providing systematists a first approximation to delimit taxa and rapidly assess species number (Janzen et al. 2009; Lamarre et al. 2016). Barcoding may also be used as an exploratory tool, revealing cases needing further investigation. Fortunately, analytical developments are facilitating the use of DNA sequence data in species delimitation (e.g., Yang and Rannala 2010; Ence and Carstens 2011). Although the newer approaches are not without caveats (Carstens et al. 2013; Sukumaran and Knowles 2017), these data-driven assessments provide working hypotheses for focused follow-up work. Given that the genes used in molecular taxonomy may not be functionally correlated with speciation, integrative taxonomy should embrace all available evidence (e.g., adult and larval morphology including color and pattern where relevant, molecular data, behavioral characters including mating displays and/or phenology, as well as ecology; Will et al. 2005; Astrin et al. 2012).

25.5 Community-Level Diversity

25.5.1 Genetic Data Types

DNA barcoding is commonly used to characterize metazoan biodiversity and has been successfully used to assess biodiversity (Gibson et al. 2014), bypassing shortfalls of other molecular diagnostic methods (Armstrong and Ball 2005). This approach proposes to use information within a single-standard short-gene region common across all taxa and to access that information by DNA sequencing across species and laboratories (Hebert et al. 2003). It relies on the assumption that sequences in a ~650-bp fragment of COI are more similar among members of the same species than to sequences of any other species. There is a growing literature demonstrating that COI reliably discriminates species-level differences for a diverse set of animals. However, increasing the spatial scale of sampling often reduces its success (Bergsten et al. 2012), and the rate of success of barcoding also varies across insect orders (e.g., Meier et al. 2006; Pentinsaari et al. 2014). Furthermore, the reliability of a COI barcode as species identifier has been debated, given cases of high intraspecific diversity (Moritz and Cicero 2004). Consequently, additional DNA markers are sometimes used to complement COI (e.g., mtDNA 16S ribosomal RNA gene or nuclear DNA loci; Astrin et al. 2012; Dupuis et al. 2012).

25.5.2 Overview of Research Questions and Findings

The new era of DNA data has cascading effects on saproxylic community biology. For example, from a taxonomic diversity perspective, these data provide tools to help with delineating species entities and with developing efficient mass sample identification strategies, whereas from a functional perspective, they shed light on trophic relationships and interaction networks among species. In addition, from a phylogenetic perspective, DNA data allow for computation of distances among species, as well as diversity indices based on tree topology.

The success of a DNA-based species identification system depends on the completeness and the consistency of a barcode reference library (Cristescu 2014). Comprehensive libraries for several focal saproxylic insect groups (e.g., Coleoptera, Isoptera, and Diptera) need to be developed to permit and streamline reliable identification of species. These barcode libraries are being built in collaboration with expert taxonomists using well-curated natural history collections. Data processing pipelines have recently been developed to detect inconsistencies in large DNA barcode datasets, before submitting them to public data repositories like the Barcode of Life Data System (BOLD) or GenBank (Rulik et al. 2017). The sequencing success from collection material identified down to the species-level in some groups (e.g., beetles) is lower than others. Nevertheless, the current developments offer new opportunities to increase throughput, reduce cost, and improve the success rate of sequencing when DNA is limited in quantity or degraded, as is the case for very small invertebrates or when working with material preserved for several years. Although the application of high-throughput sequencing to generate individual-based DNA barcodes was initially limited by short sequence reads as well as the cost and operability of tagging a large number of specimens, these restrictions are now being overcome (Shokralla et al. 2015). Accordingly, the transfer of DNA barcode library construction from routine Sanger sequencing toward the use of this newer technology is becoming feasible.

