

Chapter 11

Ambrosia Beetles



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11.1 Ambrosia Beetle Biology

11.1.1 Taxonomic Identity

The term “ambrosia beetles” refers to an ecological strategy shared by thousands of species of wood-boring weevils from multiple lineages, rather than a single taxonomic group. Most ambrosia beetle groups evolved from within the bark beetles (Curculionidae: Scolytinae), which are a diverse group of weevils which bore into trees and whose progeny develop by feeding on the host tree tissue. Ambrosia beetles do not consume the tree tissue; instead, they introduce symbiotic fungi into their tunnels, which comprise the majority or entirety of the ambrosia beetle diet. Ambrosia fungus farming has evolved at least sixteen times within bark beetles (Johnson et al. 2018) (Fig. 11.1).

There are over 3,000 species of ambrosia beetles (Hulcr et al. 2015), making them far more species-rich than other fungus-farming insect groups, such as the fungus farming ants, termites, and wood wasps. It has been suggested that the diversity of ambrosia beetles is derived from the ecological success of the fungus-farming strategy. However, only a few ambrosia beetle lineages are particularly diverse, and in those lineages, other factors likely contribute to their high diversity. For example, the rapid and extensive diversification of Xyleborini may be better explained by their haplo-diploid genetic system rather than fungus farming (Gohli et al. 2017). Several other ambrosia lineages are diverse because they are old and not because they are speciating faster than other weevil groups, such as the Platypodinae. They

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Fig. 11.1 Ambrosia beetle galleries. Left, a cavity of *Coptodryas pubifer* (Xyleborini) in Sabah, Malaysia; new adults, larvae and the white fungal growth, the top right specimen is the haploid male. Right, an unidentified *Corthyloxiphus* in Ecuador: the male (diploid), and larval chambers with individual larvae and fungus. Other types of gallery arrangements exist. Photos: J. Hulcr. *Corthyloxiphus* was identified by Sarah M. Smith

now comprise approximately 1,400 species and are estimated to have been farming fungi for over 100 million years (Jordal and Cognato 2012; Poinar Jr and Vega 2018; Vanderpool et al. 2018).

The most practical biological unit for classification and discussion of ambrosia symbioses is not any single taxonomic level, such as species or genus. Instead, it is better to use the concept of evolutionary symbiotic unit because both the beetle and the fungus partners have been coevolving and speciating together. The coevolutionary unit represents an independent event of an evolutionary beetle-fungus association and includes its evolutionary offshoots—beetle and fungus species or genera that retain that association.

11.1.2 Relationships with Fungi

Ambrosia symbioses are most often considered reciprocally obligate mutualisms. The beetles depend on their fungi as a food source and the fungi depend on the beetles for dispersal to new trees. It is likely that at least some ambrosia fungi have retained the ability to disperse by other means such as fruiting bodies that eject spores. At least some ambrosia fungi have retained the ability to produce sexual stages (Musvuugwa et al. 2015; Mayers et al. 2017; Jusino et al. 2020), but whether they are also able to disperse independently of the beetles is not known. This capacity is known in fungal associates of other insects, including fungus growing termites (Johnson et al. 1981) and siricid woodwasps (Talbot 1977).

Ambrosia fungi originated from at least seven separate fungal clades (Alamouti et al. 2009; Hulcr and Stelinski 2017). Improved systematics and phylogenetic sampling continue to reveal more independent evolutionary origins of ambrosia fungi within well-known ambrosia fungus taxa because many are polyphyletic, particularly

within the Ophiostomatales (Vanderpool et al. 2018; de Beer et al. 2022) and Ceratocystidaceae (Mayers et al. 2015). Additionally, the increasing research interest and DNA-based studies continue to uncover a rich diversity of ambrosia fungi that are not directly related to previously known ambrosia fungi, many of which have remained unnoticed until recently (Bateman et al. 2016; Li et al. 2017).

