Chapter 10
Bark Beetles

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10.1 Introduction

In general, the term "bark beetle" most commonly applies to the weevil (Curculionidae) subfamily Scolytinae (Fig. 10.1). The Scolytinae also includes ambrosia beetles that feed on symbiotic fungi and these are addressed in Chapter 11. The lifecycle of these small (0.05–10 mm) snoutless weevils occurs almost exclusively in the interior of plant tissues. As adults and larvae, bark beetles feed on plant tissues including twigs, branches, trunks and roots, xylem, piths, fruits, and cones. Adults bore into the plant tissue and create a chamber to mate, lay eggs and for larvae to grow, pupate, and eclose as adults. Most often this plant tissue is dead or dying and bark beetles serve as primary decomposers (Stokland et al. 2012), and create pathways into the wood for other decomposers.

A minority of bark beetles kill healthy trees, although at the time of attack, these healthy trees are often experiencing stressful conditions (e.g. due to drought or lightning strikes). Populations of tree-killing bark beetles can increase in size to a level where they can overcome the resistance of healthy trees and cause mass destruction of forests resulting in tremendous economic and ecological damage. It is these few species that give bark beetles their nefarious reputation and demand the attention of forest entomologists.

This chapter introduces the reader to bark beetle natural history, diversity, evolution and management. **Natural history** is organized by feeding ecology, mating strategies, and intra– and interspecific interactions. **Evolution and diversity of bark**

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Fig. 10.1 Examples of bark beetles representing different tribes. Unlike most other weevils, scolytines lack an elongated rostrum, have oval or kidney shaped eyes, and antennae with round or conical clubs. a. *Scolytus aztecus*, b. *Chramesus crenatus*, c. *Cactopinus burjosi*, d. *Pseudips mexicanus*. Photos courtesy of Thomas Atkinson, www.barkbeetle.info
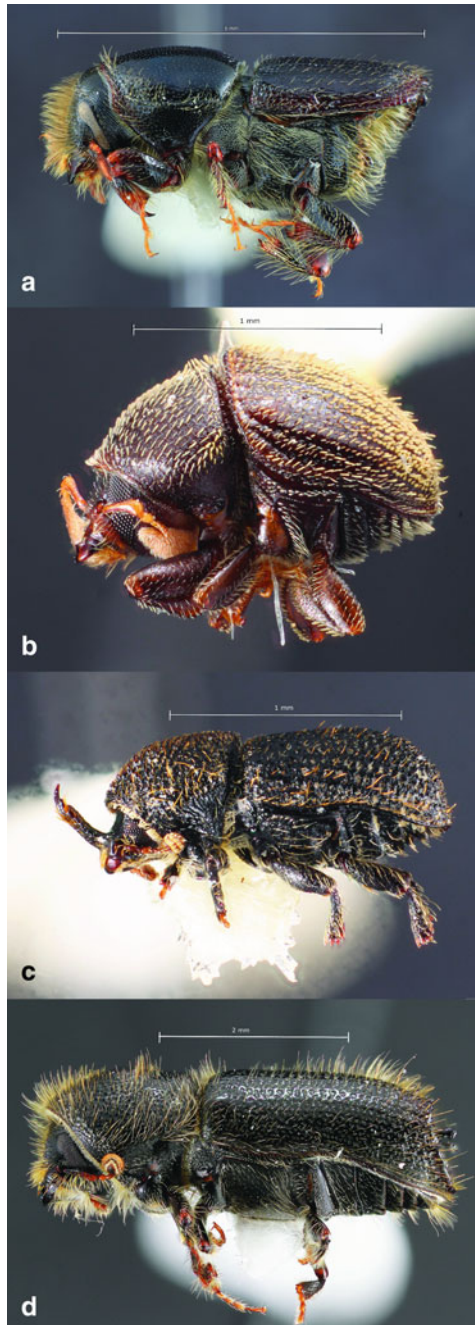
beetles includes discussion of phylogeny, timing of evolutionary events and an anno-
tated and illustrated list of bark beetle genera important to forest entomologists.
Management and control covers efforts to reduce losses to bark beetle destruction
of forests and plant products. Finally, we present case studies, including outbreak
events, which have resulted in vast economic and ecological loss.

10.2   Natural History

10.2.1   Feeding Ecology

Upon emerging from their natal host, progeny adults search for a suitable host.
Dispersal flights are usually short, consisting of a few hundred meters, but some
species have the potential to fly more than 30 km (Zumr 1992; Yan et al. 2005). For
most beetle species, a suitable host is limited to a certain tree taxon in a suitable
physiological condition for infestation. The pioneer sex, first to arrive at the host,
can vary depending on the mating system of the beetle.

Host specificity ranges widely for bark beetles from a few species restricted to
one tree species to some that exploit entire plant families. Most bark beetles that
attack living trees exploit hosts within the Pinaceae, whereas species that breed in
angiosperms are usually saprophagous. Specificity to one tree species is uncommon,
occurring in approximately 1% of all bark beetles, whereas specificity to tree family
is more common (Kirkendall et al. 2015). The ability to feed in both gymnosperms
and angiosperms is rare and has been documented only for *Polygraphus grandiclava*
(Avtzis et al. 2008).

Maturation feeding outside the maternal gallery can occur, including feeding
on fresh shoots from the natal or a new host (Raffa et al. 2015). Adults usually
overwinter in host material. Larvae are generally not able to survive cold weather.
In some species of *Ips*, groups of individuals will bore into a tree and "roost" for
the winter (Cognato 2015). *Dendroctonus frontalis* and *D. micans* are exceptions
that are able to overwinter in all life-stages (Luik and Voolma 1990; Hain et al.
2011). During overwintering, beetles stop feeding and reduce their water content,
accumulating compounds such as glycerol and ethylene glycol in their hemolymph
to withstand freezing conditions (Gehrken 1985, 1989).

Successful colonization of the host tree depends on the population level of the
available beetles to produce aggregation pheromones and on the vigor of the tree,
which determines the defensive response. The great evolutionary success of conifers,
for example, is directly related to their complex defense mechanisms to deter herbi-
vores and pathogens through the production of resin (Trapp and Croteau 2001). The
relationship among aggregation pheromones, conifer resin defenses and bark beetle
mass attacks probably reflects the coevolution of bark beetles and their hosts (Borden
1982; Franceschi et al. 2005). Pheromones, highly important for the achievement of

rapid and massive attacks, have been suggested to have originated as detoxification products of host monoterpenes (Lindgren and Raffa 2013).

Because wood is a nutritionally poor substrate, most bark beetle feeding occurs in the phloem. This tissue is a relatively thin layer, and there are different minimal requirements of phloem thickness for different bark beetle species. To increase nitrogen intake, several species feed on either fungus or fungus-infected phloem (Bleiker and Six 2007). Many bark beetles feed on fungi as well as plant tissues both as larvae and as adults. Symbiotic fungi, carried by many species in specific integument structures called mycangia or directly in the exoskeleton, are inoculated in the galleries where they grow into the host tissue (Happ et al. 1976). Females of *Dendroctonus frontalis* for example, possess mycangia in which they carry their symbiotic fungi, most commonly *Entomocorticium* (Basidiomycota) species and *Ceratocystiopsis* (Ascomycota) species, the predominant source of nutrition for the larvae (Barras and Perry 1972; Bridges 1983; Six and Wingfield 2011; Harrington et al. 2021). Other fungal species, such as the ascomycetes *Ophiostoma* spp., also alter tree condition which facilitates larval development (Barras and Taylor 1973; Goldhammer et al. 1989; Six and Wingfield 2011). These fungi, like the rest of the Ophiostomatales, are well adapted for insect dispersal, as most produce long sexual fruiting bodies with sticky spores that facilitate contact with the vector (Kirisits 2007). Interestingly, these ophiostomatalean symbionts supress wood decomposition through competitive interactions with decay fungi (Skelton et al. 2020). Moreover, it may increase feeding by subterranean termites (Little et al. 2012; Riggins et al. 2014; Clay et al. 2017).

10.2.1.1   Host Location and Acceptance

Visual and chemical cues, such as vertical silhouettes, host volatiles, and/or pheromones, are important for orientation and initial landing on the host (Person 1931; Vité and Gara 1962; Wood 1982a; Payne 1986; Saint-Germain et al. 2007). Gustatory and olfactory stimulants are important in the boring phase subsequent to host location, when the beetle determines the quality of the host in terms of nutrition and humidity (Webb and Franklin 1978). Several sensory receptors located in the antennae and mouthparts are involved in the perception and location of the host tree (Payne 1979).