For saproxylic beetles, DNA barcodes can distinguish species remarkably well (Pentinsaari et al. 2014; Hendrich et al. 2015; Rougerie et al. 2015a). Large numbers of European saproxylic beetle species have already been barcoded and are publicly available in BOLD as part of national barcoding campaigns carried out in Europe (Hausmann et al. 2013; Huemer et al. 2014; Pentinsaari et al. 2014; Hendrich et al. 2015; Rougerie et al. 2015a). For example, Pentinsaari et al. (2014) performed a comprehensive test of the effectiveness of DNA barcodes as a tool for Scandinavian beetle identification by sequencing the COI region from 1872 species. A high proportion (98.3%) of these species possessed distinctive barcodes, and furthermore, the Barcode Index Number system in BOLD coincided strongly (in 92.1% of all cases) with known species boundaries. Similarly, Jordal and Kambestad (2014) also demonstrated strong congruence between morphology-based identification and sequence clusters for 151 species in 40 genera of bark and ambrosia beetles. Lower identification success rates have been reported for non-exclusively saproxylic insect groups (e.g., Diptera, Meier et al. 2006). In these cases, mismatches were due to considerable overlap between intra- and interspecific genetic divergence. In beetle studies, the few cases of barcode identification failures involved closely related species that are often difficult to identify by morphological characters, and whose species status is controversial, as indicated by high intraspecific genetic variability, low between-species genetic distances, and evidence for introgression/hybridization at contact zones. Even though COI is a highly discriminant marker for many beetles, Jordal and Kambestad (2014) noted that the occurrence of nuclear mitochondrial pseudogenes (NUMTs), detected in 8 out of 151 bark beetle species, demands a stronger focus on data quality assessment in the construction of DNA barcoding databases. NUMTs are indeed a major pitfall in the few cases where they have been prevalent among sequences produced by standard protocols (Haran et al. 2015). That said, close examination of sequence characteristics can reduce error considerably (Song et al. 2008), and high-throughput sequencing should make it easier to detect NUMTs.

25.5.2.1 Metabarcoding

Using Sanger sequencing of single specimens in ecological studies with hundreds of thousands of specimens to be processed is prohibitively costly and time-consuming (Shokralla et al. 2015). Accordingly, the advent of affordable high-throughput sequencing technologies is revolutionizing the field of biomonitoring (Shokralla et al. 2012; Taberlet et al. 2012a). Metabarcoding is a technique that involves high-throughput sequencing from a bulk mixture of DNA from all sampled specimens (Taberlet et al. 2012a; Yu et al. 2012). This approach is much faster and yet can still be as reliable as biodiversity datasets assembled with Sanger sequencing (Ji et al. 2013). Metabarcoding has been used for assessing the diversity in bulk samples of soil animals such as earthworms (Bienert et al. 2012; Pansu et al. 2015), terrestrial arthropods (Yu et al. 2012; Ji et al. 2013; Zhou et al. 2013; Yang et al. 2014), and associated microbiota (Gibson et al. 2014). This technique has also been used in ecological studies to estimate alpha and beta diversity (Yu et al. 2012; Yang et al. 2014). The underlying technology is advancing quickly, with improved efficiency and resolution (Deagle et al. 2014; Schnell et al. 2015). However, despite the great potential of metabarcoding, few studies have applied this technique for ecological assessment (Aylagas et al. 2014; Pawlowski et al. 2014).

To date, most studies that have applied high-throughput sequencing of DNA recovered from deadwood focus on bacteria (Hoppe et al. 2015) or fungi. In some of the latter cases, assessment of fungal species richness and composition has been based on direct molecular detection of in situ mycelia, often from sawdust and shavings obtained by drilling logs through sapwood and heartwood (Cuadros-Orellana et al. 2013). These recent bacterial and fungal studies were mainly conducted in Palaearctic boreal and temperate forests (Ovaskainen et al. 2010; Rajala et al. 2011, 2012; Kubartova et al. 2012; Ovaskainen et al. 2013; Jang et al. 2015; Ottosson et al. 2015; Runnel et al. 2015; Van der Wal et al. 2015; Yamashita et al. 2015; Baldrian et al. 2016; Hoppe et al. 2016) or, more rarely, in neotropical forests (Purahong et al. 2017; Vaz et al. 2017). Except for Rougerie et al. (2015b), no other metabarcoding study has addressed the sampling of saproxylic insect communities, but some focused on other insect guilds such as belowground arthropods (Cicconardi et al. 2017), grassland/forest-edge arthropods (Morinière et al. 2016), flying insects (Yu et al. 2012), and bees (Tang et al. 2015). Now that metabarcoding of "biodiversity soups" of insect DNA is becoming reliable (Rougerie et al. 2015b), there is considerable scope for advances in understanding the diversity and composition of saproxylic insect communities and, by extension, for identifying environmental predictors of this diversity (e.g., Lindenmayer et al. 2000; Grove 2002b; Woodman et al. 2006).

