

Chapter 12

Woodborers in Forest Stands



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12.1 Introduction

The term woodborer is used to describe a polyphyletic group of insects that primarily inhabit the wood of angiosperm and conifer trees in various stages of decay. In the broadest sense, this term includes any insect that inhabits tissues of living woody plants or wood at any stage of the decay process. Common wood associates include Coleoptera (beetles), Hymenoptera (ants, wasps), Lepidoptera (moths), Diptera (flies) and Blattodea (termites and cockroaches). For this chapter, however, we focus on woodborer families that represent the majority of both ecologically and economically important species worldwide. These will include members of two beetle families (Buprestidae, Cerambycidae) as well as woodwasps (Hymenoptera: Siricidae) (Fig. 12.1). Another woodborer group, ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are covered in depth in Chapter 11. Finally, while there is some overlap in pests of urban and natural forests, this chapter will focus on woodborers of natural and managed forested ecosystems.

While woodborers have gained notoriety based on invasion success of a few species, such as the emerald ash borer (*Agrilus planipennis* Fairmaire) in

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Fig. 12.1 Examples of common woodborers, including **a** *Dicerca divaricata* (Buprestidae), **b** *Monochamus scutellatus* (Cerambycidae), and **c** *Sirex noctilio* (Siricidae). Photo credit: Kevin Dodds

North America and Russia, Asian longhorned beetle [*Anoplophora glabripennis* (Motschulsky)] in North America and Europe, and Sirex woodwasp (*Sirex noctilio* F.) throughout much of the Southern Hemisphere, the majority of insects in these families provide important ecosystem services and rarely develop into epidemic populations that cause economic losses or severe ecological impacts. Most of these species inhabit dead woody material, with the exception being species colonizing and sometimes killing living, healthy trees. Woodborers are cornerstones of decay processes through material fragmentation, introduction of fungi, and wood digestion (Edmonds and Eglitis 1989; Martius 1997; Hadfield and Magelssen 2006; Parker et al. 2006; Ulyshen 2016). They create and/or facilitate access to habitat for other

species (Georgiev et al. 2004; Buse et al. 2008) and are important components of forest food webs (Murphy and Lehnhausen 1998; Hunt 2000).

The Buprestidae and Cerambycidae represent diverse families that can be found in all woody plant parts and most wood decay stages. Worldwide, there are between 12,000 and 15,000 species of Buprestidae (Bright 1987; Bellamy 2002; Evans et al. 2004), while there are approximately 36,300 cerambycid species (Monné et al. 2017). Siricidae have much less diversity in the family compared to buprestids and cerambycids, with ~122 species worldwide from 10 genera (Schiff et al. 2012).

12.2 Natural History/Ecology of Woodborers

12.2.1 Woodborer Habitat

Some cerambycids and buprestids are found in vines and herbaceous plants (Bellamy and Nelson 2002), however, the majority, along with siricids, are found in hardwood and conifer tree tissues. Collectively, these insects inhabit all vertical portions of trees, from the roots up to small twigs in crowns, and even within leaves (Hespenheide 1991; Bellamy and Nelson 2002). Horizontally in wood, all tissues from the outer bark to heartwood are also colonized by woodborers during some portion of the decay process, with insects and their associates capable of gaining nutrition from even seemingly poor habitat (Haack and Slansky 1987). Woodborers spend most of their lives developing within host material, then emerge to locate hosts, mate, and reproduce. Eggs are laid on or within specific plant tissues on which early instar larvae establish and feed. Some species may feed sequentially on different tissues in later instars as development progresses (Donley and Acciavatti 1980; Hu et al. 2009).

Generically, woodborers are often referred to by the plant tissues or tree portions on which they feed, such as phloem, sapwood, heartwood, root and bole borers, or twig girdlers. In regard to nutrition, phloeophagous species gain all their nutrition from the phloem/cambium layer, but some may also enter the sapwood for further feeding and/or pupation (e.g. *Monochamus* Guérin spp., *Anoplophora* Hope spp.). Xylophagous species generally gain most of their nutrition from sapwood and/or heartwood and are found deeper inside trees. However, some of these species may briefly feed in the phloem. Aside from the outer bark that is of limited nutritional value, nutritional quality diminishes from the bark of trees inwards to the heartwood (Haack and Slansky 1987). Outside of the phloem/cambium layer, tissues are dominated by cellulose, hemicellulose, and lignin, all compounds that are more difficult to digest and require specialized enzymes to aid in acquisition (Stokland 2012). Woodborers developing within these tissues may take longer to develop (Haack and Slansky 1987). In addition to vertical and horizontal feeding on trees, there is a temporal aspect to food resources where woodborers are often associated with

specific stages of tree death or wood decay (Howden and Vogt 1951; Saint-Germain et al. 2007; Ulyshen and Hanula 2010; Ferro et al. 2012).

Both spatial and temporal partitioning occurs with woodborers that utilize the same habitat. For example, succession and resource partitioning, similar to what has been observed in conifer inhabiting bark beetles (Paine et al. 1981; Ayres et al. 2001) likely occurs among woodborers in dying or recently dead conifers. On available stressed or dying trees, or fresh stumps and windfall, woodborer genera such as *Tetropium* Kirby and *Asemum* Eschscholtz may colonize lower bole positions (Lowell et al. 1992), while genera such as *Monochamus*, *Sirex*, and *Xylotrechus* Chevrolat colonize mid- and upper-bole positions. Other genera of buprestids and cerambycids also colonize the crowns. Horizontal partitioning can occur simultaneously to vertical partitioning, with some cerambycids, buprestids, and siricids in the sapwood, while other species of buprestids and cerambycids feed primarily in the phloem and occur only shallowly in the sapwood.

Temporally, phloeophagous woodborers arrive early where some may compete with bark beetles colonizing the same material (Dodds and Stephen 2002). Some of these woodborers, like *Monochamus* spp., utilize kairomones (e.g. host volatiles, bark beetle pheromones) to locate freshly killed or stressed trees quickly (Allison et al. 2001; Miller 2006; Miller et al. 2011). Species that specialize on sapwood or heartwood may arrive later. Their colonization period may be longer as their habitat is less ephemeral and remains suitable longer after tree death. As trees begin to decay, species such as *Orthosoma brunneum* (Forster) that specialize on more decayed material arrive and colonize the trees or logs (Craighead 1950).

12.2.2 *Live Tree Inhabitants*

With the exception of invasive species, it is rare for woodborers to kill healthy living trees. However, living trees do provide habitat for cerambycid and buprestid species. Tree roots, boles, crowns, and leaves provide habitat for specialized species that can tolerate or avoid host defenses. For example, some *Prionus* F. species colonize roots of living host trees (Duffy 1946; Benham and Farrar 1976). Bole specialists, like the sugar maple borer [*Glycobius speciosus* (Say)] and locust borer [*Megacyllene robiniae* (Forst.)], colonize living trees and cause damage through their feeding activities (MacAloney 1971) (Fig. 12.2a). The buprestid *Coraebus undatus* (F.) colonizes the boles of living cork oak trees and can negatively impact cork harvesting (Jiménez et al. 2012). In some cases, these trees may be slow growing or under some other form of stress that allows the establishment of these woodborers (Newton and Allen 1982; O'Leary et al. 2003). Feeding damage by woodborers often causes stem failure, or further degrade of tree health that eventually results in tree mortality (Galford 1984).

Another woodborer guild of live tree inhabitants specializes in colonizing crowns of trees and includes twig girdlers, twig pruners, and leaf-mining species. Twig girdlers such as *Oncideres cingulata* (Say) can damage >40% of twigs (Forcella 1984), and as a result can reduce timber quality and height growth in hickory

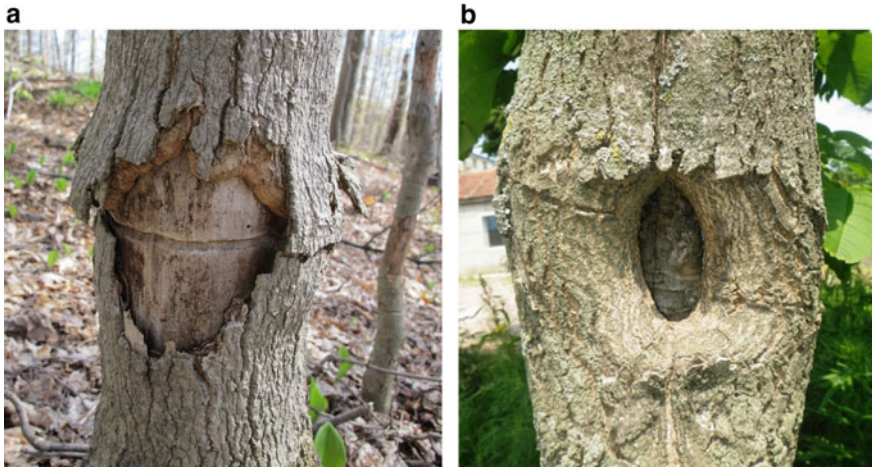


Fig. 12.2 Two examples of woodborer damage to living trees: **a** Damage caused to a living sugar maple (*Acer saccharum*) by the sugar maple borer, *Glycobius speciosus* in central New York, USA. **b** Wound periderm surrounding an unsuccessful attempt at colonization by *Agrilus planipennis* on stem of a *Fraxinus mandshurica* tree in Jilin province, China. The typical sinusoidal larval gallery is apparent but lack of an exit hole indicates the larva did not complete development. Photo credits: **a** Kevin Dodds; **b** Jon Sweeney

(Kennedy et al. 1961). Even though trees attacked by twig girdlers may appear healthy, there is some evidence that these beetles are attracted to stressed trees (Ansley et al. 1990). Twig pruners, such as *Anelaphus villosus* (F.) that colonizes various hardwoods, have larval stages that feed within branches, effectively killing those sections of trees. Similarly, some buprestids, such as *Agrilus arcuatus* Say in hickories, colonize and kill branches of healthy trees (Brooks 1926). Some species of buprestids are leafminers and do not bore in wood at all (Weiss and Nicolay 1919; Bellamy 2002; Queiroz 2002).

While few woodborers use living trees for larval development, many species use living plant material as an adult food resource. Adult feeding in woodborers is common in cerambycids and buprestids (Bright 1987; Hanks 1999; Bellamy 2002; Haack 2017) but does not occur in siricids. Many buprestids and cerambycids feed as adults and need a period of maturation feeding before mating and oviposition can occur (Linsley 1961; Hanks 1999; Poland and McCullough 2006; Lopez and Hoddle 2014). The primary source of nutrition for woodborer adults that do feed is plant material, including phloem tissue, floral resources (nectar, pollen, etc.), thin bark tissue, and leaves and needles (Linsley 1959; Hanks 1999).