Antennal sensillae are highly responsive to pheromones and host-derived volatiles, where each antennal receptor cell contains multiple sites that interact with the chemicals. Sensillae from maxillary and labial palps are also important in host selection and food discrimination, as suggested in morphological studies from *D. ponderosae* and *I. typographus* (Byers 2007). These chemicals are not only relevant in recognizing suitable hosts, but also help to avoid colonized or decaying hosts. Pine monoterpenes, such as α-pinene, are present in the oleoresin and can serve as part of the tree defense system in high concentrations. Moreover, they also function as kairomones for bark beetles, attracting them to suitable hosts, sometimes in combination with sex pheromones (Vité and Gara 1962; Wood 1982a; Payne 1986; Seybold et al. 2000,

2006). Conversely, when a large number of bark beetles are present in the host tree, a deterrent or anti-aggregation pheromone, such as verbenone, signals that the tree is no longer suitable for colonization in some species (Pitman and Vité 1969; Renwick and Vité 1970; Etxebeste and Pajares 2011). For example, in *D. frontalis*, females are initially attracted by kairomones (α-pinene) released by the host trees. Soon after the initial colonization, females release the pheromone frontalin attracting both males and females, resulting in a mass attack that overcomes tree defenses. Males later produce (+)-endo-brevicomin, an antiaggregation pheromone in high concentration (Sullivan et al. 2007).

Bark beetles can be attracted to susceptible hosts by tree volatiles (Lindelöw et al. 1992; Tunset et al. 1993), but encounter rates are also based on random alightment with no need of kairomones (Wermelinger 2004). Host location can also be influenced by abiotic effects. For example as sun-exposed trees are more likely to be attacked than trees in the shade (Lobinger and Skatulla 1996).

10.2.2   Mating Systems

Most bark beetles outbreed, but there is variation among the mating systems (Kirkendall et al. 2015). In the early colonization phase, when reproductive pairs form, conflict in the gallery entrances between conspecifics of the same sex are common in bark beetles (Kirkendall et al. 2015). In female-initiated mating systems, such as in *Dendroctonus* and *Tomicus*, male-male competition is common. Males wander and attempt to enter active galleries, but are usually blocked by already established males. Both chemical and acoustic communication are involved in gaining access to galleries and during courtship (Barr 1969; Oester et al. 1981; Ryker 1984). Females can re-emerge from the initial gallery and lay eggs in a new gallery constructed in the same host or disperse to a new tree. Eggs are commonly laid in individual niches on one or both sides of the gallery. Before re-emerging, females feed in the gallery, likely to regenerate wing muscles (Sauvard 2007).

Monogyny is the most ancestral and predominant mating system in bark beetles, and is present in almost every genus (Kirkendall 1983). In monogamous species, females typically select the host and initiate colonization. Males are subsequently attracted by female-released pheromones (Raffa et al. 2015). Exceptions exist among the Bothrosternini and Pityophthorina, where some genera are known to have male-initiated monogyny (Beaver 1973). This tends to occur with species that breed in resources where no more than one female can breed because of interbrood competition (Kirkendall 1983). A few species may have females that mate with siblings or with a newly arrived male before emergence (Bleiker et al. 2013). Depending on the species, mating occurs on the bark or in the gallery. Bigyny, where males regularly have two females, occurs in 19 genera but is most common within the Micracidini. Given that scolytines are the only insects to engage in simultaneous bigyny in nature, it has been suggested that it may be related to geometric constraints on egg tunnel construction. More than two colonizing females would decrease host real

estate, resulting in increased competition among larvae and subsequently greater larval mortality due to diminished resources (Kirkendall et al. 2015).

In polygamous species, males initiate the attack, build a nuptial chamber, and are joined by several females. Harem polygyny (simultaneous polygyny) has evolved at least 12 times in Scolytinae and is found in 26 genera, being predominant in the Ipini, and common in the Corthylini and Polygraphini (Kirkendall et al. 2015). The evolutionary context of why females would join already mated males is hypothesized to be related to resource quality (Kirkendall 1983). Because resource quality is variable, some males will have high-quality resource patches to support several females, whereas other males initiate their attacks in low-quality patches that would not be able to support multiple females.

Colonial polygyny is found in a few genera and is based on having multiple males and multiple females in the same network of interconnected tunnel systems (Kirkendall et al. 2015). Colonial polygyny has been reported for *Aphanarthrum* and *Crypturgus* (Crypturgini), and *Cyrtogenius* (Dryocoetini) (Chararas 1962; Roberts 1976; Jordal 2006). Inbreeding polygyny is most common in ambrosia beetles, but also exists in several genera of bark beetles that usually do not show phloeophagous feeding habits (Kirkendall et al. 2015). The few phloeophagous inbreeders are atypical for bark beetles. Some species within *Ozopemon* (Dyocoetini), *Hypothenemus* (Cryphalini), and *Dendroctonus* (Hylurgini) breed in large chambers with larvae feeding communally (Kirkendall 1993). Partial inbreeding can also occur in *Dendroctonus micans* and *D. punctatus*, which produce small males and female-biased sex ratios (Kirkendall 1983).

Different forms of parthenogenesis are found in the Scolytinae. Arrhenotoky is the most commonly known; observed in the most successful ambrosia beetle clade, the Xyleborini. Pseudo-arrhenotoky, where daughters are sexually produced and the paternal genome is eliminated, is known from the genus *Hypothenemus*, having been demonstrated in *H. hampei* (Vega et al. 2015). Pseudogamy, where females are produced clonally, are genetic copies of their mothers, and fertilization is required but male genomes are not passed to the offspring, occurs in some species of the spruce-feeding *Ips* in North America (Lanier and Kirkendall 1986).

10.2.3   Social Behavior

Bark beetles are largely considered sub-social, with aggregated breeding and, to some extent, parental care for offspring (Jordal et al. 2011). Sub-sociality is facilitated by their subcortical lifestyle, which offers a protected abundant resource and, by inoculating it with symbiotic fungi, an easily assimilated food substrate (Kirkendall et al. 2015).

Males typically stay within galleries with females for at least days or weeks. Mate guarding, increased offspring number and survivorship, and mate attraction, have been suggested as some of the reasons for male post-copulatory residence in galleries (Kirkendall et al. 2010). For example, blocking the entry of natural enemies into the

gallery would positively affect offspring survivorship. Experiments conducted for *Ips pini* suggest that the presence of males in the galleries increases the number of eggs laid by females by removing female-produced frass, and significantly reduces the number of predators in the egg galleries (Reid and Roitberg 1994). Clearing frass from egg tunnels, one of the most widespread forms of parental care, is conducted by either males or females depending on the species, using elytral declivities to push it out of the galleries (Wichmann 1967). Aggregated breeding through multiple colonization may occur without the production of pheromones, such as in species of *Hylastes* (Hylastini) or *Tomicus* (Hylurgini), where individuals are attracted by host volatiles.

10.2.4   Communication

Interactions between bark beetles and their hosts involve different stimuli such as semiochemicals (Blomquist et al. 2010). For example, feeding induces the production of aggregation pheromones that attract both sexes during a mass attack, such as ipsdienol and ipsenol in the genus *Ips*, and frontalin in some species of *Dendroctonus*. Pheromonal communication, which may have been co-opted from the detoxification of terpenes (Franceschi et al. 2005), is essential in this attraction-based system, which for some species helps to overcome tree defenses. Host colonization starts with the ability to locate a suitable host, followed by the attraction of conspecifics, and finally, as tree defenses decline and colonization proceeds, the emission of anti-aggregation pheromones to reduce competition (Wood 1982a). The same compounds produced by bark beetles to stop aggregation on a host, among other aggregation compounds, serve as kairomones and are attractive to a large number of organisms, including predators (Reeve 1997).

Acoustic signals are also important stimuli for intraspecific interactions within a host, with stridulatory organs present in one or both sexes depending on the species. Acoustic signals, commonly used by insects in the context of mating, have been associated in bark beetles with arrival announcement of the stridulating sex, or premating species recognition (Barr 1969; Oester et al. 1981; Ryker 1984). Stridulatory organs can be located on different parts of the body depending on the species, and play an important role in mate choice and male competition. For example, the elytra-abdominal stridulatory structure of *Dendroctonus valens* is capable of producing several distinct chirps, that males produce to induce female acceptance into the gallery (Lindeman and Yack 2015).

10.2.5   Interspecific Interactions

It is common in multiple species of bark beetles to feed on a common resource and therefore, there are several strategies for reducing direct competition (Raffa et al.

2015). In the broad sense, many bark beetle species achieve resource partitioning by having different host preferences. On a smaller scale, such as within a single tree, bark beetles can achieve resource partitioning by utilizing different parts of the tree. This within-tree niche partitioning by multiple species is usually not absolute and involves an opportunistic extension of the galleries in the absence of other species. For example, in the southeastern US, *Dendroctonus terebrans* can be observed at the base of the trunk in trees previously attacked by *D. frontalis* (Payne et al. 1987). Species of *Ips* will subsequently attack the higher portions of the trunk according to their size, with *I. calligraphus* colonizing larger diameters and *I. grandicollis* and *I. avulsus* colonizing smaller diameters and branches in the crown (Paine et al. 1981). This partitioning is also explained by chemical communication, as their pheromones have both intraspecific and interspecific effects on the distribution of the species across the tree (Birch 1980). Moreover, bark beetle predators and parasitoids can exploit pheromone signals to locate prey (Ayres et al. 2001).