As a result of their diverse origins, ambrosia fungi inherited various ecological strategies. Despite the shared strategy of symbiosis with insect vectors, the metabolic profiles of these fungi do not seem to be convergent. Instead, both the substrate use and the metabolic products (the beetle food) of each ambrosia fungus clade are more similar to closely related free-living fungi than to other ambrosia clades (Huang et al. 2019, 2020). Some newly discovered symbiotic fungi have metabolic capabilities and ecological strategies that were previously unknown from ambrosia fungi. For example, beetles in the genera *Ambrosiodmus* and *Ambrosiophilus* (beetle genera in the scolytine tribe Xyleborini) farm the basidiomycete genus *Irpex* (formerly *Flavodon*). Fungi in this genus are exceptional among ambrosia fungi because they are truly lignicolous and degrade the structural components of wood (Kasson et al. 2016; Jusino et al. 2020). This is in contrast to other ambrosia fungi which extract labile resources within the wood but do not decompose the wood itself.

The dichotomy between bark and ambrosia beetles is convenient, but imperfect. Many scolytine species blur the boundary between the phloem-feeding (phloephagous) bark beetles and fungus-feeding (mycetophagous) ambrosia beetles. While most bark beetles feed within bark and phloem, many species also consume wood, seeds, herbaceous plant tissue, and tissues with varying amounts of fungi. In fact, some of the best-known forest pests, such as species in the genera *Dendroctonus*, *Ips* and *Tomicus*, are phloeomycetophagous. This means that the larvae develop in phloem but eat primarily fungal mutualists, similar to ambrosia beetles. Similar to true ambrosia beetles, the adults of some of these phloeomycetophages even have mycangia for transporting specific fungal mutualists to new trees. Furthermore, not all ambrosia beetles are strictly fungivores. Some entire genera are xylomycetophagous: the larvae chew and ingest a mixture of wood and the mycelium of a fungal mutualist (Roeper 1995).

Phloeomycetophagous bark beetles and xylomycetophagous ambrosia beetles show similar specificity to their fungi. For example, the pine-inhabiting phloeomycetophages in North America are associated with only a few species of highly derived species of *Entomocorticium*, *Ophiostoma*, *Grossmania*, and/or *Ceratocystiopsis* (Harrington 2005). Similarly in Europe, the phloeomycetophagous species of *Ips acuminatus* and *Tomicus minor* are each primarily associated with a single species of *Ophiostoma* (Francke-Grosmann 1967; Seifert et al. 2013).

Another fungus-related strategy among bark beetles is sapromycetophagy: consuming degraded plant tissues rich in various fungi. A number of pygmy borers in the genus *Hypothenemus*, for example, occupy twigs and branches pre-colonized by fungi. Their larvae do not drill individual tunnels but instead develop in extensive communal spaces lined with mycelium. What exactly they consume, and whether there is any specificity to this beetle-fungus relationship, remains unexplored.

11.2 Who Is the Host and Why Does It Matter?

In many symbioses, the roles of host and symbiont are often obvious. The larger organism hosts the symbionts, which are usually smaller and more numerous. The host bears the brunt of interacting with the environment, while the symbionts experience only a subset of environmental factors. This environmental shielding and reduced population size affects symbiont evolution. For example, microbial endosymbionts often evolve reduced genetic complexity (Moran and Wernegreen 2000; McCutcheon and Moran 2011).

Ambrosia symbioses are different because the role of host and symbiont alternates throughout their shared life cycle. During dispersal, the beetle is the host to its fungal symbiont. The fungus is sheltered and nourished within the beetle's body in the mycangium. However, once a dispersing ambrosia beetle establishes a new gallery, the ambrosia fungi are released from the mycangium into the wood. At this point, they must colonize resources, sequester energy and nutrients, compete with other microbes, and resist or detoxify plant-produced defensive chemicals. Meanwhile, larvae and newly emerged adult ambrosia beetles feed primarily or exclusively on their fungal symbionts within the stable and protected environment of the fungi-laden gallery. At this stage, ambrosia fungi arguably act as the host to their beetles because the fungi bear the burden of interacting with a variable and often hostile environment. This stage comprises the majority of the life cycle of this symbiosis, and therefore incorporating a fungus-centric view with an entomological perspective will improve our understanding of the biology of the ambrosia symbiosis.