12.2.3 *Generic Life Cycle*

The following is a generalized life cycle and given the size of the guild, it is not surprising that exceptions exist. The woodborers covered in this chapter are all holometabolous insects. Sexual reproduction is typical for buprestids and cerambycids, while siricids are parthenogenetic and can lay viable eggs (males) without mating. Fertilized eggs are necessary to produce female brood. Mating generally occurs on the host plant for most woodborers, with females laying eggs on the bark or under bark scales, in the phloem/cambium region or directly into the sapwood. In most species, males are not present when the female oviposits. However, post-copulation mate guarding does occur in some species (Hughes 1979; Hanks et al. 1996a; Wang and Zeng 2004; Godínez-Aguilar et al. 2009). Developing larvae of all woodborers either feed directly on plant tissue, or on associated fungi that females inoculate into trees (Madden 1981; but see Thompson et al. 2013), or on plant material that has been partially digested and broken down by associated organisms (Adams et al. 2011; Thompson et al. 2014). Larvae may go through as few as 3 or as many as 15 larval instars before they pupate; the number of instars varies both intra- and interspecifically and can be affected by temperature, photoperiod, and food quantity and quality (Esperk et al. 2007). Most species developing in the phloem tissue pupate in this region (Ness 1920) or go into the sapwood to pupate (Webb 1910) but some in the Lepturinae subfamily leave the larval host and pupate in the soil (Iwata et al. 2004). Most sapwood colonizers pupate within the same region where larval development occurs. After successful pupation, newly formed adults chew through the sapwood and/or bark to emerge and disperse from host trees.

12.2.4 *Importance of Symbionts*

There has been a longstanding understanding that symbionts are important in the nutrition of wood-feeding insects (Graham 1967) and molecular techniques are illuminating the diversity and function of these relationships (Grünwald et al. 2010). Common symbionts of cerambycids include bacteria, fungi, and yeasts (Douglas 1989; Schloss et al. 2006; Grünwald et al. 2010; Calderon and Berkov 2012). These symbionts can aid insects in several ways, but a primary role is the conversion of difficult-to-digest plant material (lignin, cellulose, hemicellulose) into useable nutrients (Delalibera et al. 2005). Some buprestids can digest cellulose (Martin 1991), but less is known about symbionts in this family. Siricids have an obligate symbiotic relationship with associated white-rot fungi (Gilbertson 1984). Cerambycids and siricids also ingest fungal enzymes that help break down wood (Kukor and Martin 1983, 1986; Kukor et al. 1988).

12.3 Population Regulation

Woodborer populations are affected by many abiotic and biotic factors and their interactions. Temperature, rainfall, and other weather variables affect woodborers directly (e.g. development rate, overwintering survival, foraging activity) as well as indirectly through the host plant (e.g. trees stressed by drought, flooding, wind storms or disturbances are often more susceptible to woodborer colonization) (Juutinen 1955; Hanks et al. 1999) and their impact on symbionts. The relative impact of these factors on woodborer populations varies among species according to their life histories, and within species, both temporally and spatially. We provide some examples of how climate, fire, and other disturbances affect the distribution and abundance of woodborers. We then discuss the influence of biotic factors on woodborer populations, including bottom-up effects like host tree availability and host defenses, intra- and interspecific competition, and top-down effects like parasitoids, predators, and pathogens.

12.3.1 Abiotic Factors

12.3.1.1 Climate

Each species has optimum temperatures for development and activity as well as minimum and maximum lethal temperatures and these play a large role in determining its geographic range. These temperature optima and limits may vary depending on the life stage and season, especially in temperate climates (Wellington 1954). There are also minimum and maximum threshold temperatures for development of each life stage and a minimum number of heat units (e.g. degree-hours or degree-days = accumulated time between the minimum and maximum threshold temperatures) required to complete development. For example, emerald ash borer larvae need at least 150 frost-free days for feeding (Wei et al. 2007) and have a 2-year life cycle in the most northern province of Heilongjiang in China (Yu 1992), a 1-year life cycle in the more southern Liaoning Province (Zhao et al. 2004) and a 1–2 year life cycle at intermediate latitudes in Jilin province (Wei et al. 2007) and the USA (Tluczek et al. 2011).

Rate of egg and larval development (Schimitschek 1929) as well as adult woodborer activity (Sánchez and Keena 2013) normally increases with temperature above the minimum threshold until temperatures exceed the optimum, beyond which development rate and survival are reduced (Keena and Moore 2010). Temperatures experienced by woodborer larvae in the microclimate under the bark of host trees often differ from ambient air temperatures, and this can affect predictions of overwintering mortality and development rates (Bolstad et al. 1997). For example, the minimum daily temperatures measured under the bark of ash trees were significantly warmer than those measured in the air (Vermunt et al. 2012). Although temperature is a

dominant factor affecting woodborer development rate, host condition also affects development rate, i.e. healthy vs. stressed or moribund, as discussed in Sect. 12.2.1.

Upper lethal temperature thresholds vary with species, life stage, and duration of exposure. For example, brown spruce longhorn beetle, *Tetropium fuscum* F., adults died after 30 min exposure to 40 °C and 15 min exposure to 45 °C, whereas mortality of pre-pupal larvae required 30 min exposure to 50 °C or 15 min exposure to 55 °C (Mushrow et al. 2004). Larvae of the emerald ash borer, on the other hand, have survived 30 min exposures to 60 °C (Myers et al. 2009). However, few life stages of woodboring species appear to survive exposure to temperatures >55 °C for 30 min (Pawson et al. 2019) and thus, heat treatment is a common phytosanitary treatment for solid wood packaging used for international shipping of goods. The International Standard for Phytosanitary Measures 15 (ISPM 15) requires that wood packaging be either fumigated or heated to 55 °C for 30 min to reduce the risk that it contains live woodborers (Humble 2010).

In temperate regions, overwintering success is a critical factor affecting the potential geographic range of woodborer populations. Cold hardiness is the capacity of insects to survive exposure to cold temperatures and it varies with species, developmental stage, season, intensity, frequency and duration of exposure, and nutritional status (Lee 1989; Marshall and Sinclair 2015). Some insects avoid freezing and enhance their cold hardiness by increasing the concentration of cryoprotectants (e.g. glycerol, glycogen) in the hemolymph (Danks 2000). The supercooling point (SCP) is the temperature at which ice crystals form in the hemolymph and is a useful index of cold hardiness. In general, the lower the SCP, the greater the cold hardiness. The SCP may vary significantly among species, among different geographic populations within species, and among individuals within populations (Feng et al. 2014). Cold hardiness also varies with time of year, e.g. the SCP of Japanese sawyer beetle larvae (*Monochamus alternatus* Hope) ranged from -6 °C in the summer to -15 °C in the winter (Ma et al. 2006). If minimum winter temperatures increase because of climate change, then distributions of woodborer populations may shift northwards, similar to what has been documented in bark beetles (Lesk et al. 2017). In addition to affecting development and survival of immature life stages, temperature affects adult activity and flight in wood boring beetles, e.g. in a mark-release-recapture study of the Eucalyptus longhorned beetle, *Phoracantha semipunctata* (F.), Hanks et al. (1998) concluded that adult dispersal flights declined sharply as air temperature dropped below about 22 °C.

12.3.1.2 Natural Disturbances

Natural disturbances can significantly increase populations of some woodborer species by greatly increasing the volume of weakened or freshly-felled host trees suitable for colonization (Gandhi et al. 2007). Haack et al. (2017) list many cerambycid genera whose populations increase following disturbances like drought, ice and windstorms, and fire, due to increased availability of stressed host trees. Infestations of *Tetropium* spp. and *Monochamus* spp. increased in spruce forests weakened

by windstorms in eastern North America, and their damage far exceeded that of the spruce beetle, *Dendroctonus rufipennis* (Kirby), which often erupts following severe wind events (Gardiner 1975). Both drought and flooding can increase tree moisture stress and susceptibility to woodborer colonization (Craighead 1937, 1950; Mattson and Haack 1987). Larval survival and damage by the locust borer, *M. robiniae*, increased during drought conditions (Craighead 1937). Drought is considered to be an important factor associated with the unprecedented outbreak of red oak borer, *Enaphalodes rufulus* (Haldeman), in red oak forests in Arkansas from 1999 to 2003 (Stephen et al. 2001; Haavik and Stephen 2010; Haavik et al. 2012b).

Fire can significantly affect woodborer populations by changing the distribution and abundance of suitable host trees and can directly suppress woodborer populations by destroying brood in infested trees. Felling and burning of infested trees in winter is sometimes used in sanitation control of satellite infestations of invasive woodborers, e.g. the brown spruce longhorn beetle in Nova Scotia, Canada (Fig. 12.3). Depending on the severity and extent of a forest fire, and the species of woodborer, fire can have positive and negative effects on host availability. For example, conversion of a mature forest to an early successional stage by a severe fire will reduce host availability for many years for woodborer species that favor large diameter, mature trees or other structural components associated with these forests. On the other hand, many species of woodborers prefer to colonize trees weakened or freshly killed by fire, so fires may greatly increase host availability and increase populations of these woodborers (Costello et al. 2013). Females of the longhorn beetle *Arhopalus ferus* (Mulsant) prefer to lay eggs on trees that have been damaged by fire (Hosking and Bain 1977) as do those of the buprestid, *Melanophila acuminata* (DeGeer) (Linsley 1943). The latter species has infrared-sensitive pit organs on the underside of their metathorax (Evans 1964, 1966) and it has been suggested that these are used to detect infrared radiation from forest fires as far away as 50 km (Linsley 1943) (Fig. 12.4).

12.3.2 Biotic Factors

12.3.2.1 Host Availability

Woodborer populations and their distribution on the landscape are significantly affected by the availability of suitable hosts, i.e. those in which broods can be successfully produced (Haavik et al. 2016), and this is affected by abiotic factors (discussed above) as well as biotic factors such as inter- and intraspecific competition (see Sect. 12.3.2.3). Host availability especially affects woodborers that specialize on one or few host species or genera and/or ephemeral host conditions. For example, *Tetropium* spp. and *Monochamus* spp. typically colonize stressed, dying or recently dead trees, and their populations have increased in conifer stands weakened by defoliator outbreaks (Basham and Belyea 1960; Haack 2017).