Phenology is another form of partitioning, with differences in flight and reproductive cycles allowing some bark beetle species to occupy the same geographic range and host with minimal competition. In the case of *Ips pini*, *I. perroti*, and *I. grandicollis*, which coexist in pine forests of the north-central United States and share the same host tree, differences in flight phenology, development time, voltinism, and spatial colonization patterns reduce congeneric competition (Ayres et al. 2001). The physiological condition of the host can also partition the resource, as different colonization patterns have been observed for different bark beetle genera among trees and snags of different physiological and decomposition states (Saint-Germain et al., 2009).

Closely related species of bark beetles with similar life histories and hosts often inhabit distinct geographic regions. For example, *Tomicus piniperda* and *T. destruens*, species of great importance across the Mediterranean region, present contrasting distributions as a result of different climate demands, where *T. destruens* occurs in locations with warmer temperatures and low altitudes and *T. piniperda* occurs in locations with colder temperatures and higher altitudes (Horn et al. 2012). Another example is the distributions of *Dendroctonus terebrans*, found throughout the eastern United States from coastal New Hampshire south to Florida and west to Texas and Missouri, and *D. valens*, which occurs from Alaska to Mexico and eastward to New England, but does not occur in the southeastern United States (Mayfield and Foltz 2005). These species are morphologically and behaviorally similar, but only co-occur in a narrow zone where their ranges overlap.

Other woodborers compete with bark beetles for resources. Cerambycids for example, such as *Monochamus* spp., feed in the phloem of recently killed pine trees and are facultative intra-guild predators of larvae of other phloem feeders, influencing bark beetle population dynamics (Dodds et al. 2001; Schoeller et al. 2012). Moreover, because cerambycids are larger, competition for phloem results in a loss of resource for bark beetles (Stephen 2011). In the southeastern United States for example, *Monochamus* spp. are common after the attack of bark beetles, such as *Dendroctonus frontalis* and *Ips* spp., attracted by host volatiles and a kairomonal response to sympatric bark beetle pheromones (Allison et al. 2001; Stephen 2011). Other species

of cerambycids, such as *Acanthosinus nodosus*, appear to colonize thicker phloem, acting as a potential competitor for several bark beetle species (Stephen 2011).

Symbiotic organisms are commonly associated with bark beetles, including mites, protozoa and nematodes (Hofstetter et al. 2015). Phoretic mites, of which there are more than 250 species associated with bark beetles, have diverse roles ranging from antagonistic parasites or predators of immature beetles, to mutualists that are mycophages or nematophages (Hofstetter et al. 2013, 2015). For example, some mites contribute to fungal diversity in the galleries by carrying different fungal species in a specialized structure (sporotheca) (Moser 1985). At least 57 species of phoretic mites have been recorded for *Dendroctonus frontalis*, and some of these mites have sporothecae that frequently contain spores of *Ophiostoma minus* and *Ceratocystiopsis ranaculosa* (Hofstetter et al. 2013). Because of its pathogenicity, *O. minus* has long been considered a critical mutualist of *D. frontalis*, but several observations suggest that *O. minus* is not always present in trees killed by the beetle, and, moreover, is not capable of killing mature pines (Klepzig et al. 2005). In addition, larvae of *D. frontalis* turn away from phloem colonized by *O. minus* and cannot survive in wood colonized by the fungus (Barras 1970). *Ips typographus* is associated with 38 species of phoretic mites (Hofstetter et al. 2015), which can potentially carry spores of several fungal pathogens that cause mortality to spruce trees (Hofstetter et al. 2013). Because of the lack of mycangia on *Ips* spp., mites are frequently associated with them and critical to the maintenance of fungal associations (Harrington 2005). Nematodes are also common symbiotic organisms associated with bark beetles, often with thousands of individuals in one single beetle, ranging from mutualistic, parasitic, or commensal relationships (Hofstetter et al. 2015).

10.3 Evolution and Diversity

Bark beetles began their diversification at least 120 million years ago as evidenced by a specimen from Lebanese amber (Kirejtshuk et al. 2009). This species, *Cylindrobrotus pectinatus,* resembles *Dryocoetes* but possesses a mixture of ancestral and derived traits leading the authors to place it in a unique tribe. In 100 million-year-old Burmese amber, *Microborus inertus*, represents an extant genus of bark beetle (Cognato and Grimaldi 2009). The variation of morphological features represented in these two species suggests that scolytine diversity was well-established and greater than its fossilized representation. Many species of their extant relatives feed on angiosperms and it is postulated that these Cretaceous species also fed on the burgeoning angiosperm diversity. This would explain the scarcity of scolytine specimens from Cretaceous coniferous ambers (Hulcr et al. 2015).

Bark beetles survived the impact of the great celestial object that was the demise of the dinosaurs and perhaps flourished with the abundance of stressed trees. The next window to their ancient diversity occurred 20 million years later. The scolytine fossil record is well represented in Baltic (45 million years ago) and Dominican ambers (20 million years ago). The Baltic amber fauna is represented mainly by *Hylurgops* and

Hylastes species and along with the plant diversity, suggests an ecosystem similar to the southeastern US (Grimaldi 1996). The Dominican amber fauna is represented mostly by tropical fungi feeding scolytines (except Xyleborini) however several bark beetle genera occur and suggest ties to the current Afrotropical fauna (Bright and Poinar 1994; Cognato 2013). By this point, much of the extant generic diversity was achieved.

Bark beetles spread throughout the world's forests over 120 million years after their origin, when vast distances of ocean separated most of the continents. Bark beetles likely dispersed between land masses by wind and within tree-flotsam and likely seeded multiple species radiations (Gohli et al. 2016; Cognato et al. 2018). There are currently 189 genera and ~ 4300 species of bark beetles. Their diversity is concentrated in the Old and New World tropics, representing half of the total diversity. This is not surprising given the great diversity of plants in the tropics. Likely, natural selection caused by the close association between tree host and beetle, influenced the diversification of scolytines (Gohli et al. 2017). Also, geographic isolation had a major influence on species diversification, as evidenced by bursts of radiation through time (Jordal and Cognato 2012; Gohli et al. 2017).

Introduction of DNA sequence data for phylogenetic reconstruction has resulted in major advances in the understanding of bark beetle relationships. Prior to the 1990's bark beetle phylogenies were mostly unknown given the lack of informative morphological characters considering the canalized scolytine body form (e.g. Cognato 2000). DNA sequences from just a few genes provided needed data to address vexing questions in taxonomy and evolution (Farrell et al. 2001; Cognato and Sun 2007; Jordal and Cognato 2012). Recent use of genomic data has produced the largest and most informative phylogenies to date (Gohli et al. 2017; Johnson et al. 2018). These and other phylogenies are important because they provide evolutionary based hypotheses to the organization of scolytine taxonomy and to the investigations of biological processes. For example, the taxonomy of some of the genera of Ipini was debated (e.g. Cognato 2000; Wood 2007). DNA-based phylogenies supported the recognition of *Pseudips* for *Ips mexicanus* and *I. concinnus*, placement of *I. latidens* and *I. spinifer* in *Orthotomicus*, and the inclusion of the ambrosia fungus feeding Premnobina within Ipini (Cognato and Sperling 2000; Cognato and Vogler 2001; Cognato 2013; see Fig. 9.4 in Cognato 2015). Additionally, behavioral traits can be mapped on phylogenies to identify evolutionary patterns. For example, mapping food preferences on a phylogeny, reveals evolutionary patterns and in this case, that feeding in phloem occurred prior to feeding in other plant parts or on fungi (e.g. Kirkendall et al. 2015).

Phylogenies can also be used to predict a behavior or control method for a new bark beetle pest based on its relationship to other known species. Thereby, the cost for developing management strategies for a potential pest will be reduced. For further detailed examples of bark beetle evolution and diversity see reviews of Kirkendall et al. (2015) and Hulcr et al. (2015).

10.3.1 Ten High Impact Bark Beetle Genera and Selected Case-Studies

10.3.1.1 *Conophthorus*

Conophthorus species are similar to *Pityophthorus,* but species within *Pityophthorus* are smaller. They are distinguished by the gradual transition from asperate to punctate in the pronotum and the costal margin of the declivity descending towards the apex.