11.2.1 *Biology of the Coevolutionary Units is Dictated by the Fungus*

There is a tendency for research on agricultural symbioses to focus on the “farmers” as the dominating partner and to expect that their crops are passive or enslaved participants in the symbiosis. However, in insect/fungus farming, and even human agriculture, there is evidence that crops also exert significant selection on their farmers, especially during the early stages of the evolution of agricultural symbioses (Schultz et al. 2005). Support for this view comes from comparative studies of ambrosia fungi and closely related non-ambrosia fungi. The ancestors of various ambrosial lineages had distinct metabolic abilities and ecological niches, and each ambrosia lineage has retained the metabolic capacities of its recent ancestors (Huang et al. 2019). The inherited metabolic capacity of beetle-associated fungi is correlated with the diversity and taxonomic composition of the trees that the fungi utilize (Veselská et al. 2019), suggesting that the ecological niche breadth of an ambrosia beetle may be constrained by the niche of its fungal symbiont.

The contemporary ecology of each coevolutionary ambrosia beetle/fungal symbiont unit seems to be predicted more by the ancestral ecology of the fungus than

by the ancestral ecology of the beetle. For example, beetle taxa that farm *Ambrosiella* and the closely related genus *Meredithiella* utilize substrates that are prone to drying such as twigs and smaller branches. These beetles include unrelated groups, such as the *Xylosandrus* clade within Xyleborini, *Corthylus* spp., *Scolytotlatypus*, all of which independently evolved the colonization of twigs or branches, but rarely trunks. Conversely, essentially all the ambrosia beetles that colonize the bases of tree trunks, which remain moist, have fungal symbionts in the genus *Raffaelea* (sensu lato) and related Ophiostomatales. These beetle clades—including multiple Xyleborini genera, Platypodinae, corthyline genera *Monarthrum* and *Gnathotrichus*, and Premnobiina—are not closely related. Even within the hyper-diverse tribe of ambrosia beetles Xyleborini, there are several separately derived coevolutionary units, and the beetle members of each unit typically follow the ecological strategy of the fungus, not the ancestral strategy of the beetles. This diversity of fungal traits and the resulting ecological variability among the fungus-beetle coevolutionary units suggests that there are many functionally diverse ambrosia symbioses, rather than a single convergent type.

In addition to influencing a beetle's ecological niche, the ecology of ambrosia fungi may also be tied to mating systems, and perhaps facilitate the evolution of sociality. This is the case especially in systems where the growth of the fungus garden lasts long enough to support multiple overlapping generations of the beetles. Most ambrosia gardens are short lived, because almost all ambrosia fungi stem from lineages of saprotrophic or plant-pathogenic ascomycetes. These fungi typically lack the ability to degrade the lignin-containing structural components that comprise the majority of wood biomass. Instead they rely on more readily digestible resources such as sugars and amino acids, but those are abundant only in living trees or fresh dead wood. This forces each new generation of most ambrosia beetles to seek new substrate, largely preventing the overlap of generations. However, there are notable exceptions. *Ambrosiodmus* and *Ambrosiophilus* beetles are the only ambrosia beetles currently known to farm ambrosia fungi capable of degrading lignin, the compound that makes wood remarkably difficult to enzymatically degrade. By partnering with *Irpex subulatus*, a true wood degrading basidiomycete, *Ambrosiophilus* and *Ambrosiodmus* can remain in the same log longer as it is slowly decomposed, and display signs of sub-social arrangement such as overlapping generations (Kasson et al. 2016). Similar delay of dispersal and acceleration of reproduction was documented in other ambrosia beetles which live in environments where the ambrosia garden is long-lasting, such as *Xyleborinus* and *Austroplatypus* (Kent and Simpson 1992; Biedermann and Taborsky 2011).