Some woodborer species are polyphagous while others breed in a single plant genus or species. For example, the linden borer, *Saperda vestita* Say, breeds only



Fig. 12.3 Sanitation burn of red spruce trees and stumps suspected of infestation by the brown spruce longhorn beetle, *Tetropium fuscum*, at a satellite infestation near Glenholme, Nova Scotia. Photo credit: Wayne MacKinnon, Natural Resources Canada, Canadian Forest Service

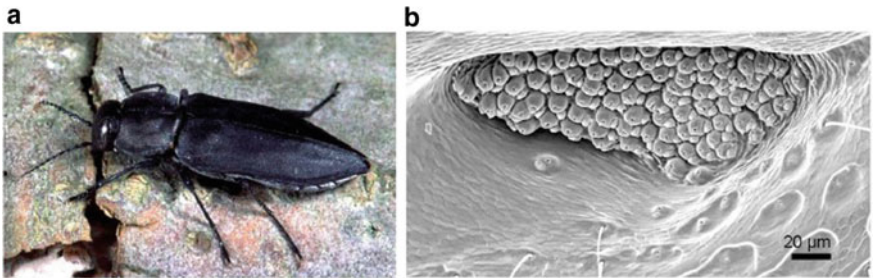


Fig. 12.4 **a** Adult of the “fire-loving” jewel beetle *Melanophila acuminata*; **b** Scanning electron microscope image of one of two infrared (IR) pit organs located between the base of the middle legs on the underside of the beetle’s thorax. Each IR pit organ has about 70 hemi-spherical IR sensilla. Reproduced with permission from Schmitz et al. (2009)

in dead and dying linden trees, *Tilia* L. spp. (Yanega 1996), whereas *Neoclytus acuminatus* (F.) breeds in at least 26 genera of broadleaf trees (Haack 2017). Larval feeding by most of the >3000 described species of jewel beetles in the genus *Agrilus* is restricted to a single genus or family of host plants, but there are several exceptions,

e.g. *Agrilus viridis* (L.) will colonize many genera such as *Betula* L., *Salix* L., and *Fagus* L. (Jendek and Poláková 2014).

Typically, species that feed in healthy trees tend to specialize on one or few host genera whereas those that feed in dead hosts tend to be polyphagous (Hanks 1999). But there are exceptions like *Anoplophora chinensis* (Forster) whose larvae can complete development in live healthy plants from at least 13 different genera (Sjöman et al. 2014). Even for polyphagous woodborers, there are differences among host species in terms of preference (by ovipositing females) and performance (survival and reproduction of offspring). For example, *A. glabripennis* has been recorded from 24 tree genera (Sjöman et al. 2014) but extensive surveys of infestations in Toronto, Canada (Turgeon et al. 2016) and Chicago, USA (Haack et al. 2006) found that *Acer* L. and *Ulmus* L. were clearly preferred to other tree species. Similarly, *A. glabripennis* has been recorded in seven genera in Northern Italy but 98% of infested trees belonged to only four genera (*Acer*, *Ulmus*, *Salix*, *Betula*) and both oviposition and larval survival was greatest on *Acer* (Faccoli and Favaro 2016). There are also differences in host preference or performance within genera. For example, oviposition and reproductive success of *A. glabripennis* were greater on *Acer rubrum* L. than on *A. platanoides* L. or *A. saccharum* Marsh. (Dodds et al. 2014b), emerald ash borer females lay significantly more eggs on highly susceptible North American ash species than on the more resistant Manchurian ash (*Fraxinus mandshurica* Rupr.) (Rigsby et al. 2014), and reproductive potential of *Monochamus galloprovincialis* Olivier was greater on *Pinus sylvestris* L. than on *Pinus nigra* Arnold (Akbulut 2009).

Host suitability also varies within tree species according to variables such as tree vigor, diameter, and bark thickness. Host condition (e.g. healthy *versus* stressed live trees, recently dead *versus* partially decomposed) affects the preference and/or performance of many wood boring species (Haack 2017). For example, colonization success of *P. semipunctata* larvae in *Eucalyptus* was significantly greater in fresh logs and moisture-stressed trees than in healthy trees (Hanks et al. 1991). As trees die and advance through stages of decay, there are successional changes in the woodborer community following changes in host condition and suitability for different species (Haack 2017).

Variability in host quality combined with the inability of woodborer larvae to move from the brood host selected by females may be responsible for the large intraspecific variation in adult body size (Andersen 1983). According to the preference-performance hypothesis (Jaenike 1978), females should preferentially oviposit in hosts that optimize offspring fitness. Results of some woodborer studies have supported this hypothesis and others have not. Survival and development rate of brown spruce longhorn beetles were greater in stressed than in healthy spruce (Flaherty et al. 2013a) and females landed 10 times more frequently and laid 3 times as many eggs on stressed trees than on healthy trees (Flaherty et al. 2013b). However, Hanks et al. (1993) found that survival of eucalyptus longhorn beetles in field trials was actually lower in preferred hosts, due to high larval densities and intense intraspecific competition; brood survival was greater in the preferred hosts only when larval densities were kept artificially low in laboratory studies.

12.3.2.2 Host Defenses

Tree defenses may be constitutive (always present) or induced (e.g. by herbivore feeding or fungal infection) and both types can significantly reduce survival and colonization success of herbivores, including woodborers (Raffa 1991; Phillips and Croteau 1999). Constitutive and induced resins (complex mixtures of phenolics and terpenoids) may prevent establishment of early instar larvae physically by drowning them or chemically by reducing food digestibility. Drowning of early instar larvae in host oleoresin is a major mortality factor in *T. fuscum* (Juutinen 1955), *Semanotus japonicas* Lacordaire (Shibata 1987, 2000; Kato 2005), and other woodborers that attack live but weakened hosts.

Trees may also increase toxin concentrations at the site of feeding and surround larvae with tougher, less digestible wound periderm tissue (Lieutier et al. 1991). Establishment and survival of early instar buprestid larvae in healthy trees is usually low due to callus formation (Evans et al. 2004; Chakraborty et al. 2014) (Fig. 12.2b). When trees are stressed, these defenses are reduced and larval establishment, colonization success, and woodborer populations increase. For example, incipient root rot in *Eucalyptus* was correlated with attack by the bullseye borer, *Phoracantha acanthocera* (Macleay) (Farr et al. 2000), extensive areas of *P. sylvestris* weakened by root rots were infested and killed by *Phaenops cyanea* (F.) in Germany in the late 1960s (Evans et al. 2004), and oaks undergoing temporary periods of stress from defoliation may be colonized and killed by *Agrilus biguttatus* (F.) in Europe (Moraal and Hilszczanski 2000) and *Agrilus bilineatus* (Weber) in North America (Dunbar and Stephens 1975).

Tree defenses are also less effective at preventing woodborer colonization of naïve hosts, i.e. tree species that have not coevolved with a woodborer species introduced to a new range. A good example of this phenomenon is the devastating mortality of North American ash, *Fraxinus* L. spp., caused by the exotic invasive emerald ash borer compared to the relatively benign effect of this insect on *Fraxinus* spp. in its native range (Poland and McCullough 2006; Herms and McCullough 2014). Similarly, “evolutionary naïve” Eurasian species of birch are far more susceptible to colonization and mortality by the Nearctic bronze birch borer, *Agrilus anxius* Gory, than are North American species of birch (Muilenburg and Herms 2012).

Development rate and survival of woodborer larvae that normally attack weakened hosts (e.g. brown spruce longhorn beetle, emerald ash borer) is lower in healthy trees than in stressed trees, likely due to differences in defensive compounds or host nutrients (Flaherty et al. 2011, 2013a; Tluczek et al. 2011). Growth rate of *Hylotrupes bajulus* L. larvae was negatively correlated with increases in secondary carbon-based compounds in *P. sylvestris* (Heijari et al. 2008). Low host nutritional quality and low moisture content can also prolong the development time of cerambycids and buprestids, with several cases where adults emerged from finished wood products up to 40 years after the presumed oviposition (Duffy 1953; Haack 2017).

Resistance of *Eucalyptus* L'Hér. to colonization by *P. semipunctata* is related to bark moisture content (Hanks et al. 1991) and resistance of *Populus tomentosa* Carr. to colonization by Asian longhorned beetle is related to bark glycoside and phenolic

acid content (Wang et al. 1995). The maintenance of healthy, vigorous trees is the best defense against attack by most species of cerambycids and buprestids (Evans et al. 2004). In addition to “bottom-up” factors like host availability and host defenses, woodborer populations are also regulated by “top-down” factors, i.e. natural enemies like parasitoids and predators, and these are discussed in Sect. 12.3.2.4.

12.3.2.3 Competition

Woodborers must compete for limited food and space with conspecifics as well as other species of woodborers and other insects and microorganisms that exploit the same host species and tissues. For example, 27 different species of longhorn beetles, plus a few species of buprestids, curculionids and other beetles were recorded co-inhabiting branches and small saplings of *Leucaena pulverulenta* (Schlect.) Benth. that had been girdled by the twig-girdler, *Oncideres pustulata* LeConte (Hovore and Penrose 1982).

Woodborers may be subject to indirect or exploitative competition, in which larvae that establish later have less food or space for development than earlier colonists (Ikeda 1979), or direct competition, i.e. cannibalism or intra-guild predation (Rose 1957; Anbutsu and Togashi 1997b; Dodds et al. 2001; Ware and Stephen 2006), or both (Powell 1982; Shibata 1987). Lower survival of brown spruce longhorned beetle in cut logs than girdled trees was partially attributed to interspecific competition with other species of phloem-feeding insects which were more numerous in cut logs than girdled trees (Flaherty et al. 2011). The impact of cannibalism on woodborer survival increases with larval densities (Richardson et al. 2010) and later colonists (i.e. smaller larvae) are usually the victims (Anbutsu and Togashi 1997b). Intraspecific competition resulting from overcrowding can be a major mortality factor of *P. semipunctata* (Powell 1982; Way et al. 1992; Hanks et al. 2005) and *Monochamus* spp. (Shibata 1987; Dodds et al. 2001; Akbulut et al. 2008). Larvae of the red oak borer will sometimes cannibalize one another (Ware and Stephen 2006) but subsequent life table studies indicated that intraspecific competition was not an important mortality factor (Haavik et al. 2012a).

Another form of intraspecific competition is when polygamous male cerambycid species compete with other conspecific males for access to females for mating, e.g. larger males of *Glenea cantor* (F.) have greater mating success than smaller males (Lu et al. 2013). Mate guarding, in which the male remains in copula or stays close to the female after copulation to prevent copulation with other males, occurs in several species of cerambycids (Fig. 12.5).

Fig. 12.5 Pair of *Moechtypa diphysis* adults on the stem of *Quercus mandshurica*. Note the pair are not in copula but the male remained mounted on the female for a prolonged period, possibly as a form of mate guarding to prevent her from mating with other males. Photo credit: Jon Sweeney



12.3.2.4 Natural Enemies

Parasitoids

Woodborers are parasitized by many species, mainly wasps (Hymenoptera), particularly the families Ichneumonidae and Braconidae, but also flies (Diptera: Tachinidae) and beetles (Coleoptera: Bothrideridae). Most woodborer parasitoids attack host larvae but some species exploit eggs and pupae (Yu et al. 2016). Some species are ectoparasitoids that feed externally on hosts while others are endoparasitoids that feed internally. Parasitoids can also be classified as idiobionts that kill or paralyze their host immediately following oviposition or koinobionts that allow their host to continue developing and consume it at a later stage (Askew and Shaw 1986). Koinobionts tend to have a narrower host range than idiobionts (Spradbery 1968) possibly because they have had to evolve defenses against host immune systems (Gauld 1988).