Using mtDNA metabarcoding, three alternative workflows could be applied to saproxylic insect samples. Workflow 1 involves extraction of pooled insect DNA directly from the preservative solution (Fig. 25.1). For example, it has been demonstrated by Shokralla et al. (2010) and Hajibabaei et al. (2012) that ethanol, commonly used as a preservative medium for trapping and/or storing specimens, contains DNA from stored organisms that can be directly used for downstream amplification and sequencing. Hajibabaei et al. (2012) reported that using "free DNA" from ethanol preservative was effective in providing sequence information for 87% of taxa identified individually from mixture, as compared to 89% in conventional tissue-based DNA extraction methods. Missing taxa were from species with the lowest abundance (e.g., one individual) in the species mixture. This approach does not require the mashing and mixing of all organisms to form homogenized slurry, and consequently does not result in destruction of individual specimens, thereby rendering subsequent morphological analyses possible. The effectiveness of community ethanol-based DNA nonetheless seems to decrease when preservative liquid has been changed in time (Rougerie et al. unpubl. data). In contrast, workflow 2 involves individual-based DNA extraction from voucher specimens and is therefore more time-consuming yet can retain information that ties a particular specimen to a specific mtDNA sequence (Fig. 25.1). Workflow 3 also involves a time-consuming presorting step but streamlines DNA extraction into a single bulk sample; this approach can yield approximately 30% more high score

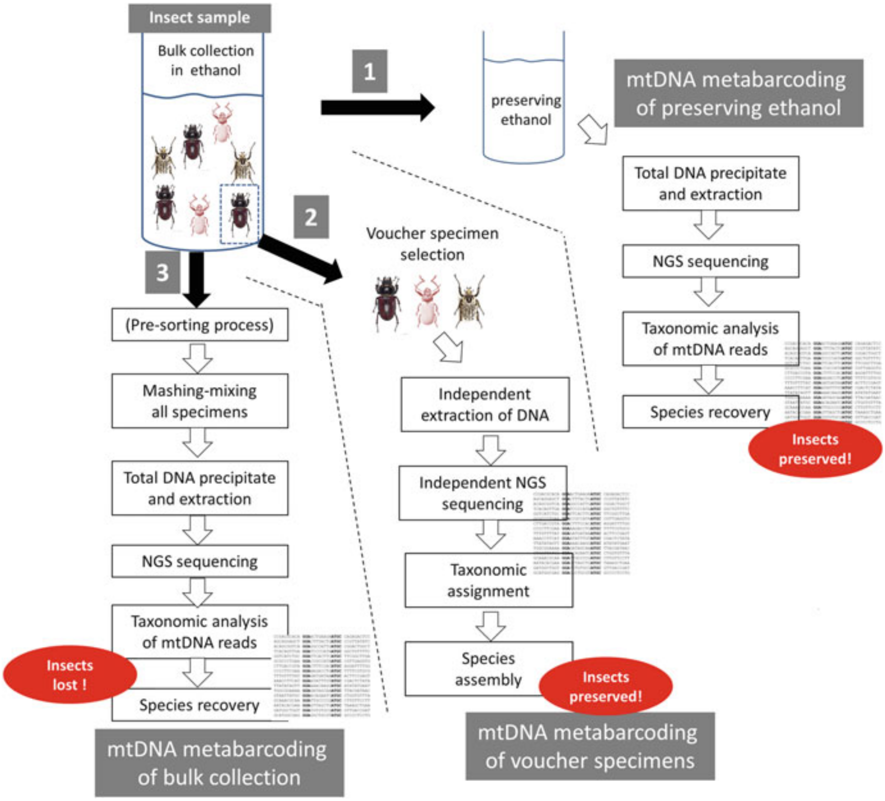

Fig. 25.1 Three alternative workflows for mitochondrial DNA metabarcoding using next-generation sequencing (NGS), each of which could be applied to saproxylic insect bulk collections. Workflows 1 and 2 preserve insect specimens, thereby rendering subsequent morphological study possible, whereas workflow does not

barcode index numbers compared to a non-sorted sample (Morinière et al. 2016; Fig. 25.1).

Once DNA has been extracted, PCRs are usually performed in several replicates and at different annealing temperatures to diminish amplification bias, and products are pooled before sequencing to correct for within-sample variation (Zhan et al. 2014) and to avoid spurious overestimation of operational taxonomic unit (OTU) diversity. The use of Illumina MiSeq or HiSeq sequencing platforms ensures that sufficient read depth is obtained for the detection of rare species in the samples. For each sample, the DNA is tagged with specific sequence identifiers, to ensure the traceability of the OTUs and species identification from the sequences back to the collecting event (or individual specimens, depending on the workflow used; see Fig. 25.1). The development of bioinformatics pipelines to determine OTUs from high-throughput sequence data is a rapidly advancing field, and existing tools are becoming more efficient (Yu et al. 2012). Most pipelines involve removal adaptor sequences and low-quality reads, followed by the assembly of high-quality sequences, and then the assignment of sequences to different OTUs based on overall sequence similarity. However, OTU delimitation can differ among taxa (Fontaneto et al. 2015). Several clustering methods (Zhang et al. 2013) exist to infer the taxa present in the samples in an effort to unify the definition of OTUs and streamline analyses. The RESL approach in BOLD (Ratnasingham and Hebert 2013) has been effective in objectively delimiting the OTUs and assigning a species name through sequence matching to barcode index numbers in saproxylic beetles (Pentinsaari et al. 2014; Rougerie et al. 2015a).