11.2.2 *Mycangia*

A mycangium can be one of various anatomical structures that maintains living fungal propagules in dormant and/or dispersing adult beetles. These structures are key adaptations that are essential to the evolution and maintenance of ambrosia

symbioses (Mayers et al. 2022). Mycangia facilitate the persistence of associations between beetle and fungal lineages across generations. Mycangia provide an interface for the discrimination of mutualistic versus non-mutualistic fungi and a bottleneck, through which antagonistic fungal parasites and competitors are purged (Skelton et al. 2019a). Mycangia vary among beetle lineages in their size, complexity, anatomical location, sex associations, and specificity to fungal species. There is a rich literature describing the detailed morphology of these structures, identifying their fungal and bacterial contents (Hulcr and Stelinski 2017), and devising classifications according to their anatomy and complexity (Six 2003).

More than just passive containers for fungal spores, bark and ambrosia beetle mycangia support the growth of fungi during strategic moments of beetle development (Francke-Grosmann 1956; Batra 1963; Kajimura and Hiji 1992). While some mycangia are fixed structures, some are dynamic. The mesothoracic mycangium in the genera *Xylosandrus*, *Anisandrus*, and relatives are flattened in young adults, inflate with fungal matter after symbiont uptake and during dispersal, and deflate again after the new garden is established (Li et al. 2018b). These observations suggest that maintaining a mycangium that is full of active fungal tissue is a costly investment for these beetles and that selection favors precise timing and control over fungal growth.

Mycangia provide a mechanism to promote specificity in beetle-fungus relationships. Beetles in the genus *Xylosandrus* farm fungi in the genus *Ambrosiella*. Their mycangium is able to accept several species of *Ambrosiella* in no-choice situations. However, the probability of uptake of any *Ambrosiella* by the new generation of beetles is lower for species that are not the specific coevolved symbiont, and minimal for non-*Ambrosiella* genera (Skelton et al. 2019a). Likewise in *Xyleborus* and Platypodinae, the mycangium can transfer multiple species of *Raffaelea*, *Harringtonia* or *Dryadomyces*, but routinely only one species is numerically dominant in the mycangia of each beetle species, and other fungal genera are vectored in lesser abundances and low frequencies (Carrillo et al. 2014; Li et al. 2018a). Further experimental work is needed to determine if the dominance of particular species is enforced by selectivity of the beetles' mycangia, or additional/alternative mechanisms such as beetle behavior, substrate choice, or fungal competition.

In some beetles, the ambrosia farming lifestyle is evident from galleries lined with luxuriant fungal growth, yet the presence of a mycangium is yet to be confirmed [e.g. *Sueus* and several Platypodinae, (Li et al. 2020)]. Other beetles possess small external structures that frequently hold a few fungal cells, but their function is uncertain. Such "pit mycangia" are common in Platypodinae and have been proposed for other beetle taxa. In *Xyleborinus* and some *Xyleborus* (Scolytinae, Xyleborini), the putative elytral mycangia are also very small, and symbiotic fungi have been isolated from other body parts (Biedermann et al. 2013). It remains unclear whether these pit and elytral mycangia are truly co-evolved adaptations for bearing the propagules of fungal mutualists, or if they are simply anatomical features with an as yet unknown function and a coincidental tendency to collect spores. Uniquely, *Xyloterinus* and some *Euwallacea* beetles appear to have two types of mycangia, each occupied by

a different fungus (Abrahamson and Norris 1966; Mayers et al. 2020; Spahr et al. 2020).