Table 12.1 lists some parasitoid genera recorded from cerambycids, buprestids and siricids, along with some features of their biology. Due to the cryptic nature of most woodborers, obtaining accurate host records of parasitoid species is not straightforward, but the associations of parasitoid genera with woodborer families in Table 12.1 may be considered accurate. In simple collections of parasitoids and woodborers that emerge from the same log or tree, it is generally not possible to know from which woodborer species the parasitoids emerged when more than one potential host woodborer species emerges. Molecular techniques have been used to a limited degree to associate emerging parasitoids from trees with more than one brood species (Foelker et al. 2016). Unequivocal woodborer species-parasitoid associations have generally been determined either by manipulative experiments that expose a single woodborer species to parasitoids or by isolating individual woodborer larvae from infested trees and then recording parasitoids that emerge.

Apart from a few pest species like *P. semipunctata*, emerald ash borer, *S. noctilio*, Asian longhorned beetle, and *M. galloprovincialis*, natural enemies of woodborers have not been the subject of much research, and few studies have documented their

Table 12.1 (continued)

Order/family/subfamily/genus	Cerambycidae		Buprestidae			Siricidae			
	EC	C	I	EC	BC	I	EC	C	I
<i>Odontocolon</i> Cushman	EC	C	I						
<i>Xorides</i> Latreille	EC	C	I	EC	BC	I			
Aulacidae									
Aulacinae									
<i>Pristaulacus</i> Keiffer	EN	C		EN					
Stephanidae									
Stephaninae									
<i>Foenatopus</i> Smith					B				
Schletteriinae									
<i>Schlettererius</i> Ashmead							EC	C	I
Braconidae									
Doryctinae									
<i>Callithormius</i> Ashmead	EC	B	I	EC	B				
<i>Doryctes</i> Haliday	EC	BC	I	EC	B				
<i>Ephyllus</i> Foerster	EC		I	EC	B				
<i>Heterospilus</i> Haliday	EC	BC	I	EC	B	I	G		
<i>Jarra</i> Marsh & Austin	EC	B	I						
<i>Leluthia</i> Cameron	EC		I	EC	B		G		

(continued)

Table 12.1 (continued)

Order/family/subfamily/genus	Cerambycidae			Buprestidae			Siricidae		
	EC	B	I						
<i>Onistra</i> Cameron	EC	B	I						
<i>Pareucorystes</i> Tobias	EC		I	EC	B				
<i>Polystenus</i> Foerster				EC	B	I			
<i>Rhoprocentrus</i> Marshall	EC	B	I	G					
<i>Spathius</i> Nees	EC	B	I	EC	BC	I			
<i>Syngaster</i> Brullé	EC	B	I						
Braconinae									
<i>Atanycolus</i> Foerster	EC	BC	I	EC	BC	I			
<i>Coeloides</i> Wesmael	EC	BC	I	EC	C	I			
<i>Cyanopterus</i> Haliday	EC	C	I						
<i>Digonogastra</i> Viereck	EC	C	I						
<i>Iphiaulax</i> Foerster	EC	BC	I	G	B	I	G		
<i>Megalomium</i> Szepligeti	EC	B	I						
<i>Monogonogastra</i> Viereck				EC	B	I			
Helcominae									
<i>Helcon</i> Nees	EN	BC	K						
<i>Helcomidea</i> Viereck	EN	C	K						
<i>Cenocoelius</i> Westwood	EN	B	K	EN	B	K			

(continued)

Table 12.1 (continued)

Order/family/subfamily/genus	Cerambycidae			Buprestidae			Siricidae		
	EN	BC	K	S	EN	B			
<i>Wroughtonia</i> Cameron	EN			S	EN	B			
Eulophidae									
Entedoninae									
<i>Entedon</i> Dalman					EN	B	K		
<i>Pediobius</i> Walker					EN	B			
Euderinae									
<i>Euderus</i> Haliday	EN	B			EN	B			
Tetrastichinae									
<i>Aprostocetus</i> Westwood	EN	B							
<i>Baryscapus</i> Foerster					EN	B			
<i>Quadrastichus</i> Girault					EN	B			
<i>Tetrastichus</i> Haliday					EN	B	K	S	
Encyrtidae									
Encyrtinae									
<i>Avetianella</i> Trjapitzin					E	B	I		
<i>Ooencyrtus</i> Ashmead					E	B	I		
<i>Oobius</i> Trjapitzin	E	B	I	S	E	B	I	S	
<i>Orianos</i> Noyes					E	B	I		

(continued)

Table 12.1 (continued)

Order/family/subfamily/genus	Cerambycidae	Buprestidae	Siricidae
Eupelmidae			
Calosotinae			
<i>Balcha</i> Walker		EC B I	
<i>Calosota</i> Curtis		EC B	
Eupelminae			
<i>Eupelmus</i> Dalman		E B	
Neanastatinae			
<i>Metapelma</i> Westwood		B	
Pteromalidae			
Clyonyminae			
<i>Cleonymus</i> Latreille	B		
<i>Oodera</i> Westwood		B	
Pteromalinae			
<i>Trigonoderus</i> Westwood		EC B	
<i>Zatropis</i> Crawford		B	
Chalcididae			
Chalcidinae			
<i>Phasgonophora</i> Westwood		B K S	

(continued)

Table 12.1 (continued)

Order/family/subfamily/genus	Cerambycidae			Buprestidae			Siricidae		
Ibalidae									
Ibaliinae									
<i>Ibalia</i> Latreille							EN	BC	K S
Bethylidae									
Epyrinae									
<i>Sclerodermus</i> Latreille	EC	B	I	G	EC	B	I	G	
Diptera									
Tachinidae									
Dexiinae									
<i>Billaea</i> Robineau-Desvoidy	EN	BC							
Coleoptera									
Bothriideridae									
<i>Dastarcus</i> Walker	EC	B		G					

Note ^akleptoparasite on *Rhyssa* spp.

Adapted from Kenis and Hilszczanski (2004), Schimitschek (2004), Finlayson (1969), Raske (1973), Wanjala and Khaemba (1987), Duan et al. (2009, 2016), Kenis and Hilszczanski (2004), Naves et al. (2005), Petrice et al. (2009), Li et al. (2010), Flaherty et al. (2011), Van Achterberg and Mehrmejad (2011), Coyle and Gandhi (2012), Schiff et al. (2012), Taylor et al. (2012), Roscoe et al. (2016), Triapitsyn et al. (2015), Golec et al. (2016), Jennings et al. (2017), Yu et al. (2016), and Paine (2017)

impact on woodborer population dynamics (Paine 2017). A multi-year life table study of the red oak borer concluded that competition and natural enemies contributed very little to mortality during the crash of the outbreak, and that tree defenses were more likely responsible (Haavik et al. 2012a). Similar results have been reported with the woodwasp *S. noctilio* (Haavik et al. 2015), although factorial exclusion trials suggest that biotic factors (e.g. competitors and their associated fungi, and natural enemies) may also be important in parts of the range (Haavik et al. 2020). However, relatively high parasitism rates have been recorded in some species, e.g. 20–75% mortality of *Tetropium gabrieli* Weise and *T. fuscum* in Europe (Schimitschek 1929; Juutinen 1955) and 22–28% mortality of *S. noctilio* (Long et al. 2009; Zylstra and Mastro 2012), suggesting parasitoids may be important in regulating populations of some woodborer species. Further evidence for this comes from successful biological control programs that are discussed in Sect. 12.7.2.3.

An interesting question is how parasitoids locate cryptic woodborer hosts beneath the bark and wood of a tree. Increased parasitism of bark beetles in stressed trees vs. healthy trees suggests that parasitoids may use volatiles emitted from stressed trees as olfactory cues associated with their hosts (Sullivan et al. 1997). Percent parasitism of *Tetropium* spp. (Flaherty et al. 2013a) and *Semanotus japonicus* (Shibata 2000) was greater in stressed trees than in healthy trees. After landing on a tree, some parasitoids use auditory cues to locate their hosts. Ichneumonid wasps in the Cryptini tribe have hammer-like structures on their antennae that they use to echo-locate wood boring larvae and pupae of both cerambycids and buprestids (Laurenne et al. 2009), and the braconid, *Syngaster lepidus* Brullé, uses chordotonal organs to detect the vibrational cues of *P. semipunctata* larvae feeding under the bark (Joyce et al. 2011). Aspects of a woodborer's host tree can affect the foraging success of its parasitoids. For example, the ovipositor of *Tetrastichus planipennis* Yang cannot penetrate >3.2 mm of bark so its effectiveness against emerald ash borer is restricted to smaller diameter trees (Abell et al. 2012). On the other hand, parasitism of *S. noctilio* by *Ibalia leucospoides ensiger* Norton peaked at bole diameters of 15 cm but was not affected by bark thickness (Eager et al. 2011).

Predators

Woodborers are attacked by a variety of predators (vertebrate and invertebrate), including beetles in the families Cleridae (e.g. *Thanasimus dubius* (Fabricius)), Trogossitidae (e.g. *Trogossita japonica* Reitter), and Elateridae (e.g. *Athous subfuscus* Müller), flies in the families Asilidae (e.g. *Laphria gibbosa* (L.)), Lonchaeidae (e.g. *Lonchae chorea* (F.)), Odiniidae (e.g. *Odinia xanthocera* Collin), Pallopteridae (e.g. *Palloptera usta* (Meighen)), crabronid wasps (e.g. *Cerceris fumipennis* (Say)), lacewings (e.g. *Raphidia xanthostigmus* Schummel), and earwigs (e.g. *Forficula auricularia* L.) (Kenis and Hilszczanski 2004). Ants prey on eggs of *P. semipunctata* (Way et al. 1992) and the red oak borer (Muilenburg et al. 2008). Woodpeckers (Piciformes: Picidae) are common and important predators of woodborers. Cerambycid larvae are the preferred food of woodpeckers (Pechacek and