There are 13 species of *Conophthorus* in the Nearctic region, from Canada to Guatemala (Alonso-Zarazaga and Lyal 2009). Both larvae and adults feed on pine cones, although some species can infest twigs and buds. Females initiate the galleries near the base of second year cones in early summer (Kirkendall 1983). As reported for several species in the genus, females attract males to the cone with the sex pheromone (+)-pityol (Miller et al. 2000). There is usually one monogamous mating pair per cone (Trudel et al. 2004). Females deposit eggs along the gallery in individual niches close to the developing seeds.

Conophthorus ponderosae is an economically important species that occurs in many *Pinus* species in western North America, ranging from Canada to Mexico (Fig. 10.3). This species can cause up to 90% cone mortality with 100% seed mortality within each cone (Bennett 2000; Smith and Hulcr 2015). It has been suggested that this species is polyphyletic and that southern populations represent a different species (Cognato et al. 2005). *Conophthorus ponderosae* can be distinguished from other *Conophthorus* species by the absence of tubercles on the declivital interstriae 1, and by the lateral convexities on the declivity.

10.3.1.2 *Dendroctonus*

The genus *Dendroctonus* is distinguished by its flattened and rounded antennal club, 5-segmented funicle, steep convex declivity, and an entire compound eye. Species can be confused with *Hylurgus* or *Tomicus*, but these genera have a conical antennal club with a 6-segmented funicle.

There are 20 described species of *Dendroctonus* distributed across the Nearctic region (18 species), and two species in the Palearctic region (Armendáriz-Toledano et al. 2015; Six and Bracewell 2015). *Dendroctonus* contains some of the major conifer-killing bark beetles in the world. Most species colonize *Pinus*, and five reproduce in *Picea*, *Pseudotsuga*, or *Larix*. Females initiate colonization and build a nuptial chamber, followed by a male that is attracted by sex pheromones and/or host kairomones. After mating, females lay eggs in a newly constructed gallery in the phloem. In this monogamous genus, females typically build galleries that are packed with frass. Some re-emergence and re-mating can occur, as well as sib-mating in a few species (Six and Bracewell 2015). Larvae usually feed on phloem and symbiotic fungi. Larger individuals can fly further, produce more pheromone and offspring, and have a greater overwintering success (Six and Bracewell 2015). Attack of the

basal portion of a living tree by some species involves a few individuals with gregarious larval feeding that usually does not kill the tree in usual climatic conditions. However, other representatives of the genus conduct a pheromone-based mass attack that results in the death of the tree and potential massive outbreaks (Raffa et al. 2008).

The southern pine beetle, *Dendroctonus frontalis*, is the most destructive native pest of pine trees in the southeastern United States, Mexico, and Central America (Fig. 10.2) (Thatcher et al. 1980; Coulson and Klepzig 2011). During outbreaks, southern pine beetle infestations often begin in weakened or injured trees, but high beetle populations can mass-attack and kill healthy trees (Cara and Coster 1968; Hain et al. 2011). Uncontrolled infestations may grow to thousands of acres in size, persisting for multiple beetle generations, until depletion of hosts, cold temperatures, direct control, or other factors intervene (Billings 2011). Trees attacked by southern pine beetle often exhibit hundreds of pitch tubes on the outer bark. Beetles feed on phloem and bore S-shaped galleries which can girdle a tree, causing its death. This species is distinguished by its small size (2 to 3 mm) and the convex elytral declivity with the striae distinct and impressed. Males have a distinct notch in the frons and females have a transverse ridge (mycangium) along the anterior pronotum (Fig. 10.3).

Southern pine beetle outbreaks have been cyclical in occurrence, occurring on six to 12 year-intervals and generally last for two to three years after they begin. It has shown a dramatic decline in outbreak activity over much of the southeastern United States since the turn of the twenty-first century compared to previous decades (Birt

Fig. 10.2 Southern Pine Beetle (*Dendroctonus frontalis*) damage in Honduras. Photograph by Ronald Billings, US Forest Service

Fig. 10.3 From left to right, top to bottom, lateral view of *Conophthorus ponderosae*, *Dryocoetes confuses*, *Dendroctonus frontalis*, *Dendroctonus ponderosae*, *Ips typographus*, *Pityophthorus juglandis*, *Polygraphus proximus*, *Polygraphus ruffipenis*. Scale bar: 1.0 mm. Photographs by Demian F. Gomez, University of Florida

2011; Clarke 2012; Clarke et al. 2016; Asaro et al. 2017). The major outbreak, from 1998 to 2002 in the southern Appalachian Mountains, affected more than 400,000 hectares with an economic loss of more than US$ 1 billion (Nowak et al. 2008; Clarke and Nowak 2009).

Female *D. frontalis* carry symbiotic fungi in their mycangia, most commonly *Entomocorticium* and *Ceratocystiopsis* species (Yuceer et al. 2011; Six and Bracewell 2015; Harrington et al. 2021). These fungi are introduced into the phloem and serve as the predominant source of nutrition for larvae. The beetles also inadvertently carry blue-stain fungi such as *Ophiostoma minus* in association with phoretic mites

(Moser 1985; Moser and Bridges 1986; Hofstetter et al. 2006). Despite the ongoing controversy over the role of these fungi in tree death, it is known that it has a limited impact compared to the actual beetle attack (Six and Wingfield 2011).

Dendroctonus ponderosae is the most destructive species of bark beetle, colonizing weak *P. ponderosa* and *P. contorta*, and producing extensive outbreaks in healthy trees facilitated by drought and warming climate (Raffa et al. 2008; Creeden et al. 2014) (Fig. 10.3). This species caused the death of more than 11 million hectares of pine trees in a 13-year period in North America, responsible of 50% of tree mortality in the western United States (Ramsfield et al. 2016). Historically distributed in western North America, it has been increasing its natural range mainly because of a warming climate through northern British Columbia towards new regions in Alberta, Canada (Robertson et al. 2009). Obligate symbionts are carried in the mycangia to provide nutritional supplementation, increasing nitrogen availability for larvae (Bleiker and Six 2007). *Grosmannia clavigera*, *Leptographium longiclavatum*, and *Ophiostoma montium* are common symbions of *D. ponderosa* (Six and Bracewell 2015). These fungi can vary within a population due to changing nutrient and moisture profiles in the host, competition among the fungi, and temperature (Six and Bentz 2007). *Dendroctonus ponderosae* can be distinguished from other *Dendroctonus* species by the absence of tubercles in the frons, the large punctures in the pronotum (larger than the distance between them), and the impressed interstria 2 on the elytral declivity.

10.3.1.3 *Dryocoetes*

Dryocoetes species can be recognized by their 5-segmented funicle, the truncated antennal club with corneous first segment, and the short, steep, and unarmed elytral declivity. This genus is similar to *Coccotrypes*, but it can be distinguished by the broad oral region and the non-aciculate frons.

There are 46 species in the genus *Dryocoetes* distributed in the Holarctic and Oriental regions, with seven species occurring in North America (Smith and Hulcr 2015). This genus is mostly phloeophagous feeding in broadleaved and conifer hosts. During colonization, males initiate the attack and build the nuptial chamber in the phloem (Furniss and Kegley 2006). Depending on the species, between 2–6 females will join and construct star-shaped egg galleries. Males remove the frass through the entrance hole after females remove it from the egg galleries. Larval galleries are short and development time may vary according to temperature and altitude, ranging from 1 to 2 years (Smith and Hulcr 2015).

Dryocoetes confusus is the most destructive species in the genus, causing severe damage mainly to *Abies lasiocarpa*, but it can also attack other firs (Garbutt 1992; Smith and Hulcr 2015) (Fig. 10.3). This species can colonize fallen trees as well as kill over-mature trees (i.e. beyond the stage of desirable or optimal development or productivity) in association with the fungal pathogen *Grosmannia dryocoetis* transmitted through a mandibular mycangia. Successfully attacked hosts also show less

induced resinosis and less radial growth than unsuccessfully attacked trees, and mortality typically occurs in spots (groups of infested trees) (Bleiker et al. 2003; McMillin et al. 2003).

10.3.1.4 *Ips*

Ips species are distinguished by the three to six spines that line the lateral margin of the elytral declivity. They can be confused with *Orthotomicus* and *Pseudips*; however, in these genera, the elytral declivity is steep and the sutures of the antennal club are slightly to distinctly procurved.

There are 37 *Ips* spp. distributed throughout the Holarctic and most species diversity lies in North America (23 spp.) followed by Eurasia (14 spp.) (Cognato 2015). The adults and larvae feed and complete their life cycle under the bark of the conifer genera *Abies*, *Pinus*, *Picea*, and *Larix*. Most species are specific to *Pinus* or *Picea*, but two Asian species are specific to *Larix*. When *Ips* spp. are restricted to one or two hosts, this appears to be the result of host availability within specific geographic areas. Adult *Ips* males initiate mating by locating a suitable dead or dying host and bore into the phloem to create a nuptial chamber. Males produce aggregation pheromones while feeding, which attract conspecifics to the tree. *Ips* spp. are polygamous and 3–7 females may join the male in the nuptial chamber where they mate. The females then create a tunnel where they lay eggs in niches along the tunnel walls. The hatched larvae feed by tunneling through the phloem. The larvae complete their development in 6–8 weeks depending on temperature.