25.5.2.2 Community Diversity and Structure

Pipelines that use high-throughput DNA sequencing generate molecular operational taxonomic units (MOTUs), based on pairwise distance and a user-defined sequence divergence cutoff. MOTU-based metrics are useful species surrogates to describe community richness. From these data, information on evolutionary relationships among MOTUs is easily attainable. The value of phylogenetically based measures of biodiversity has been advocated for some time, but a wider appreciation of their broad utility, including in high-profile study systems, has occurred only recently (e.g., King 2009; Morlon et al. 2011; Frishkoff et al. 2014). Indeed, phylogenetically derived biodiversity metrics are useful for assessing ecosystem functioning (Paquette et al. 2015). One such metric, phylogenetic diversity, quantifies the amount of shared evolutionary history (total branch lengths) among lineages that occur within a location, the context of a tree estimated from all lineages that were sampled across all locations (Faith 1992, 2002). Another metric, phylogenetic endemism, measures the spatial restriction of phylogenetic diversity (Rosauer et al. 2009). Together, these can be viewed as phylogenetic analogs of species richness and turnover, respectively.

In addition to providing opportunities for unbiased measures of local biodiversity in saproxylic arthropods, DNA sequence data may also enable taxonomic assignment of specimens to named species using reference DNA barcode libraries. In such cases, metabarcoding provides accurate measurements of species richness from bulk and environmental samples at an affordable cost. However, one of the limitations relates to the occurrence of natural DNA contaminants, such as sequences derived from prey in gut predatory insects. Another limitation of assessing diversity using metabarcoding is that PCR amplification may cause strong biases, thereby preventing the use of read numbers to estimate the relative abundances of different taxa, and so the technique produces occurrence data only. Recent studies have proposed targeting whole mitochondrial genomes instead of a single or few DNA fragments, and to use shotgun sequencing of bulk or environmental samples, thus bypassing PCR amplifications and inherent biases (i.e., amplification stochasticity, taxon biases, loss of quantitative data; Zhou et al. 2013; Andújar et al. 2015; Gomez-Rodriguez et al. 2015; Tang et al. 2015). This approach would ideally be used in conjunction with the assembly of reference mitogenome libraries for the focal groups. So far, results of this PCR-free mitogenomic approach have been encouraging for bulk samples with relatively few species and individuals (Andújar et al. 2015; Gómez-Rodríguez et al. 2015).

Measures of changes in functional community structure and food webs require species-level identifications to allow linking species counts to pre-existing databases of functional traits (except in the case of work on intraspecific trait variability; Violle et al. 2012). Whereas the roles of abiotic factors in shaping local forest communities have been well studied, the role of species interactions has received little attention. Most current biomonitoring programs ignore the complex ecological networks of species interactions, which are crucial to take into account if we want to understand the ecological responses of communities to environmental stressors (Gray et al. 2014). Taking tree-insect-parasitoid ecological networks as an illustration, Evans et al. (2016) argued that combining DNA metabarcoding approaches with ecological network analysis presents important new opportunities for understanding large-scale ecological processes. PCR-based molecular gut content analyses may be used to characterize predator-prey or host-parasitoid interactions. Only one PCR-based molecular gut content analysis is known for communities of saproxylic insects (Schoeller et al. 2012), but several studies exist for communities of other insect groups (e.g., Foltan et al. 2005; Eitzinger et al. 2013; Paula et al. 2016). Using gut DNA content screening, Schoeller et al. (2012) characterized interactions between field-collected *Monochamus titillator* (F.) and other wood borers and demonstrated facultative intra-guild predation. Moreover, employing DNA barcoding to identify their morphologically indistinct immature life stages illustrated the power of molecular data to complement and enhance the morphological approach to insect diagnoses. Given the importance of larvae in saproxylic food webs, molecular identification could improve our understanding of saproxylic networks.