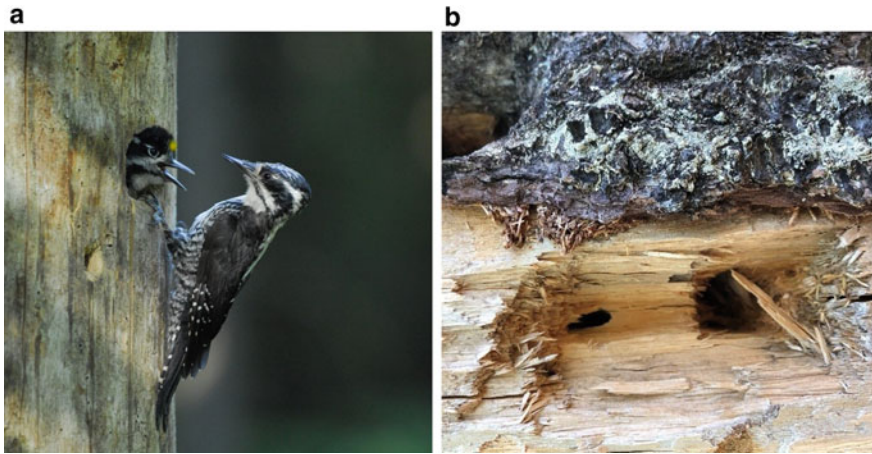


Fig. 12.6 **a** Three-toed woodpecker, *Picoides tridactylus* is a common predator of woodboring larvae in Europe. **b** Woodpeckers often excavate deeply into trees to find woodboring larvae. Photo credits: **a** Dariusz Graszka-Petrykowski; **b** Kevin Dodds

Kristin 2004) and their availability is critical to the reproductive success of the three-toed woodpecker, *Picoides tridactylus* L. in Europe (Fayt 2003) (Fig. 12.6). Woodpeckers mainly consume mature larvae and pupae and predation rates often increase as larval density increases (McCann and Harman 2003; Lindell et al. 2008; Flaherty et al. 2011) but not always [e.g. woodpecker-caused mortality of *P. semipunctata* decreased with increasing larval density in trap logs (Mendel et al. 1984)]. Wood-borer mortality from woodpeckers can be considerable, e.g. woodpeckers have been reported to consume 65% of oak branch borer, *Goes debilis* LeConte larvae (Solomon 1977) and 32–42% of emerald ash borer larvae (Duan et al. 2012).

Pathogens

Woodborers may be infected and killed by various pathogens like nematodes [e.g. *Steinernema carpocapsae* (Weiser)] and fungi [e.g. *Beauveria bassiana* (Bals.-Criv.), Vuill.] (Morales-Rodríguez et al. 2015; Liu et al. 2016). *Beauveria bassiana* caused significant natural mortality of the pine sawyer, *M. galloprovincialis* (Naves et al. 2008). *Beauveria pseudobassiana* Rehner & Humber, isolated from natural populations of the pine sawyer in Spain was highly virulent in lab tests, killing 100% of adults and significantly reducing adult lifespan and number of eggs laid, both via direct contact and by mating with infected beetles, i.e. horizontal transmission (Álvarez-Baz et al. 2015).

Entomopathogenic fungi such as *Beauveria* spp. and *Metarhizium anisopliae* (Metsch.) Sorok. have shown potential for applied control of woodborers. For example, direct application of aqueous suspensions of *B. bassiana* conidia (or

mitospores) to ash trees infested with emerald ash borer significantly reduced larval densities and the number of emerging adults in the next generation (Liu and Bauer 2008). Wrapping non-woven fabric strips impregnated with fungal conidia around host tree trunks was effective at infecting and killing *M. alternatus* Hope (Shimazu and Sato 1995; Shimazu 2004) and reducing longevity and fecundity of *A. glabripennis* (Dubois et al. 2004). Another method that has been tested for woodborer control is auto-dissemination, in which the target species is attracted to a trap baited with pheromone and/or host volatiles where it receives a dose of fungal conidia and is allowed to escape and horizontally transmit the pathogen within the local population (Klein and Lacey 1999; Lyons et al. 2012; Francardi et al. 2013; Sweeney et al. 2013; Álvarez-Baz et al. 2015; Srei et al. 2020).

One of the most interesting and successful examples of microbial control of woodborers is the use of the nematode, *Deladenus siridicola* Bedding for control of *S. noctilio*. The nematode does not kill the woodwasp but infected insects become sterile and the female spreads the nematode from tree to tree when depositing nematodes instead of eggs (Bedding and Akhurst 1974). For a more complete story on the woodwasp and its control by the nematode, see Chapter 17.

12.4 Ecological Roles

The vast majority of woodborers serve important ecological functions while inhabiting dead or stressed materials and provide critical services that benefit forested ecosystems. Important contributions from woodborers include facilitating nutrient cycling (Edmonds and Eglitis 1989; Cobb et al. 2010), influencing forest structure (Feller and McKee 1999), creating habitat (Buse et al. 2008), and providing food for predaceous invertebrates and vertebrates.

12.4.1 Nutrient Cycling

Saproxyllic woodborers are an important group of insects that help drive nutrient cycling in forested environments through the breakdown of dead wood (Fig. 12.7). Woodborers are some of the earliest arriving insects at stressed trees and dead wood (Savely 1939; Saint-Germain et al. 2007) and a successive community of these species colonize wood throughout the decay process (Graham 1925; Howden and Vogt 1951; Stokland and Siitonen 2012). Through their feeding and tunneling behavior, woodborers begin the process of fragmentation and nutrient cycling as well as exposing wood to other organisms, such as decay fungi, which are also important decomposers (Harmon et al. 1986; Edmonds and Eglitis 1989; Hadfield and Magelssen 2006; Parker et al. 2006). Woody debris is an important forest structure and can contain large sources of nutrients (Harmon et al. 1986). The return of nutrients to the soil through decomposition of dead wood is a critical ecosystem service and one that is aided by woodborers and other organisms (Edmonds and Eglitis 1989; Ulyshen 2016).

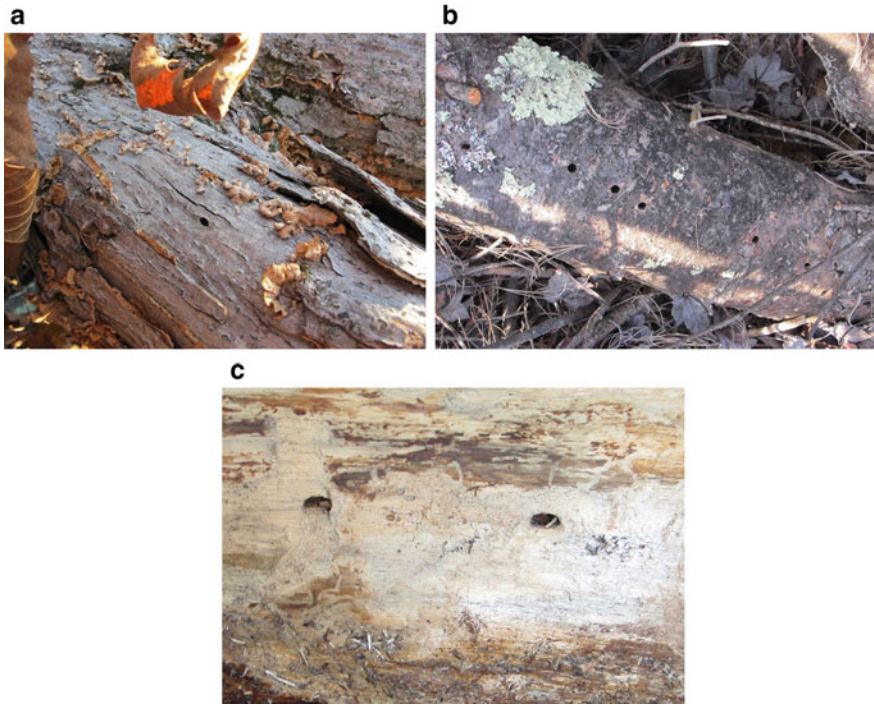


Fig. 12.7 Coarse woody debris at various stages of decay, including **a** wood with evidence of Buprestidae emergence and decay fungi, **b** Siricidae emergence, and **c** *Monochamus* sp. sapwood entrance holes. Photo credit: Kevin Dodds

While the relationship between woodborers and wood decay and nutrient cycling is well known, few studies have attempted to quantify this relationship. *Monochamus scutellatus* (Say) was an important contributor to Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco] log decay, most likely through providing pathways for decay fungi into larger diameter logs (Edmonds and Eglitis 1989). At small scales, *M. scutellatus* larval activity can influence total carbon and nitrogen in soil around infested logs (Cobb et al. 2010). Cerambycids were also a factor in decay of both deciduous and coniferous standing snags (Angers et al. 2011).

12.4.2 Forest Structure

Forest structural diversity, including standing snags and downed wood of various decay classes, is an important component of natural forests and an important reservoir of organic matter and forest nutrients (Harmon et al. 1986). Insects, such as woodborers and bark beetles, play a critical role in the creation of these structural

components either through directly killing trees, or colonizing this material and facilitating decay, thus creating additional habitat for saproxylic (Buse et al. 2008) and other organisms. Woodborers can drive changes in the structure (crown characteristics, bark attachment) and physical properties (wood density, moisture) of coarse woody debris. These changes to coarse woody debris are critical to maintaining biological diversity and help support healthy forest ecosystems (Harmon et al. 1986; Jia-bing et al. 2005).

In addition to the obvious contributions that woodborers make to forest structure through the breakdown and decay of standing and downed wood, they also influence stand structure through impacts on living trees. For example, the cerambycid, *Elaphidion mimeticum* Shaeffer is important for creating small-scale gaps in mangrove forests and subsequently promoting understory regeneration (Feller and McKee 1999). Black locust (*Robinia pseudoacacia* L.), an early successional tree species in North America, can be killed from successive years of *M. robiniae* attacks. Through this mortality, canopy gaps are created that allow more shade-intolerant tree species to become established (Boring and Swank 1984). Red oak borer in combination with other factors, can kill overstory trees that results in changes to residual forest structure (Heitzman et al. 2007; Haavik et al. 2012b). Stand structure in pine stands is also influenced by attack patterns of woodborers. For example, *S. noctilio* preferentially attacks and colonizes smaller suppressed trees (McKimm and Walls 1980; Dodds et al. 2010a). Species such as *Plectodera scalator* F. that colonize lower bole and root positions on trees can structurally weaken stems to a point where they break. Through these actions, *P. scalator* may influence the spatial structure of stands and regeneration.

The behavior of branch girdlers can also have an impact on forest structure. The cerambycid *Oncideres rhodosticta* Bates influences crown architecture of honey mesquite (*Prosopis glandulosa* Torr.) through its stem girdling behavior (Martínez et al. 2009) and the resultant branch-heavy crowns may be a critical factor in increased desertification in parts of the Chihuahuan Desert (Duval and Whitford 2008). Similarly, twig girdlers influenced understory crown architecture of *Dicorynia guianensis* Amshoff. (Caraglio et al. 2001). *Oncideres humeralis* Thomson influenced forest composition and structure in a Brazilian forest through species-specific tree attacks that likely allowed other tree species to respond to increased resources (Romero et al. 2005). Through their actions, these species can also influence the invertebrate community in these stands (Calderón-Cortés et al. 2011) and provide habitat for many other species (Lemes et al. 2015).