Ips typographus, the European spruce bark beetle, is the most destructive species of the genus attacking primarily *Picea*, but it can also breed in *Abies* and *Pinus* (Fig. 10.3). The species is distributed across Europe and Asia and although it usually behaves as a secondary pest attacking and killing trees under some level of stress, mass attacks on neighboring healthy trees and enormous economic losses have been reported (Wermelinger 2004). This species can be identified by the four spines on the dull elytral declivity, and the impunctate interstriae on the basal half of the elytral disc.

During the last decade of the twentieth century in Europe, storms caused severe damage to spruce forests, triggering outbreaks of *Ips typographus*. The extent of the damage was highly significant, with millions of cubic meters of spruce killed and large amount of public money spent to manage the outbreaks (Wermelinger 2004). In recent years, severe storms, windthrow events, and high temperatures, have caused the return of new outbreaks in several European countries and parts of Asia (Lausch et al. 2013; Mezei et al. 2017).

Outbreaks depend on weather, drought, storms, and the availability and susceptibility of host trees. Unmanaged forests do not necessarily have higher populations of *I. typographus*. However, after a disturbance, the populations of beetles in unmanaged forests are more likely to increase to epidemic levels (Schlyter and Lundgren 1993). Site and silvicultural characteristics, such as water availability and slope, are

related to attack probability. The maintenance of heterogeneous stands is recommended to reduce attacks in managed spruce forests, as multi-tree species forests are often less susceptible to bark beetle attack (Wermelinger 2004). Aggregation pheromones, biosynthesized from tree resin compounds, play a role in attracting *Ips typographus* to suitable breeding hosts. Colonization usually occurs in windthrown trees and large trunks are most commonly attacked.

Ips acuminatus has recently increased the frequency and intensity of outbreaks in *Pinus sylvestris* of the south-eastern Alps (Colombari et al. 2012). In Belarus, timber losses accounted for more than 184,000 ha in the last ten years. This species often initiates attacks in the upper bole of mature trees and may infest twigs as small as 2 mm in diameter. Trees are subsequently attacked by second-generation *I. acuminatus* and by *Ips sexdentatus* in the lower part of the trunk. *Ips acuminatus* can be identified by the three spines in the elytral declivity, of which the third is flattened and acuminate in the male.

10.3.1.5   *Pityophthorus*

Pityophthorus can be distinguished by the pronotal asperities on the anterior half of the pronotum and by the presence of a sclerotized septum in both antennal sutures of the club. Species of *Pityophthorus* can be confused with the genus *Araptus*, however, species of the latter genus do not have a sclerotized septum in the antennal club.

There are 386 species in the genus *Pityophthorus* distributed mostly in North and Central America, but also ranging from the Palearctic to the Oriental Region (Alonso-Zarazaga and Lyal 2009). This genus typically infests twigs and branches from a broad range of hosts, such as conifers, woody shrubs, vines, hardwood trees, and herbaceous plants (Bright 1981). In North America, most species develop in *Pinus*, with a few colonizing *Abies*, *Picea*, *Pseudotsuga*, and *Larix*. Mating systems vary widely in this genus from polygamy to monogamy and thelytokous parthenogenesis. In phloeophagous species, males initiate the attack and build a nuptial chamber, joined by 3–5 females attracted by aggregation pheromones (Smith and Hulcr 2015). Females then excavate egg galleries radiating from the central nuptial chamber. Females of myelophagous species feed and construct galleries in the pith of small twigs.

Most species in this genus are secondary pests and usually are not of economic importance, with the exception of a few species that vector fungi such as the conifer pathogen *Fusarium circinatum* or the walnut pathogen *Geosmithia morbida*. *Pityophthorus juglandis*, endemic to Mexico and the southwestern continental United States, is the most economically important species in the genus (Fig. 10.3). *Pityophthorus juglandis* causes black walnut tree mortality when they colonize branches and trunks in high numbers and cankers develop around the galleries as a result of its association with *G. morbida* (Kolařík et al. 2011; Rugman-Jones et al. 2015). After 3 years, trees show symptoms of die-back and flagging. The combination of the insect and the fungus threatens the $500 billion black walnut industry in the eastern United States (Newton et al. 2009). However, the pathogenicity of *G. morbida* has recently

been questioned as different strains may cause different effects, and therefore, the consequences of *P. juglandis* colonization are dependent on the pathogenicity of the *G. morbida* strain and environmental factors (Sitz et al. 2017).

10.3.1.6 *Polygraphus*

Polygraphus species are distinguished from other related genera such as *Carphoborus*, by the divided eye, the antennal club with no sutures, and the absence of a scutellum. There are 101 species distributed through the Holarctic, Oriental, and Ethiopian regions (Alonso-Zarazaga and Lyal 2009). All the species within this genus are phloeophagous, feeding mainly on Pinaceae (*Abies*, *Cedrus*, *Larix*, *Picea*, and *Pinus*) and hardwoods (Wood and Bright 1992). *Polygraphus* spp. are polygamous, with males usually initiating attack and excavating the nuptial chamber. Attracted to male aggregation pheromones, 2–4 females can join and start individual egg galleries that can reach up to 10 cm length (Smith and Hulcr 2015).

Polygraphus proximus, distributed in the eastern Palearctic region, attacks several species of *Abies*, and is one of the main factors contributing to the destruction of large areas of Siberian forests since the early 2000s (Krivets et al. 2015) (Fig. 10.3). This species typically colonizes weakened or dying trees, but when population levels are high healthy trees are attacked (Kerchev 2014). Trees usually die after 2–4 years of attack. The ophiostomatoid fungus *Grosmannia aoshimae*, is symbiotic with *P. proximus*, considered an aggressive phytopathogen (Pashenova et al. 2011) and likely contributes to tree mortality. *Polygraphus proximus* can be distinguished from other European species by the pointed antennal club, yellow legs, and elytral base slightly wider than pronotum (Pfeffer 1995).

Polygraphus rufipennis, common across the Nearctic region, is a secondary species that usually colonizes stumps, trunks, or branches of *Picea,* particularly *P. glauca.* In association with the blue stain fungus *Ophiostoma piceaperdum*, it can cause mortality to trees previously weakened by other biotic factors (Fig. 10.3). For example, *P. rufipennis* often colonizes trees weakened by *Dendroctonus rufipennis* or the spruce budworm (*Choristoneura* spp.) (Simpson 1929). This species has one generation per year, with females emerging in mid-summer to establish a second brood. *Polygraphus rufipennis* is distinguished by the stout body, the obtusely pointed antennal club, and by the densely punctured frons in females (Wood 1982b).

10.3.1.7 *Pseudohylesinus*

Pseudohylesinus species are distinguished by the scaled vestiture, the seven-segmented funicle, and the antennal club with the first segment larger. *Pseudohylesinus* species are similar to those of *Xylechinus* and *Hylorgupinus*, but *Pseudohylesinus* can be distinguished by the two-color pattern of dark and light scales covering the body.

There are 13 species of *Pseudohylesinus*, all endemic to North America, distributed from Alaska and western Canada and contiguous United States, to Mexico (Wood and Bright 1992). Species in this genus are all phloeophagous and are attracted to host compounds, feeding mostly on *Abies*, whereas a few species also develop on *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*. Only a few severe outbreaks have been recorded for species within this genus, but the common observed damage is in discrete patches or individual trees (Carlson and Ragenovich 2012). This genus is monogamous, with females initiating the attack and boring the entrance tunnel (Bright 1969). Once the male joins, they both excavate branched egg galleries (1 or 2 ramifications), and females deposit individual eggs along the gallery and cover them with boring dust.

Pseudohylesinus granulatus, the most economically important species of the genus, is distributed from British Columbia to California and attacks mostly *Abies amabalis* (Fig. 10.4). It can kill overmature trees in association with the brown-staining fungus *Ophiostoma subannulatum*, but usually colonizes fallen trees (Carlson and Ragenovich 2012). Mortality can occur as a result of girdling from accumulated attack patches over several years (Smith and Hulcr 2015). *Pseudohylesinus granulatus* can be distinguished by the large and deep pronotal punctures and by the slender body (Wood 1982b).

10.3.1.8   *Pseudopityophthorus*

Pseudopityophthorus can be distinguished by the reduced or absent striae in the elytra, the convex elytral declivity with abundant hair-like to scale-like setae, and the septate and procurved sutures in the antennal club. Species in this genus can be confused with *Pityophthorus*, but the absence of striae in *Pseudopityophthorus* differentiate them.