25.5.2.3 Molecular Insect Monitoring

There is an increasing need for real-time, large-scale biomonitoring with immediate feedback into management frameworks. The current monitoring programs of forest biodiversity are taxonomically constrained and ill equipped to cover large geographic scales. Traditional biomonitoring schemes are too labor intensive and costly to handle large numbers of specimens, given that they involve examining each individual separately (Lebuhn et al. 2013). In addition, biomonitoring is often biased toward certain taxa, avoiding groups for which taxonomic expertise is unavailable. Invertebrates are rarely used as study groups despite their ecological importance because of their hyperdiversity and the taxonomic impediment (Ebach et al. 2011). Furthermore, traditional biomonitoring schemes often use morphospecies as surrogate of species, thus underestimating actual species numbers, especially in the richest taxa that require careful examination in the laboratory (Derraik et al. 2002). These studies are also unable to account for immature stages in most groups. The combination of emerging genomic technologies and bioinformatics in DNA metabarcoding is strengthening our capacity to process many samples collected at a large scale for long-term ecological studies that measure the impact of global change on biodiversity. Numerous tools already exist varying in complexity, accuracy, and costs, for biomonitoring marine (e.g., Aylagas et al. 2014) and freshwater ecosystems (Woodward et al. 2013). Biomonitoring pipelines that streamline the identifications of large numbers of specimens and provide accurate, rapid, and cost-efficient measurements of saproxylic insect diversity are needed. Also, few metabarcoding studies to date have focused on groups for which a library was available beforehand. Approaches that can go beyond assigning sequences to MOTUs followed by examination of alpha and beta diversity will bring much more insight into ecological questions. These perspectives strengthen the importance of developing reliable reference databases for species identification.

DNA barcoding allows the rapid and accurate identification of alien and pest species, including morphologically indistinct taxa. It is now widely employed in contexts ranging from monitoring pests (Ashfaq et al. 2016) to supporting the detection of invasive species (Armstrong and Ball 2005). In China for instance, DNA identification of *Xyleborus* species (i.e., ambrosia beetles associated with solid wood-packing materials and very commonly intercepted at ports) has been successfully developed to monitor and prevent invasion (Chang et al. 2014).

High-throughput sequencing allows the detection of an organism following secondary transfer of its DNA to environmental samples. Metagenomic techniques are already in place for preparation of environmental DNA from soil or water (Lodge et al. 2012; Yoccoz et al. 2012; Schmidt et al. 2013; Bohmann et al. 2014). A specifically designed workflow could be developed to treat large volumes of substrate and enable detection of insect larvae in deadwood or in tree-related microhabitats (e.g., wood mold in tree cavities, lignicolous fungus sporocarp). These techniques have already been used to detect deadwood-associated fungi (e.g., Cuadros-Orellana et al. 2013). Several studies have shown promising results for invertebrate species identification from frass (Sint et al. 2015). The analysis of wood samples has the potential to revolutionize forest biomonitoring by allowing foresters to obtain accurate measures of biodiversity, including insects, from dead branches without complex and expensive sampling procedures. The processing of a large volume of substrate and its physical structure may however prove challenging for DNA extraction, although recent results on large volumes of soil (Taberlet et al. 2012b) are encouraging. Crucial steps for wood samples would be the homogenization of large volume of substrate in a grinding mill, and protocol optimization of DNA extraction from wood as secondary compounds, such as terpenoids, might inhibit subsequent PCR amplifications.

25.6 Emerging Directions

Many of the same research questions and molecular approaches highlighted above have been applied to other groups of saproxylic invertebrates [e.g., velvet worms (Sunnucks and Wilson 1999; Trewick 2000; Oliveira et al. 2011; McDonald and

Daniels 2012), terrestrial flatworms and springtails (Alvarez-Presas et al. 2011; Garrick et al. 2012 and references therein), land snails (Hugall et al. 2002), pseudoscorpions (Ranius and Douwes 2002), spiders (Beavis et al. 2011), and millipedes (Walker et al. 2009)]. Accordingly, trends seen in insects may be representative of a broader array of studies that have attempted to understand distributions of diversity in this functionally important ecological community. Indeed, given the taxonomic and geographic breadth of studies published over the past two decades, a broad synthesis of insights from genetics for conservation of saproxylic invertebrates as a whole should now be possible. It is also noteworthy that genomic and transcriptomic tools are increasingly being applied to saproxylic invertebrates [e.g., velvet worms (Roeding et al. 2007), termites (Cameron and Whiting 2007; Zhou et al. 2008; Tartar et al. 2009), wood roaches (Hayashi et al. 2017), and springtails (Wu et al. 2017)]. These genome-wide molecular datasets, coupled with comparative and/or functional analyses, are now enabling previously intractable questions to be addressed.

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Index

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