12.4.3 Ecosystem Services

Woodborer larvae represent a relatively large source of nutrition for animals foraging in wood. Woodpeckers are commonly seen foraging on dead standing or downed trees, and woodborers are a common prey item taken (Hanula et al. 1995; Murphy and Lehnhausen 1998; McCann and Harman 2003; Nappi et al. 2015). Crows have

also been reported to use twigs to extract larvae from wood (Hunt 2000). Adult cerambycids are reported as prey for bats (Medellín 1988), owls (Haw et al. 2001), pitcher plants (Cresswell 1991), lizards (Vitt and Cooper 1986) and passerines (Tryjanowski et al. 2003). Predaceous insects attack all stages of woodborers and are important factors in population regulation as previously discussed in section “Predators”.

Pollination is an important ecosystem service carried out by a diverse group of insects that includes woodborers. Cerambycids, especially from the subfamily Lepturinae, feed on pollen as adults (Linsley and Chemsak 1972) and are frequently found with pollen on their integument (Willemstein 1987). Buprestids have also been commonly associated with plants as pollinators (Williams and Williams 1983). Siricids, however, with their lack of adult feeding, are not known to serve a role in pollination.

Because of their impacts on plants, several woodborers have been introduced into new environments as biological control agents against unwanted invasive plants. Several species have been introduced targeting the invasive plant, *Lantana camara* (L.), including the cerambycids *Plagiohammis spinipennis* (Thomsom) in Hawaii (Broughton 2000) and *Aerenicopsis championi* Bates in Australia (Palmer et al. 2000). Australia has successfully introduced other woodborer species for invasive plant management including the cerambycids *Aldidion cereicola* Fisher targeting *Harrisia* Britton cactus (McFadyen and Fidalgo 1976) and *Megacyllene mellyi* (Chevrolat) for *Baccharis halimifolia* L. management (McFadyen 1983), and the buprestid *Hylaeogena jureceki* Obenberger targeting cats claw creeper (Dhileepan et al. 2013). South Africa has also released *A. cereicola* for *Harrisia* cactus management (Klein 1999) and *H. jureceki* for cats claw creeper (King et al. 2011). North American woodborer releases have included *Oberea erythrocephala* (Schrank) (Cerambycidae) targeting leafy spurge (Rees et al. 1986), and the buprestids *Sphenoptea jugoslavica* Obenb. and *Agrilus hyperici* (Creutzer) for knapweed (Powell and Myers 1988; Harris and Shorthouse 1996) and St. Johns wort (Campbell and McCaffrey 1991), respectively.

12.4.4 Woodborer Conservation

Some species of woodborers are rarely observed and may be in danger of extirpation due to loss of suitable habitat and hosts. Many species feed in dead and decaying heartwood of ancient “veteran” trees and these trees have become increasingly rare in Europe (Nieto and Alexander 2010). Forestry practices that leave less dead wood in the forest have resulted in declining populations of some wood boring beetles, e.g. *Cerambyx cerdo* L. is listed as “near threatened” in Europe (Evans et al. 2004). Similarly, populations of species that depend on old growth forests or which feed in large diameter wood may decline as the area of old growth forest declines; more than 80% of land in Europe is under some form of direct management (Anonymous 2007). Risk of longhorn beetle extinction increases with larval host plant specialization and length of generation time (Jeppsson and Forslund 2014). The hoptree borer, *Prays*

atomocella (Dyar) (Lepidoptera: Praydidae) is listed as an endangered species in Canada because its sole larval host is the “common” hoptree which is limited to a very narrow range in southwestern Ontario (Harris 2018; Anonymous 2020).

The International Union for Conservation of Nature (IUCN) assessed 431 species of saproxylic insects in Europe (of which 153 species were cerambycids and 1 species was a buprestid) and designated 2, 27 and 17 as critically endangered, endangered or vulnerable, respectively (Nieto and Alexander 2010). More than half of these species are endemic to Europe and found nowhere else in the world. The drivers of this decline are habitat loss due to forest harvesting and a general decrease in old growth “veteran trees” on the landscape (Nieto and Alexander 2010). Other threats include agricultural and urban expansion, forest fires and climate change. It is more than a little ironic that invasive woodborers may threaten populations of native woodborers and other arthropods. The community of arthropods on ash trees in the state of Maryland, USA, included 13 orders, 60 families and 41 genera (Jennings et al. 2017) and the decimation of North American *Fraxinus* species by the invasive emerald ash borer may threaten woodborers and other herbivores tightly associated with ash (Herms and McCullough 2014).

The IUCN identifies species at risk of extinction (so called Red Lists) and promotes their conservation by increasing public awareness and conserving wildlife habitat (Rodrigues et al. 2006). When it comes to woodborers and other insects, Red Lists often reflect a lack of knowledge of species range and population trends rather than actual extinction risk (Cardoso et al. 2012). According to the European Red List, 14% of saproxylic beetles have declining populations but the trend is unknown for more than half of the species (57%) on the list (Nieto and Alexander 2010).

In an effort to conserve species that rely on old growth forests, some countries have forest management regulations in place that mandate conservation of coarse woody debris, snags, and dead wood in the forest. Many countries are signatories to the 1979 Bern Convention on the Conservation of European Wildlife and Natural habitats and the 1992 Convention on Biological Diversity, which provide official impetus for conserving wildlife biodiversity, including woodboring insects. Each member state is required to identify threatened species and their respective habitats, and then develop management plans to protect these natural areas. In Europe, this makes up the Natura 2000 network, a coordinated network of protected areas home to rare and threatened species that makes up 18% of the European Union’s land base and 10% of marine territory (European Commission, Directorate-General for Environment and Sundseth 2021). While the goal of conserving biodiversity is valid, the effectiveness of the Natura 2000 network for conserving saproxylic beetles has been questioned (D’Amen et al. 2013). In Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) meets twice a year to review and assess the status of wildlife species, including arthropods, and submits an annual report to the federal Minister of Environment and Climate Change. Species listed as extirpated, endangered, threatened or of special concern are considered for legal protection and management under the *Species at Risk Act* (SARA). Only two wood boring insects are currently listed as endangered in Canada: the hoptree borer, *Prays atomocella* (Dyar) (Lepidoptera: Praydidae) and the Aweme borer, *Papaipema aweme* (Lyman)

(Lepidoptera: Noctuidae) (Anonymous 2020). Ultimately, woodborer species richness depends on the quantity and diversity of living and dead wood in the forest, forest size and fragmentation, and management practices.

12.5 Chemical Ecology

As discussed above, adult woodborers usually live a few days to a few weeks and are host specific both in terms of the species and physiological condition of the host. This specificity can result in a heterogeneous spatial and temporal distribution of suitable hosts across the landscape and variance in larval performance in hosts. For example larval survival, developmental time, and adult size are all affected by host quality in *P. semipunctata* (Hanks et al. 1993, 1995). In addition to this variance in host quality, due to their short life-span, a delay in mate or host location of only a few days can have significant fitness consequences. Cumulatively, these factors generate selection for rapid host and mate location. Not surprisingly, most adult woodborers typically have highly developed sensory systems while immature life stages do not.

The dominant modality that woodborers use to obtain information about their biotic and abiotic environment is olfaction. The advantages of olfaction include: (i) the availability of a large number of “channels” due to the diversity of chemicals woodborers and their host plants can synthesize and that woodborers can perceive. As a result, chemical signals and cues can have high information content and be highly specific; (ii) volatile chemicals can be transmitted over large distances and around obstacles; and (iii) woodborers can perceive and discriminate among chemical cues and signals with high levels of sensitivity and precision. The disadvantages of olfaction include the fact that: (i) they cannot be transmitted quickly over large distances; (ii) the primary direction of transmission is determined by wind direction; and (iii) they require complex behaviors [e.g. optomotor anemotaxis, see Cardé (2016)] to locate the odor source.

Interest in and our knowledge of the chemical ecology of woodboring insects has increased dramatically in the past 20 years. For example, while fewer than 10 attractant pheromones were known for the family Cerambycidae in 2004 (Allison et al. 2004), approximately a decade later pheromones and likely pheromones (i.e. attraction observed in the field but production and release not yet demonstrated) were known for more than 100 species of Cerambycidae (Hanks and Millar 2016). This increase has been driven by the realization that woodborers can have significant economic impacts (particularly in plantation and urban trees), recognition that they are among the most common and damaging exotic insects (Brockerhoff et al. 2006; Haack 2006) and increased awareness of the importance of the ecosystem services that they deliver.

In general, woodboring insects use volatile sex pheromones to mediate mate location over large distances and low volatility cuticular hydrocarbons for mate recognition at close range (Allison et al. 2004; Hanks and Millar 2016; Millar and Hanks

2017; Silk et al. 2019). A large number of studies have reported the identification of pheromones and the demonstration of attraction to known pheromones and their analogues in the Cerambycidae and we refer readers to the review by Millar and Hanks (2017) for an excellent synthesis of this literature. In brief, two general patterns of volatile pheromone use in the Cerambycidae have emerged: (i) male-produced pheromones are released in large quantities, attract both sexes and occur in the subfamilies Cerambycinae, Lamiinae and Spondylidinae; and (ii) female-produced pheromones are released in small quantities, only attract males and occur in the subfamilies Prioninae and Lepturinae. Volatile pheromones are only known for a single species in the Buprestidae and Siricidae, the emerald ash borer (Silk et al. 2011) and *S. noctilio* (Cooperband et al. 2012), respectively. In the emerald ash borer, it is a female-produced pheromone and male response to it is synergized by host volatiles [synergy of the response to pheromone by host volatiles has also been reported in the Cerambycidae (Allison et al. 2012; Millar and Hanks 2017)]. The putative pheromone in *S. noctilio* is male-produced and behavioral activity has been demonstrated in laboratory trials (Cooperband et al. 2012; Guignard et al. 2020) but field trials did not observe activity (Hurley et al. 2015).

Although the active space of these attractant pheromones has not been quantified empirically for any woodborer, mark-release-recapture trials with several species of Cerambycidae suggest they may range from ca. 50 to 500 m (Maki et al. 2011; Torres-Vila et al. 2013, 2015). These estimates are consistent with research in moths which suggests that attraction likely occurs over a distance of a few meters to a maximum of a few hundred meters (Cardé 2016). Often the release of volatile pheromones is sex-specific, occurs from specific habitats (e.g. host material) (Hanks 1999) and is facilitated by “calling” behaviors (Lacey et al. 2007).