There are no known instances in which an obligate dependence on fungus farming has been secondarily lost in bark and ambrosia beetles. However, several lineages of ambrosia beetles have secondarily lost their mycangium in favor of a “mycocleptic” strategy. These beetles bore their galleries adjacent to the galleries of mycangium-bearing ambrosia beetles. The mycoclept’s offspring feed on the parasitized fungal gardens as the fungi extend into the gallery of the mycoclept (Hulcr and Cognato 2010). Mycoclepts are perfect examples of evolutionary cheaters because they exploit the ambrosia mutualism by benefiting from the nutritional spores produced by ambrosia fungi, while they do not reciprocate by facilitating the dispersal of the ambrosia fungus (Skelton et al. 2019a).

11.2.3 Relationships with Trees

Ambrosia beetles are often said to colonize “stressed, dead or dying” trees. However, it is important to discriminate among these types of resources. From the beetle and fungus perspective, plant tissues that are stressed but still alive present a much different environment than tissues which are dead or nearly so. Grouping them together obscures significant differences between the ecology of beetles and fungi that are able to colonize stressed but living trees, and those that only colonize trees which will not recover. The ability of some species to colonize stressed live tissue explains their tendencies to become forest or silvicultural pests.

Only very few ambrosia beetle species and their fungal associates are able to colonize healthy living trees. Some beetles, such as the black twig borer *Xylosandrus compactus*, attack only the twigs of healthy trees causing the end of the twig to die, but they typically cause no serious harm to the tree unless they are present in very high abundance. There is only a single case in which an ambrosia beetle causes tree mortality by infecting the tree with a systemically pathogenic fungus: the redbay ambrosia beetle *Xyleborus glabratus* which carries the systemic laurel pathogen *Harringtonia lauricola*. Although these pest species are more studied and better known than harmless species, they do not represent the typical ambrosia ecological strategy.

Trees that are stressed while still alive are attractive to several other groups of specialized ambrosia beetles, including the common and widely introduced species *Cnestus mutilatus*, *Xylosandrus crassiusculus*, and *Xylosandrus germanus*. As a result, these beetles are prominent pests on intensively managed trees such as in nurseries and young orchards. The remaining ambrosia beetle species are not known to colonize healthy living trees, and only rarely colonize stressed trees. Instead, most ambrosia beetles seek freshly dead trees which no longer possess functioning defense mechanisms.

Several groups of ambrosia beetles prefer to colonize wood tissue already pre-infested by their respective fungus, instead of seeking new hosts. For example, the

tea shot-hole borer *Euwallacea fornicatus* establishes large colonies by re-infesting the same portions of trees, and only when the particular tree part is no longer suitable to support the fungus, the emerging beetles take flight and seek new hosts (Mendel et al. 2017). Similarly, beetles associated with the wood decaying ambrosia fungus *Irpex* (*Ambrosiodmus*, *Ambrosiophilus*) are often found colonizing tree parts infected with *Irpex* inoculated by previously colonized beetles of either genus (Kasson et al. 2016; Li et al. 2017).

The question of taxonomic host tree specificity of ambrosia fungi and beetles is not yet fully resolved. On one hand, a seemingly unlimited taxonomic range of tree hosts is sometimes reported (Beaver 1979; Hulcr et al. 2007), however these analyses are typically based predominantly on beetles that associate with the polyphagous species of the polyphyletic fungal genus *Raffaelea*. There are many observations suggesting that other groups of ambrosia beetles and fungi display preferences for particular host tree families. For example, in Asia there are entire genera of Xyleborini specific to dipterocarps and species from various genera specific to Lauraceae (including the pestiferous *X. glabratus* associated with *H. lauricola*). In North America there are several phloeomycetophagous semi-ambrosial beetles that farm *Entomocorticium* and only colonize trees in the Pinaceae (Harrington 2005). There are even species that are specific to certain host tree species, such as some *Corthylus* (Roeper et al. 1987). This pattern further supports the notion that there is not one, but many different types of ambrosia symbiosis and a corresponding diversity of ecologies.