There are 27 species of *Pseudopityophthorus*, distributed mostly in the Nearctic region, but some species occur in the Neotropical and eastern Palearctic region (Wood 1986; Alonso-Zarazaga and Lyal 2009). Species of *Pseudopityophthorus* are phloeophagous and mainly found on *Quercus,* although other Fagaceae have been reported as hosts. Males initiate the colonization process in this monogamous genus by excavating the entrance tunnel and a short longitudinal gallery in cut, broken, or fallen branches or trunks (Wood 2007). The female then joins and begins a transverse egg gallery in the opposite direction from the male gallery. Larval galleries are longitudinal and almost straight.

Pseudopityophthorus minutissimus (Fig. 10.4) and *P. pruinosus* (Fig. 10.4)*,* have been implicated as vectors of the oak wilt fungal pathogen, *Bretziella fagacearum* in North America, although different roles of the beetle as a vector have been suggested for this pathogen (Berry and Britz 1966; Ambourn et al. 2006). These beetles produce two generations per year through most of the disease range. *Bretziella fagacearum* causes a vascular wilt in more than 30 species of *Quercus* and kills thousands of trees every year in urban landscapes of the United States (Tainter and Baker 1996). *Pseudopityophthorus minutissimus* can be identified by the reticulate frons, the confused

Fig. 10.4 From left to right, top to bottom, lateral view of *Pseudohylesinus granulatus*, *Pseudopityophthorus minutissimus*, *Pseudopityophthorus pruinosus*, *Scolytus multistriatus*, *Scolytus quadrispinosus*, *Scolytus schevyrewi*, *Scolytus ventralis*. Scale bar: 1.0 mm. Photographs by Demian F. Gomez, University of Florida

elytral punctures, and by the uniformly short and confused elytral setae (Wood 1982b). *Pseudopityophthorus pruinosus* is similar to *P. minutissimus* but is larger with larger elytral punctures, and with a row of scales on interstria 1 and 3.

10.3.1.9 *Scolytus*

The genus *Scolytus* can be distinguished by the single curved process in the outer margin of the protibiae, the flattened antennal club, the seven-segmented funicle, and by the slightly sloped elytra (Smith and Cognato 2014). This genus is similar to *Cnemonyx*, but the indistinct declivity in this genus differentiates them.

There are 213 species in the genus *Scolytus* distributed in the Holarctic, Oriental and Neotropical regions. They are phloeophagous and colonize either Pinaceae, such as *Abies*, *Larix*, *Picea*, *Pseudotsuga*, and *Tsuga*, or hardwoods. Host selection is usually mediated by host volatiles and severe attacks are usually stress related, commonly associated with drought or other insects (Smith and Cognato 2014). All Holarctic *Scolytus* species are monogamous and Neotropical species are bigamous or polygamous (Smith and Hulcr 2015). In monogamous species, females colonize the host and start the construction of the nuptial chamber. Males join the entrance tunnel where mating occurs. The female then excavates 1 or 2 egg galleries (depending on the species) with eggs deposited individually inside niches. Males leave the gallery after the egg gallery is complete and females typically die in the entrance hole. Maturation feeding in twigs has been reported for some species.

Scolytus multistriatus is a Palearctic species that has been introduced in the Americas, Australia, and New Zealand (Fig. 10.4). Through the production of an aggregation pheromone, females colonize stressed native and exotic *Ulmus* species. This species is the principal vector of the pathogen *Ophiostoma novo-ulmi*, that causes Dutch elm disease, responsible for the death of millions of elm trees in North America (Furniss and Carolin 1977; Bloomfield 1979). Adults, covered in fungal spores of *Ophiostoma novo-ulmi* upon emergence, inoculate the trees with the pathogen during maturation feeding in the twigs. This species can be identified by the presence of lateral teeth on ventrites 2–4 and by a median conical spine on ventrite 2 (Smith and Cognato 2014).

Scolytus quadrispinosus, a native species in North America, is one of the most destructive pests of hardwoods, in particular species of the genus *Carya* (Fig. 10.4). It usually attacks and kills single trees through mass attack and subsequent girdling of the host, but can develop outbreaks during periods of drought (Blackman 1922). Males are distinguished by the apical margin of ventrite 3 armed by three spines, ventrite 4 armed by one median tooth, and ventrite 1 apically descending (Smith and Cognato 2014). Females are distinguished by the flattened and longitudinally aciculate frons.

Scolytus schevyrewi, a Palearctic species that has been introduced in North America, colonizes stressed *Ulmus* trees and is attracted by host volatiles (Fig. 10.4). This species is a less effective vector of the Dutch elm disease pathogen than *S. multistriatus* (Jacobi et al. 2013). *Scolytus schevyrewi* resembles *S. piceae*, but it can be

distinguished by the subapical carina on ventrite 5 located just before the end of the segment (Smith and Cognato 2014).

Scolytus ventralis, native to North America, attacks several *Abies* species and can cause significant mortality, being the most destructive conifer-feeding species in the genus (Fig. 10.4). This species is associated with the symbiotic fungus *Trichosporium symbioticum*, introduced by females in the gallery (Bright and Stark 1973). Development time varies from 41 to 380 days depending on latitude and elevation. Males of this species can be distinguished from females by the elevated base of ventrite 2, the surface of ventrite 2 flat, the apical margin of ventrite 2 often bearing a median denticle, and by the glabrous ventrite 2 (Smith and Cognato 2014). Females are distinguished by the weakly aciculate and strongly punctate frons and by the apical margin of ventrite 1 flush with basal margin of ventrite 2.

10.3.1.10 *Tomicus*

Tomicus species can be differentiated by the 6-segmented antennal funicle, an ovate club with straight sutures, the pronotum wider than long, and the convex declivity with interstrial granules and erect setae. This genus is similar to *Hylurgus*, but *Tomicus* can be distinguished by the shiny frons and declivity, and by the less hairy vestiture.

Tomicus is comprised of eight species distributed across the Palearctic region with one species introduced in North America (Lieutier et al. 2015). Five species occur only in Asia, one in Europe and northern Africa, and two widely distributed in Eurasia. All species are phloeophagous and usually colonize trunks or branches of weakened *Pinus* species, and one species utilizes *Picea.* Maturation feeding occurs in the shoot of healthy and vigorous pines, causing severe problems to young plantations when a large number of shoots are destroyed resulting in growth loss. This maturation feeding, revealed by the existence of entrance holes surrounded by resin, can occur in a different tree than the natal host; therefore, their life cycle would not necessarily occur in the same tree as in most scolytines. Species of this genus are monogamous and have one generation per year, with females excavating egg galleries with individual niches.

Tomicus destruens is among the most damaging pests across the Mediterranean region and attacks native and exotic pine species through attraction to several host volatiles from stressed trees, such as ethanol, α-pinene, β-myrcene, and α-terpinolene (Faccoli et al. 2008) (Fig. 10.5). *Tomicus destruens* can be distinguished by the weakly impressed elytral declivital interstriae 2 with dense and confused punctures, and by the uniformly yellow or yellow–brown antennae (Kirkendall et al. 2008).

Tomicus piniperda, the most widespread species, can colonize several *Pinus* species but prefers *P. sylvestris* (Fig. 10.5). This species has been introduced in eastern North America where it causes damage to the Christmas tree and nursery industries (Haack and Poland 2001). Host kairomones (α-pinene) and aggregation pheromones play an important role in colonization of the host (Poland et al. 2003). *Tomicus piniperda* can be distinguished by the interstria 2 strongly impressed and concave with uniseriate regularly spaced punctures on the declivity, the erect hairs

Fig. 10.5 From top to
bottom, lateral view of
Tomicus destruens, *Tomicus
piniperda*, *Tomicus
yunnanensis*. Scale bar:
1.0 mm. Photographs by
Demian F. Gomez,
University of Florida

on the declivity distinctly longer than those on disc, and by the uniformly brown
antennae (Kirkendall et al. 2008).

Tomicus yunnanensis, recorded only in Yunnan Province, China, has caused
significant damage to more than 200,000 hectares of *Pinus yunnanensis* forests in
southwest China (Liu et al. 2010) (Fig. 10.5). *Tomicus yunnanensis* can be distin-
guished by the interstria 2 strongly impressed and broadly convex with confused or
biseriate evenly spaced punctures on the declivity, and by the uniformly yellow or
yellow–brown antennae (Kirkendall et al. 2008).

10.4   Management and Control

Bark beetle epidemics are generally managed through direct and indirect control measures. Direct control involves tactics like sanitation harvests to manage current infestations, whereas the indirect approach is preventive and designed to reduce the frequency and severity of future attacks. Indirect measures involve manipulation of the stand through silvicultural practices such as thinning and prescribed burning, aimed at reducing competition among trees resulting in improved tree vigor, and selecting for favorable species composition.