For some of these species, females have been observed to deposit nonvolatile compounds while walking that males use to locate females [i.e. trail pheromones (Hoover et al. 2014)]. Alternatively, in some species males form leks and females may be attracted to these by visual (Allison et al. 2021) and olfactory stimuli (Cooperband et al. 2012; but see Hurley et al. 2015). These mechanisms (sex and trail pheromones, leks) bring the sexes into close proximity but in many woodborers mate recognition appears to be mediated by contact pheromones (Allison et al. 2004; Millar and Hanks 2017; Silk et al. 2019). In these species, males do not appear to recognize females until their antennae contact the female cuticle and they detect cuticular hydrocarbons. After contact males often begin a sequence of characteristic behaviors that culminate in copulation (Hanks et al. 1996a).

Due to the heterogeneous distribution of suitable hosts in space and time, wood-boring insects are expected to experience strong selection to rapidly locate available host material. For woodborers, oviposition can generally be considered as two separate and sequential events: host location and host acceptance. Host location is generally thought to occur first and be initiated from a distance (i.e. before landing on the host plant), whereas host acceptance does not occur until the host has been contacted. Both host location and acceptance are mediated, at least in part, by chemicals. Meurer-Grimes and Tavakilian (1997) evaluated the phytochemistry and diversity of Cerambycidae associated with 51 species of Leguminosae. The host

plants of cerambycid guilds (species sharing host plants) were taxonomically related and had similar phytochemistry. In contrast guild members were not usually related suggesting that host location and/or acceptance are mediated by phytochemicals.

In support of the hypothesis that host location and acceptance are chemically mediated, numerous studies have identified primary attractants for woodborers including floral, smoke, trunk and leaf volatiles (Allison et al. 2004; Hanks and Millar 2016; Millar and Hanks 2017; Silk et al. 2019). Some woodborers from the family Cerambycidae overlap temporally in host trees with bark beetles and are attracted by bark beetle pheromones (Allison et al. 2001, 2013). In addition to competing with bark beetle larvae for limited host tissues, larvae of these woodborers are also facultative intraguild predators of bark beetle larvae (Dodds et al. 2001; Schoeller et al. 2012). The current paradigm for host selection by phytophagous insects argues that to optimize foraging efficiency all available cues and signals should be used. Although most studies have focused on the role of attractive semiochemicals in host location and acceptance, a few studies have demonstrated that woodborers (Coleoptera: Cerambycidae) respond to repellent non-host volatiles to avoid non-host trees (Aojin and Qing'an 1998; Suckling et al. 2001; Morewood et al. 2003).

Semiochemicals produced by the host plant and conspecifics influence female oviposition behavior. The woodborer *H. bajulus* preferentially oviposits in wood infested with larval conspecifics and several monoterpenoids identified in larval frass appear to stimulate oviposition in females (Evans and Higgs 1975; Higgs and Evans 1978; Fettköther et al. 2000). In other woodborers, the presence of conspecifics reduces oviposition (Wang et al. 1990; Anbutsu and Togashi 1996, 1997a, 2000; Peddle et al. 2002). Treatment of host material with larval frass or extracts of larval frass reduced oviposition by *M. alternatus* (Anbutsu and Togashi 2002), suggesting that semiochemicals in larval frass mediate the effect. Some woodborers deposit a jelly-like substance over their eggs (Anbutsu and Togashi 1996, 1997a, 2000; Peddle et al. 2002) and females palpate the bark surface before oviposition. It has been hypothesized that semiochemicals in the material deposited over the eggs mediates the recognition and avoidance of host material already infested with conspecifics. To date, the role of phytochemicals in the induction of oviposition have only been studied in *M. alternatus*. In this species chemicals in the inner bark of the host *Pinus densiflora* Siebold & Zucc. have been demonstrated to induce oviposition in females (Yamasaki et al. 1989; Islam et al. 1997; Sato et al. 1999a, 1999b).

12.6 Economically Important Species

Most woodborers develop in dead or stressed trees, or downed wood, and provide important ecosystem services that contribute to healthy forest ecosystems. The adults of some species oviposit in stressed trees (e.g. fire, drought, and storm damaged; defoliated) and fewer in apparently healthy trees (Craighead 1950; Keen 1952; Solomon 1995). The associated larval feeding and development can result in mortality in both classes of trees. Although some woodborers are significant pests of woody plants

in their native range, exotic species are often among the most damaging species, especially in terms of causing direct tree mortality. For example, in the United States annual costs of tree removal, replacement and treatment due to invasive phloem and woodborers are estimated to be approximately \$1.7 billion USD, of which 50% is a result of the emerald ash borer (Aukema et al. 2011).

The significant economic and ecological impacts of woodborers is of concern given the increase in the number of introductions outside of their native ranges in recent years (Haack 2006; Aukema et al. 2011). As mentioned above, woodborer larvae feed cryptically within phloem and xylem tissues and development takes months to years. These traits make woodborers ideally suited for movement outside of their native ranges in wood products, wood packaging material, dunnage and nursery stock. Additionally, many species attack low quality, stressed hosts and this type of wood is often used for wood packaging and dunnage in container shipping. It is therefore not surprising that the increase in introduction of woodborers outside of their native ranges is coincident with increased movement of goods in container shipping (Haack 2006; Aukema et al. 2011).

In addition to the direct impacts on tree health, larval development and feeding and the associated invasion by fungi can result in degrade losses to wood products. Few studies have quantified these losses but degrade affecting as much as two-thirds of the inventory in log yards have been reported (Becker 1966), as well as monetary losses of 35% to logs infested by woodborers (Becker and Abbott 1960). Woodborers can also negatively affect trees by contributing to disease transmission that leads to increased stress or mortality. In North America, several species of Cerambycidae are known vectors of the tree-killing nematode, *Bursaphelenchus xylophilus* (Steiner & Buhner) Nickle (Linit 1988; Vallentgoed 1991), and this disease has been particularly problematic in Japan where it is transmitted by *M. alternatus* (Mamiya 1988). Woodborers have also been implicated in the transmission of several fungal pathogens including Dutch elm disease, chestnut blight, dieback of balsam-fir, oak wilt and hypoxylon canker on aspen (Donley 1959; Linsley 1961; Nord and Knight 1972; Ostry and Anderson 1995).

By far, the most important economic genus of Buprestidae is *Agrilus*. This genus contains over 3000 species, most of which inhabit angiosperms (Chamorro et al. 2015). Some native species are problematic on stressed trees in North America and Europe or are able to colonize non-native host trees common in more urban settings. Species such as the bronze birch borer (*A. anxius*), twolined chestnut borer (*A. bilineatus*), oak buprestid beetle [*Agrilus biguttatus* (F.)] and bronze poplar borer (*Agrilus liragus* Barter & Brown) can transition into primary tree killers given favorable environmental conditions (Barter 1957; Haack and Benjamin 1982; Dunn et al. 1986; Moraal and Hilszczanski 2000; Vansteenkiste et al. 2004) (Fig. 12.8). Exotic *Agrilus* spp. have been much more aggressive than their native counterparts in urban and forested settings in newly invaded areas. For example, the emerald ash borer has successfully invaded and spread into a large portion of North America (Herms and McCullough 2014), while also establishing and spreading in parts of Russia (Orlova-Bienkowskaja 2014). Native to eastern Asia, this species is a pest of ash throughout its introduced range. Indigenous exotic species (sensu Dodds et al. 2010b) have also

been problematic in introduced areas, including the goldspotted oak borer (*Agrilus auroguttatus* Schaeffer) and soapberry borer (*Agrilus prionurus* Chevrolat) in forests in California and Texas, respectively (Coleman and Seybold 2008; Billings et al. 2014). These are native species that were previously isolated from areas where they have inadvertently been introduced.

Several genera of Cerambycidae can have significant economic or ecological importance. *Monochamus* species are secondary species colonizing weakened or recently dead material (Baker 1972), but through their maturation feeding can transfer the pinewood nematode to pine trees (Linit 1988). Pinewood nematode has caused serious tree losses in East Asia and Portugal, and threatens European pines (Mamiya 1988; Mota et al. 1999; Shin 2008; Zhao 2008; Robertson et al. 2011). Brown spruce longhorned beetle, a European species that was introduced into maritime Canada, has caused mortality in spruce stands (Smith and Hurley 2000). Asian longhorned beetle and citrus longhorned beetle [*Anoplophora chinensis* (Forster)], both native to Asia, have been repeatedly introduced in North America and Europe where they have successfully established multiple times (Haack et al. 2010; Meng et al. 2015).



Fig. 12.8 Damage caused by twolined chestnut borer, *A. bilineatus*, in the eastern US. Trees **a** stressed by drought and *Lymantria dispar* defoliation were killed by the buprestid, while logs **b** with damage from high densities of larvae **c** were salvage logged. Photo credit: Kevin Dodds

Worldwide, the most well-known siricid is *S. noctilio*. This species has been a pest of pine plantations since the early 1900s when it was detected in New Zealand (Bain et al. 2012) and later spread to other parts of the Southern Hemisphere (Slippers et al. 2002). Because the majority of siricids are associated with dead wood, very few species have caused economic losses. *Sirex noctilio* uses a phytotoxic venom (Bordeaux et al. 2014) to help it overcome host tree defenses and colonize trees most siricids cannot occupy.

12.7 Management of Woodborers

Management to reduce populations of most woodborers is unnecessary. However, management is required for some invasive species that damage and kill live trees, or if degradation to standing salvageable trees or stored wood products by native species is a concern. Where management is necessary in forested environments, approaches taken include silvicultural treatments, aggressive tree removal, and biological control efforts with bacteria, fungi, nematodes, and other insects.

12.7.1 Native Species

For native woodborers, there are few circumstances where population management is necessary. In situations where woodborer populations are building in a forest, it is generally in association with some form of abiotic or biotic disturbance that is predisposing trees to attack by secondary insects, including woodborers. Once the disturbance has subsided, or susceptible trees have been eliminated, woodborer attacks on trees rapidly diminish because of improved vigor of residual trees. Maintaining healthy forests with suitable stocking for a given site will reduce the number of susceptible trees that could be colonized by woodborers or act as sources for initial population outbreaks.

Because some woodborers respond to recently dead trees after a large-scale disturbance (Amman and Ryan 1991) and mine through wood, they can result in degrade losses, especially related to timber salvage after a disturbance. *Monochamus* species, in particular, cause rapid decline in wood quality of various conifer species after a disturbance (Richmond and Lejeune 1945; Gardiner 1957, 1975; Prebble and Gardiner 1958) because they are attracted to injured or recently dead trees where females oviposit and larvae mine into sapwood. Timely salvage and storage practices that minimize exposure to peak woodborer populations (Post and Werner 1988) can reduce the chance of excessive woodborer damage in logs destined for markets.