11.2.4 Host Selection and Chemical Ecology

While host searching behavior has been well studied in several important species of bark beetles, it has only recently been studied in ambrosia beetles. Just as in bark beetles, several main sources of volatile chemicals are important for ambrosia beetles: host volatiles (primary attractants), non-host volatiles that are typically repellent, volatiles generated by decay or the organisms associated with decay (secondary attractants), and pheromones produced by other scolytine beetles. Pheromones exist in ambrosia beetle groups that reproduce via regular outcrossing, such as the Platypodinae (Gonzalez-Audino et al., 2005) and Xyloterini (Macconnell et al. 1977).

Primary host attraction is most important in ambrosia beetle species that attack living trees or that are specific to certain host groups. Such host-specific species are rare among ambrosia beetles, but a well-studied example is the redbay ambrosia beetle *X. glabratus*. The beetle responds to sesquiterpenes and other compounds that are characteristic for Lauraceae, its host family (Kendra et al. 2014). On the contrary, it is repelled by volatiles from other kinds of trees, as well as volatiles from the leaves of Lauraceae, indicating healthy and unsuitable host (it is, however, attracted to volatiles released from the wood) (Hughes et al. 2017). Interestingly, the effect of the most commonly used attractant of aggressive ambrosia beetles—ethanol—on *X. glabratus* is ambiguous, and may even be a repellent (Kendra et al. 2014).

Ambrosia beetle ecology differs from that of other wood borers primarily in the reliance on fungi, and that has implications also for their chemical ecology. Fungus-produced volatiles are attractive to ambrosia beetles. In some instances, vectors are most strongly attracted by volatiles from their respective symbionts (Hulcr et al. 2011). More general fungal volatiles, such as quercivorol, are attractive to a broad diversity of ambrosia beetles or serve as synergists for other volatiles (Cooperband et al. 2017).

Some volatiles seem to be attractive to many different ambrosia beetles. For example, the aforementioned ethanol and quercivorol, byproducts of plant stress and of fungal metabolism respectively, are attractive to many unrelated beetle species (Kamata et al. 2008; Ranger et al. 2010; Kendra et al. 2017). The repeated use of the same compounds in related species, or at least the use of derivatives of the same chemical structures, and the enrichment of the information content by synergy with host volatiles, has been termed semiochemical parsimony, and has been also shown in other wood boring beetles (Hanks and Millar 2013).

An important group of ambrosia beetles, the Xyleborini, is exceptional in its lack of aggregation pheromones. All species in this tribe reproduce almost entirely via inbreeding paired with haplo-diploidy. The haploid males, which are smaller than the females, flightless, and probably blind, mostly stay in their native galleries and mate with their sisters. Because the dispersing females are already mated when they arrive at a new tree and therefore do not need to attract a male, the group does not use any long-distance pheromones. Short-distance or contact pheromones are produced at least by the genus *Euwallacea* (Cooperband et al. 2017), but their practical application as long-distance pest attractants is unlikely due to low volatility.

11.3 Economic Significance

Ambrosia beetles and fungi are ecologically diverse, and the pestiferous species are no exception. Here we introduce multiple examples, especially those that display different types of damage. Many other interesting and important ambrosia pest groups exist but could not be covered here, including tropical and temperate pinhole borers and many species that cause damage to trees stressed by climate or management.

11.3.1 *Ambrosia Beetle Pests in Dead Trees*

Before the contemporary era of global biotic homogenization, ambrosia beetles were known mostly for lumber damage, the result of many tunnels at timber loading sites in logged forests. Such damage is typically regional, and unrelated to the health of living trees.

11.3.1.1 *Trypodendron*

Distributed throughout almost the entire Northern hemisphere, the genus *Trypodendron* defies many standard narratives about ambrosia beetles. Despite its wide distribution, the genus is rather species-poor, especially compared to the hyper-diverse Xyleborini or Platypodinae. *Trypodendron* species do not kill trees, but their massive colonization of freshly cut conifer trees causes many perforations in the wood and their associated fungi cause staining around the beetle galleries. This results in a significant reduction of the monetary value of lumber. Such damage to cut lumber may exceed the financial losses caused by the tree-killing bark beetles (Lindgren and Fraser 1994).