In order to apply proper control strategies, monitoring and prediction programs that gather and analyze information on the extent of infestations are essential. Aerial surveys using digital mapping are commonly used for recognizing spots of infested trees that are later confirmed in the field (Fettig and Hilszczański 2015). Remote sensing techniques are becoming more commonly used to detect bark beetle outbreaks, usually relying on near-infrared (NIR) and shortwave infrared (SWIR) satellite imagery (Hais et al. 2016). Hazard prediction systems are also utilized. Some hazard rating systems are based on stand characteristics (e.g. basal area, radial growth), and others are based on bark beetle captures. The former provides an estimate of how severely a stand might be impacted if an outbreak were to occur, while the latter attempts to estimate beetle population trends. For example, a system to forecast infestation trends (increasing, static, declining) and relative population levels (high, moderate, low) of *D. frontalis* has been developed and implemented in the southeastern United States based on the captures of the pest and its major predator, the clerid *Thanasimus dubius* (Billings and Upton 2010).

Preventive measures that reduce the amount of slash material (woody debris from logging operations or forest disturbances) can help minimize populations of some bark beetles (Fettig et al. 2007). It is also important to select the appropriate tree species for the site, as well as spacing intervals that minimize tree competition. Treatments such as thinning, are recommended to enhance tree vigor, and therefore, increase forests resilience towards bark beetles.

Thinning is a silvicultural treatment with the objective to reduce stand density to improve growth and forest health (Helms 1998). Several benefits arise from thinning, such as enhanced growing space for desirable trees, increased tree vigor, reduced fire, insect, and pathogen risks, and the production of early economic benefits. Depending on the objective of the thinning, as well as the tree species involved, different practices can be used. Low thinning removes trees from smaller diameter classes, crown thinning removes mid-canopy trees, and selection thinning removes the largest trees (Fettig et al. 2007). This is a widely used method and, if conducted properly without creating physical damage to residual trees, thinning reduces bark beetle attacks and therefore, tree mortality. For southern pine beetle for example, landscape-level preventative thinning is the most economical and sustainable approach to the mitigation of epidemics (Asaro et al. 2017). In more than 10 states, the Forest Service offers the Southern Pine Beetle Assistance and Prevention Program, which promotes

proactive management practices by reimbursing landowners for thinning, prescribed burning, or other management plans (Nowak et al. 2008).

The relationship between silvicultural thinning and significantly reduced tree mortality during outbreaks has been experimentally reported for the two most severe bark beetle pests in North America, *D. ponderosa* and *D. frontalis* (Fettig et al. 2007; Asaro et al. 2017). Thinning is usually conducted during periods of reduced beetle activity; however, for *D. frontalis* for example, thinning can be conducted during periods of beetle activity with limited risk if logging damage and slash material is minimized (Fettig et al. 2007). For secondary bark beetles, such as *Ips* spp., slash or damaged hosts are important for the growth of infestations, particularly in areas with high beetle populations. For *Ips typographus* for example, removal of windthrown timber is one of the most important management strategies. Moreover, these logs can act as trap trees if removed after infestation but before emergence (Göthlin et al. 2000).

In planted forests, breeding sites of these secondary bark beetles occur mostly in slash material produced by pruning and thinning, thus management of slash material is an essential tool for reducing bark beetle populations. Chipping slash residual has been proposed as a strategy to reduce breeding sites and retain biomass for nutrient cycling, however, some authors have shown that the high concentration of monoterpenes and other volatiles associated with chipping actually increases the risk of standing trees being attacked compared to scattered logs (Fettig et al. 2007). Prescribed fire, used to enhance wildlife habitat, reduce fuels, and control pests, can stress standing trees and increase susceptibility to bark beetles (Elkin and Reid 2004). Some studies have associated prescribed fires, when not properly conducted, to infestations of *D. frontalis* in the southeastern United States, but usually fire increases populations of less threatening bark beetles such as *Ips* spp. and *Dendroctonus terebrans* (Sullivan et al. 2003).

Direct control measures include insecticides, mass trapping, mating disruption, biological control, or sanitation harvests. These methods are costly, meaning that their implementation will depend on budget, equipment, and market conditions. Hence, the first step is to identify which spots are more likely to expand (Billings and Ward 1984).

Sanitation harvesting (cut-and-remove trees to remove pests) is the preferred control tactic for species like *D. frontalis* (George and Beal 1929) because it is still the most effective. Harvesting trees infested by the beetles, as well as a 15 to 30 m (1–2 tree lengths) buffer zone of uninfested trees, can stop spot growth (Billings 2011). However, sometimes salvage logging (harvest to recover some economic value) is not possible, either because of socio-political and economic hurdles (as has been the case with *D. frontalis* in the southeastern US recently), or because complex terrain in remote locations can make salvage impractical, as can be the case in the western US and Canada. For *I. typographus*, sanitation harvesting is the most effective direct management approach. However, trees need to be cut before adults emerge and logs need to be either debarked, burned or chipped before storing or removed from the forest. Debarking can be highly effective because it causes 93% mortality of the beetles (Dubbel 1993).

When cut-and-remove operations are not possible, cut-and-leave tactics are the next best option (Fig. 10.6). This control method is based on felling all freshly attacked or infested trees towards the center of the spot, in addition to a buffer zone of uninfested trees in the expanding front (Fig. 10.6), usually as wide as the average tree height (Billings and Schmidtke 2002; Fettig et al. 2007). This technique is effective because it increases solar radiation and causes less favorable microclimatic conditions for further bark beetle development, while also increasing competition with wood borers and other antagonists.

Insecticides are important control measures for some species, such a *D. ponderosae*, but the use is regulated by different agencies and approved chemicals vary among jurisdictions. Usually, insecticides are only utilized to preventatively protect unattacked or lightly attacked high value trees, such as the ones grown in urban environments or trees growing in progeny tests or seed orchards (Fettig and Hilszczański 2015). Most treatments involve spraying the tree trunk or any part that is likely to be attacked by the targeted species usually in late spring prior to adult flight. Injection of systemic insecticides to the trunk can also be used, as the product is transported throughout the tree. For example, the application of systemic pesticides, particularly emamectin benzoate, can protect high-value trees from the attack of *D. frontalis* during outbreaks (Grosman et al. 2009).

Semiochemicals, mainly used as attractants or anti-aggregation compounds in forest management, can also be employed for mass trapping, but usually these traps will not capture a significant portion of the population and catches do not necessarily correlate with high infestations (Weslien and Lindelow 1990; Dodds and Ross 2002). Moreover, some beetles attracted to these traps may infest adjacent trees causing additional mortality (Fettig and Hilszczański 2015). In some cases, such as in push–pull strategies, mass trapping devices are combined with repellents so to deter beetle attack of high quality stands or trees. Antiaggregation pheromones, such as verbenone for several species of *Dendroctonus*, are widely used to protect individual trees or forest stands. These inhibitors are usually placed as pouched release devices on individual trees before beetle flight. For *D. frontalis* for example, both male and female pheromones are used for monitoring purposes (Sullivan and Mori 2009). The female pheromone (frontalin) is deployed in multi-funnel traps, while the male pheromone ((+)-endo-brevicomin) is deployed a few meters away from the frontalin trap to significantly enhance its synergistic effect on *D. frontalis* attraction. For *I. typographus* pheromone traps baited with cis-verbenol, ipsdienol and 2-methyl-3-buten-2-ol are used to prevent attacks on living trees and for monitoring. However, catches depend on environmental and local conditions, such as temperature, sun exposure, and the presence of woody debris, slash, and susceptible trees (Lobinger 1995; Wermelinger 2004; Fettig and Hilszczański 2015).

Nonhost volatiles (NHV), released by nonhost angiosperm plants, have been shown to inhibit pheromone attraction and orientation response in several conifer bark beetle species (Byers et al. 1998; Zhang 2003). The combination of NHVs with anti-aggregation pheromones can provide potent treatments to protect trees, logs, or stands from attacks by bark beetles (Huber et al. 2001). Even though semiochemicals are widely used in bark beetle management, more studies on blends and delivery

Fig. 10.6 Top: Cut-and-leave management strategy for Southern Pine Beetle (*Dendroctonus frontalis*) damage in Honduras. Bottom: Buffer zone during direct control management for Southern Pine Beetle (*Dendroctonus frontalis*) damage in Honduras. Photographs by Ronald Billings, US Forest Service

systems are needed, as well as the performance of the semiochemicals on different hosts and beetle populations (Fettig and Hilszczański 2015).