12.7.2 Invasive Species

Limiting the introduction of invasive species is an important first step to keeping damaging woodborers out of new environments. Strong legislation that focuses on preventative measures for limiting the introduction of these species or curtailing their spread once established can help reduce the impacts of these organisms. Once established and causing damage, various techniques have been implemented to attempt eradication and/or management of invasive woodborers. In some cases, well-developed integrated pest management plans have been developed through decades of research (Haugen et al. 1990), and in other cases, the development of management plans continues, even long after establishment (Herms and McCullough 2014). Common components involved with invasive woodborer management in forests include silvicultural treatments (Dodds et al. 2014a), tree removal (Hérard et al. 2006; Herms and McCullough 2014), biological control (Bedding 2009; Collett and Elms 2009), and restrictions on wood movement (USDA-APHIS 2010). Chemical insecticides are rarely implemented in invasive woodborer management within forested environments, although they can be important components of managing these species in urban forests.

12.7.2.1 Silvicultural Treatments

For invasive woodborer species that behave similarly to secondary species, or species that target specific trees (e.g. trees of certain species, sizes, vigor, or crown class), forest management may provide a solution for eliminating or reducing the effects of these insects. An example of silvicultural treatments reducing the impact of an invasive species is *S. noctilio*. Early observations of *S. noctilio* behavior suggested this woodborer was targeting weakened trees growing under overstocked stand conditions (Morgan and Stewart 1966). Consequently, silvicultural options that promoted optimal growing conditions in younger stands and targeted suppressed trees during thinning in older stands (Neumann et al. 1987) have successfully reduced the impact of *S. noctilio* in pine stands (Dodds et al. 2014a).

Unfortunately, most invasive woodborer species do not concentrate attacks on specific age, size, or canopy classes in forests. Therefore, it is not possible to target specific trees for removal based on any of these characteristics. Most invasive woodborers have either a wide host breadth, attack trees of all size classes, or do both, making silvicultural options ineffective (Dodds and Orwig 2011).

12.7.2.2 Tree Removal

Attempts to eradicate woodborers from urban forests often involve large-scale tree removal efforts. These removals can target infested trees only, and in some cases infested and adjacent non-infested host trees (Turgeon et al. 2007; Straw et al. 2015).

The use of large-scale tree removals in forested settings have been limited because of logistical challenges as well as questions as to effectiveness (Herms and McCullough 2014). For example, a six mile wide ash-free zone was created in southern Ontario in an attempt to stop the spread of emerald ash borer, but after completion, the beetle was found already established behind the zone (i.e. in the area the zone was designed to prevent emerald ash borer from invading) (Poland and McCullough 2006). Preemptive salvage logging of host species, such as ash in North America, has been conducted in some situations. Removal of Asian longhorned beetle infested trees and non-infested host trees has been conducted in smaller forested stands in North America (Dodds and Orwig 2011; Dodds et al. 2014b), Europe (Krehan 2008) and Great Britain (Straw et al. 2015) (Fig. 12.9). Woodborer dispersal behavior and initial distribution upon detection are generally the deciding factor for determining if eradication through tree removal is a feasible option for a given species. Asian longhorned beetle eradication has been successful because the adult beetles often reattack natal host trees and generally do not disperse long distances (Smith et al. 2004), allowing for more containment of infestations. Invasive species that are more widely dispersed upon detection, like *S. noctilio* in North America, are most often beyond the point where eradication would be feasible or cost effective.



Fig. 12.9 Asian longhorned beetle infested trees cut as part of an eradication program in Massachusetts, USA. Photo credit: Kevin Dodds

12.7.2.3 Biological Control

Both classical (introducing biological agents from other regions into new environments to control damaging invasive species) and augmentative biological (increasing native biological agents to control damaging invasive species) control of woodborers has been attempted for several species. Classical biological control using parasitic nematodes and wasps (Ichneumonidae, Ibaliidae) to manage *S. noctilio* populations has been implemented throughout the Southern Hemisphere (Hurley et al. 2007). These species have been important components of integrated pest management plans that also include silvicultural treatments for *S. noctilio* and have been responsible for keeping populations below damaging levels in many places. Classical biological control using an egg parasitoid, *Avetianella longoi* (Hymenoptera: Encyrtidae), with parasitism rates sometimes >90%, has also been helpful for reducing *Eucalyptus* mortality and damage from *P. semipunctata* in California, USA (Hanks et al. 1996b). However, biological control against *P. recurva* using *A. longoi* has not been effective (Luhring et al. 2000).

Because some invasive woodborers are congeners of native species and colonize the same habitat, there is often overlap in population regulation factors, providing opportunities for augmentative biological control if populations become economically or ecologically problematic. Native parasitoids that attack North American siricids have been documented attacking *S. noctilio* in these same forests (Ryan et al. 2012; Standley et al. 2012; Zylstra and Mastro 2012) (Fig. 12.10). Similarly, native parasitoids have also been found attacking the invasive brown spruce longhorned beetle (Flaherty et al. 2013a) and emerald ash borer (Gaudon and Smith 2020) in North America. Asian longhorned beetle and *A. chinensis* have been colonized by parasitoids native to the invaded region as well (Brabbs et al. 2015; Duan et al. 2016).

Purely augmentative biological control using native natural enemies on the native cerambycid *Massicus raddei* (Blessig) that causes damage to oak and chestnut species has been attempted in China. The parasitic wasp *Sclerodermus pupariae* Yang et

Fig. 12.10 Two rhyssine (Ichneumonidae) parasitoids search for hosts on a *Sirex noctilio* infested Scots pine in New York, USA. Photo credit: Kevin Dodds



Yao (Hymenoptera: Bethyridae) and the beetle *Dastarcus helophoroides* (Fairmaire) (Coleoptera: Bothrideridae) have been used as biological control agents (Yang et al. 2014). Both are potential management tools for reducing the impact of *M. raddei* on native trees.

The combination of augmentative and classical biological control could be beneficial for reducing woodborer populations. This approach is currently being developed for emerald ash borer in North America. Four hymenopteran species have been approved as biological control agents for release in the U.S., including *Oobius agrili* Zhang and Huang (Encyrtidae), *Spathius agrili* Yang (Braconidae), *Tetrastichus planipennisi* Yang (Eulophidae), and *Spathius galinae* Belokobylskij & Strazanac (Braconidae) (Gould et al. 2015; Duan et al. 2019). These species are native to China, Russia, and Korea and attack eggs (*O. agrili*) or larvae (*S. agrili*, *T. planipennisi*, *S. galinae*). Native species, including *Phasgonophora sulcata* Westwood and *Atanycolus* Foerster spp. can be used as augmentative biocontrol agents (Gaudon and Smith 2020). The fungus *B. bassiana*, a native species, has also been tested to manage EAB (Lyons et al. 2012) and ALB populations (Dubois et al. 2004).

12.7.2.4 Chemical Control

Similar to tree removal, chemical control options have been used successfully on woodborers in urban forests, but their utility in natural or managed forests is limited. Several compounds are available, primarily for invasive species control, including systemic and contact insecticides. Compounds such as imidacloprid, cypermethrin, and emamectin benzoate have been used on invasive woodborers in urban settings (Hu et al. 2009). However, because of the cost associated with treatments, logistical challenges, and environmental concerns, these compounds are not seen as valid options for managing woodborers in forested environments.

12.7.2.5 Cultural Control

An important factor to limiting the spread of invasive woodborers is restricting movement of host material that may be infested by these insects. Wood products or wood packing material are often moved large distances, both intra- and inter-continently. This material, combined with the cryptic nature of woodborers, provides an efficient pathway of introduction for woodborers and associated organisms (Mamiya 1988) into new environments. Wood packing is often colonized by woodborers that are then transported in the egg, larval, or pupal stage and emerge in the new environment to seek hosts unless wood is properly handled at the destination. The most damaging woodborers worldwide, including emerald ash borer, Asian longhorned beetle, and *S. noctilio*, are all believed to be introduced via whole logs or wood packing material.

Firewood is a documented pathway for movement of invasive species in North America and likely elsewhere when this material is used for heating or recreation (USDA-APHIS 2010). It has been linked to the spread of emerald ash borer across

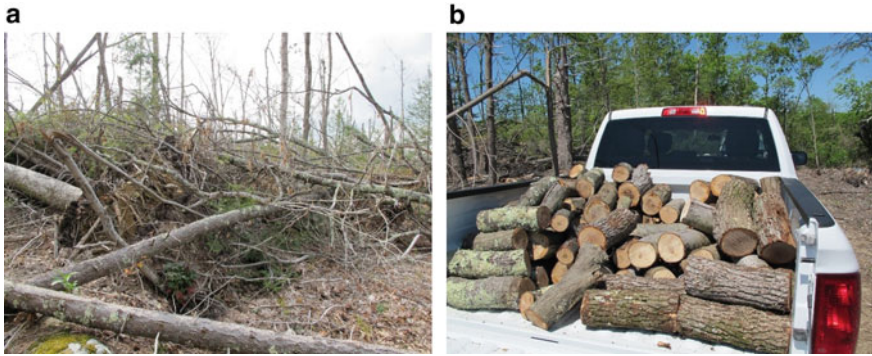


Fig. 12.11 Disturbances such as windstorms can leave large volumes of downed trees **a** that are quickly colonized by woodborers and other insects. This material is often cut into firewood **b** that can provide a pathway for insects into new environments. Photo credit: Kevin Dodds.

portions of eastern North America (Cappaert et al. 2005) and may have been the pathway for *Agrilus prionurus* into Texas from Mexico (Haack 2006) and *A. auroguttatus* into California (Coleman and Seybold 2011). Trees harvested for firewood are often recently dead and already infested with woodborers or at a stage of decay that makes them suitable for colonization (Fig. 12.11). Seasoning of trees or cut firewood also provides opportunity for insects to colonize this material. Firewood can host large communities of wood-inhabiting insects, including buprestids, cerambycids and siricids (Dodds et al. 2017) that can then be moved large distances often for recreational camping (Jacobi et al. 2011; Koch et al. 2014). If this wood is infested with invasive species, introductions into new environments can occur.

12.8 Summary

Woodborers are an ecologically important guild in forested ecosystems. They contribute to various ecological processes including nutrient cycling, forest succession, and are important components of food webs. Woodborers colonize all parts of dead or living trees, while generally causing little impact on overall tree health. Most Buprestidae, Cerambycidae, and Siricidae encountered in native and managed forests are secondary species that rarely kill trees, however, important invasive species like Asian longhorned beetle, emerald ash borer, and *S. noctilio* can have broad ranging impacts on urban, managed, and natural forests. At times, management of woodborers is necessary and includes preventative silvicultural treatment, tree removal, biological control, chemical control, and cultural methods to reduce movement of infested materials.

Various factors effect woodborer populations, including both abiotic (i.e. climate, fire, and other natural disturbances) and biotic factors (i.e. host suitability, natural

enemies, and competition). Biotic factors such as parasitic nematodes, fungi, and parasitoids have been important in management of some woodborers, including the invasive emerald ash borer and *S. noctilio*. In some forest types and regions, some woodborer species are considered threatened or endangered, primarily from habitat loss due to forest fragmentation, conversion, and loss of old trees.

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