Trypodendron damage garnered significant research attention, and consequently a considerable number of management methods that are now available for truly Integrated Pest Management (IPM) of this pest. A simple yet significant mitigation of impact can be achieved by the timing of logging and exposure of logs because *Trypodendron* spp. are distinctly seasonal (Dyer and Chapman 1965). Application of non-host volatiles, such as pine extracts, onto spruce logs achieves up to 85% protection against *T. lineatum* (Dubbel 1992). In addition, *Trypodendron* species are also highly responsive to the genus-specific pheromone lineatin, which is therefore widely used in monitoring. In heavy infestations, lineatin baited intercept traps can also trap-out significant numbers of beetles from the vicinity of the logs (Lindgren and Fraser 1994). The use of semiochemicals for the control of *Trypodendron lineatum* has been one of the most successful examples of this control technique.

11.3.2 *Global Change-Induced Damage by Ambrosia Beetles*

The health of the world's trees and forests is increasingly affected by many stressors. The two pressures most related to the spread of ambrosia beetles is the spread of planted monocultures and global climate change. In intensively managed nurseries and orchards, trees may experience multiple stressors, including poor matches to the local soil types, excessive or insufficient water regimes, and novel pathogens. Such stresses may not be apparent to a human observer, but some ambrosia beetles have evolved to be exquisitely sensitive to the semiochemical signature of a stressed tree (Ranger et al. 2010). As examples below demonstrate, from tropical plantations to temperate nurseries, ambrosia beetles attack managed trees emitting trace amounts of stress-related chemicals, while similar attacks are not reported from nearby natural vegetation. Perhaps rather than thinking about all ambrosia beetles strictly as pests and attempting to manage them as such, it may be more appropriate for tree managers to consider many ambrosia beetle species as reliable indicators of underlying poor tree health that should be improved. That increased insect activity is a symptom of poor tree health is one of the foundational elements of modern forest entomology (Manion 1981).

11.3.2.1 Tree Stress Responders: *Xylosandrus* Spp.

In the U.S. and increasingly in Europe, the invasive *Xylosandrus crassiusculus* and *X. germanus* are examples of ambrosia beetles sensitive to tree stress-related volatiles, primarily ethanol (Ranger et al. 2015). Ethanol production is triggered most often by damaged roots, for example due to frost, lack of oxygen due to saturation of soil with water, or an internal pathogen. Such stressors are common in actively managed nurseries and orchards, and therefore non-native *Xylosandrus* species are becoming notable pests in such environments.

It is important to recognize that the beetles are not the cause of the tree stress but a sign of other stressors. Focusing management on the beetle is likely going to be less effective than ameliorating the underlying causes. Ambrosia beetles are abundant throughout the landscape, difficult to monitor and even more difficult to manage. In contrast, the growing conditions and health of tree crops can be much more easily monitored and managed. If growers maintain healthy trees and optimal growing conditions, the ubiquitous ambrosia beetles will be mostly inconsequential.

Xylosandrus crassiusculus is also increasingly posing a problem to industries that process hardwood lumber. The rapidly reproducing and polyphagous beetles can colonize untreated timber in high numbers, causing extensive perforation and staining of the wood. This necessitates a much shorter turnaround of such inventory.

The third invasive and damaging species of this genus is *Xylosandrus compactus*. This minute ambrosia beetle is specialized on small living twigs, causing dieback of branch tips. Heavy infestations can cause disfiguration of trees and death of seedlings. The origin of this beetle is South East Asia (Urvois et al. 2021), and it is an increasingly common pest throughout warm regions of the US and Europe, and in coffee growing regions globally where it causes significant damage to the coffee crop (Ngoan et al. 1976; Greco and Wright 2015; Vannini et al. 2017).