Biological control using predators or parasitoids has been used with success to control bark beetle populations. In China, the predator *Rhizophagus grandis* (Coleoptera: Rhizophagidae) has been used to control introduced *Dendroctonus valens* in pine forests (Yang et al. 2014). Entomopathogenic fungi, mainly *Beauveria bassiana*, have been effective at causing high mortality in several bark beetle species (Whitney et al. 1984). Inoculating beetles collected in baited traps and then releasing them back into the field has been suggested (Kreutz et al. 2000), but more practical methods should be developed because of low infection rates in field trials compared to laboratory conditions.

10.4.1   Emerging Pests

10.4.1.1   *Acanthotomicus suncei* **Cognato**

The sweetgum inscriber, *Acanthotomicus suncei*, is a polygynous species, in which the male starts the gallery and is later joined by one to three females (Gao and Cognato 2018) (Fig. 10.7). Galleries are usually horizontal ranging from 5 to 10 cm and trees as small as 2 cm diameter can be attacked. This endemic Chinese species has been recently reported to cause severe damage to a sweetgum native to North America, *Liquidambar styraciflua*, planted as an ornamental tree in China (Gao et al. 2017) (Fig. 10.7). The outbreak occurred in nurseries and urban trees in the Shanghai area. Affected trees exude resin from wounds and branches wilt and die. As it is observed in conifer-feeding bark beetles, the accumulation of attackers eventually exhausts tree defenses and kills the tree. Outbreaks develop quickly and the extent of the damage is unknown outside the evaluated localities. Economic losses are estimated around US$ 4 million from the loss of more than ten thousand trees. Arrival of this species to North America would be cause for concern for the health of native *L. styraciflua*. A recent economic analysis suggests a potential economic loss of US$ 150 million to US forest industries (Susaeta et al. 2017).

10.4.1.2   *Cyrtogenius luteus* **(Blandford)**

Cyrtogenius luteus is an Asian bark beetle that attacks stressed or dying trees, with no economic significance recorded in its native range (Fig. 10.7). It is a polygynous species that flies mainly in summer, but colonization has also been observed in spring (Gómez et al. 2017). Irregular star-shaped galleries are bored in the phloem and eggs are laid in niches on the side (Gómez et al. 2012). Larvae will bore irregular galleries and after pupation, adults will emerge through individual exit holes. Since 2009, it has been recorded in South America (Uruguay) and Europe (Italy) (Faccoli et al. 2012; Gómez et al. 2012). More recently, it has also been reported from southern
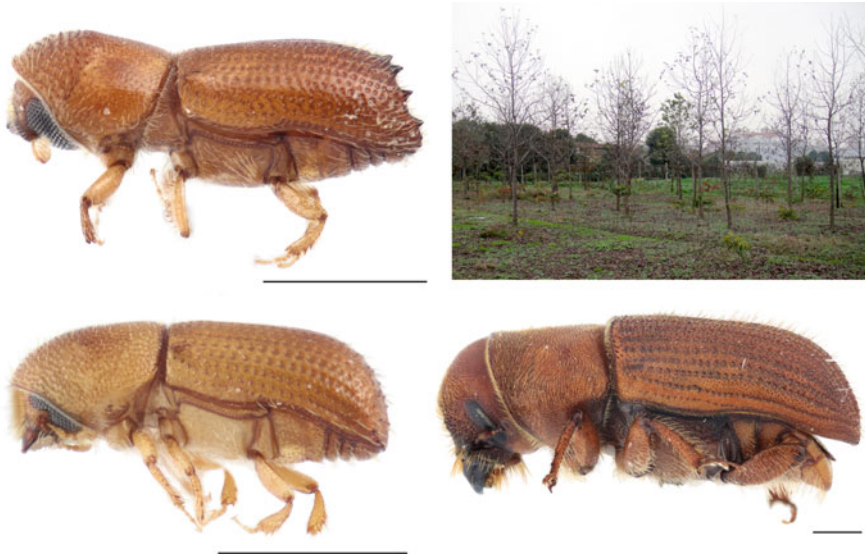
Fig. 10.7 From left to right, top to bottom, lateral view of *Acanthotomicus suncei* (photograph by Demian F. Gomez, University of Florida), commercial nursery of sweetgum attacked by *Acanthotomicus suncei* in Shanghai, China (photograph by You Li, University of Florida), lateral view of *Cyrtogenius luteus* (photograph by Demian F. Gomez, University of Florida), lateral view of *Dendroctonus valens* (photograph by Demian F. Gomez, University of Florida). Scale bars: 1.0 mm

Brazil (Flechtmann and Atkinson 2018), where it occurs since 2006. In Italy, it has been mostly recorded from traps and no economic damage has been reported. In South America, where commercial forestry has been increasing exponentially in the last two decades, *C. luteus* is usually associated with *Pinus taeda*, the most common planted pine tree species in Brazil and Uruguay. However, observations from Brazil suggest that this species might be colonizing the native Brazilian conifer *Araucaria angustifolia*, as it has only been recovered from traps deployed 30 km away from the closest pine plantation (Flechtmann and Atkinson 2018). Even though *C. luteus* appears to behave as a secondary pest in Asia, attacking only dying trees, several infested apparently healthy pine stands have been reported in Uruguay (Gómez et al. 2012). In commercial plantations of *P. taeda,* 80% of the stand is affected with losses up to 20 hectares (Fig. 10.7). However, this observation was made after significant drought periods in dense stands. In Brazil and Italy, no significant damage to live trees has been recorded (Faccoli et al. 2012; Flechtmann and Atkinson 2018).

10.4.1.3   *Dendroctonus valens* **LeConte**

Dendroctonus valens is widely distributed in North and Central America, ranging from Canada to the western United States, Mexico, Guatemala, and Honduras (Fig. 10.7). It is rarely a problem in its native range, but was introduced into China

where it has become a pest. After its first detection in the Shanxi Province in northern China in 1998, it has been spreading to adjacent provinces causing unprecedented tree mortality to *Pinus tabuliformis* (Yan et al. 2005). This beetle species has the broadest host range within the genus (Six and Bracewell 2015) and usually reproduces in living trees, but is highly attracted to injured, weakened, and dying trees (Fettig et al. 2004).

10.4.2   Bark Beetle Management in a Changing World

From a landscape perspective, the abundance and distribution of susceptible hosts play an important role in the distribution of bark beetles. Outbreaks occur when favorable environmental and host conditions occur. Silvicultural treatments that increase forest resilience may become even more important to stave off pest problems as climate change and invasive species introductions continue. Insects are attracted to highly concentrated patches of their hosts (Root 1973), and large forested areas with little heterogeneity make certain regions highly susceptible to outbreaks. As a result, the spatial arrangement of stands of similar age and species is relevant to reducing levels of tree mortality (Samman and Logan 2000; Jactel and Brocker-hoff 2007). However, this does not mean that desirable forest conditions are free of disturbances. Forests can be both productive and sustainable, but this condition in a forest ecosystem also involves dead and dying trees. From an ecological perspective, healthy amounts of insects and pathogens are needed to keep a baseline tree mortality (Castello and Teale 2011). Beyond this baseline the impacts of insects can cause mortality with more negative consequences.

Forest insects and pathogens are seen as problems when they interfere with management objectives, but the conditions that favor insect or disease problems are usually the result of past or present human activity, such as method of harvesting, and spatial and temporal patterns in tree size, tree species, among others. For many eruptive forest insects, the existing knowledge on the drivers of outbreak eruptions and crashes is insufficient to face current challenges. Biotic variables that affect bark beetle population dynamics need to be compiled, and hypotheses on their role and their interaction with anthropogenic change need to be developed (Biedermann et al. 2019).

For severe outbreaks to occur, there must be several years of favorable weather that enhance population growth, and an abundance of susceptible trees. Increasingly, climate change is playing a substantial role in these interactions. Recent examples of drought-related tree mortality suggest that all forest types are vulnerable to climate change (Allen et al. 2010). Moreover, outbreaks of bark beetles and other insect pests are increasing in severity and frequency. Climatic changes are predicted to significantly affect the frequency and severity of disturbances, as higher latitudes and elevations will be more susceptible to bark beetle outbreaks and the resulting tree mortality in the next decades (Bentz et al. 2010).

Market forces also play a significant role in bark beetle management. For example, during the SPB outbreak of 2012 in Missisipi, cut-and-leave was the primary suppression method for 407 hectares (201 spots), whereas less than 12 hectares were treated with cut-and-remove (Meeker 2013).

Despite the effectiveness of management strategies, changing forest structure to improve resiliency is perhaps the best long-term plan for coping with climate change. Regional and international networks should support countries to increase local knowledge and forest management capacity. Cooperation among forest scientists, landowners, and governmental stakeholders is key, and will ultimately help with developing long-term and evidence-based solutions to manage outbreaks of the bark beetles (Biedermann et al. 2019). Bark beetle outbreaks will keep increasing as long as susceptible forests and favorable climatic conditions coincide.

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