11.3.3 Tree-Killing Invasive Species

The killing of mature healthy trees is very rare among ambrosia beetles. Some unusual native species, such as *Corthylus punctatissimus*, naturally colonize small tree seedlings which consequently die (Roeper et al. 1987). However, the majority of ambrosia beetles that cause extensive tree mortality are non-native species, which have not coevolved with these trees.

11.3.3.1 *Xyleborus glabratus*

The most dramatic and unusual case of widespread ambrosia beetle-induced tree mortality is the case of Laurel wilt, a deadly disease of susceptible trees in the Lauraceae caused by the fungus *H. lauricola* which is vectored by the ambrosia beetle *X. glabratus*. Laurel wilt is most prevalent in the Southeastern US which used

to have high densities of susceptible Lauraceae trees. So far, the disease has had the greatest economic impact in avocado groves in South Florida (Evans et al. 2010). Ecologically, the most affected ecosystem has been the forest understory across the Southeastern US where mature individuals of several *Persea* and related lauraceous genera have been nearly eradicated. Only a fraction of the former population survives, which has consequences for many other members of the ecosystems, from insect herbivores to endangered plant pollinators (Hughes et al. 2015).

Large ecological impacts have occurred due to Laurel wilt in the Florida Everglades, where the void left by the deaths of millions of *Persea* is being filled by invasive plants (Rodgers et al. 2014). Laurel wilt also occurs in Asia, but with much lesser intensity (Hulcr et al. 2017). The greatest threat may yet be realized. Lauraceae and avocado are much more important ecologically, economically and culturally in South and Central America (Lira-Noriega et al. 2018). If Laurel wilt spreads to these regions, the effects could be catastrophic.

The ecology of the *X. glabratus* and *H. lauricola* mutualism in non-native regions is unusual in several respects. For instance, the vector beetle searches for live host trees by following specific sesquiterpenes, a behavior not known in other ambrosia beetles (Kendra et al. 2011). Similarly, the disease has unusual etiology. The prevailing hypothesis about the initial infection posits that the first beetle colonizes the living and healthy tree in error, or perhaps as a trial, and either leaves or dies within the tree (Martini et al. 2017). Should this be confirmed as the main mode of action of the disease spread, it is truly a unique situation as the pioneer beetle derives no fitness benefit and the behavior is not adaptive. The fungus-tree interaction is also unusual. Unlike the localized infections caused by other ambrosia fungi in living trees, *H. lauricola* rapidly spreads as a systemic infection, triggering extensive formation of tyloses in tracheids and vessels, diminishing the water conductivity of the xylem (Inch et al. 2012).

11.3.3.2 Euwallacea

The genus *Euwallacea* includes species that span the entire range from primary pests (attacking living, healthy trees) to saprophages (living in decaying wood). From the tree health management perspective, species that attack living trees are important, and those include the *E. interjectus*, *E. destruens*, *E. fornicatus*, *E. kuroshio*, and *E. perbrevis*. All *Euwallacea* species are primarily associated with *Fusarium* species from the specialized ambrosial *Fusarium* clade, collectively referred to as the “AFC” (O’Donnell et al. 2016). The spread of *E. fornicatus* to various regions around the world and the damage that has followed appear to suggest that this species is much more invasive and damaging than the remaining ones (Hulcr et al. 2017; Smith et al. 2019).

Observations from native regions suggest that some of these small *Euwallacea* species are able to colonize specific parts of healthy trees, such as branch joints (Hulcr et al. 2017). However, the greatest damage is typically observed in managed situations such as urban landscape vegetation or avocado groves. Some of the greatest damage

in natural systems appear to be associated with tree stress including flooding and pollution (Boland and Woodward 2019). The greater impact in managed plantations is manifested in both the invaded and the native regions. The tea shot hole borer (*E. perbrevis*) has been known to cause losses in tea plantations in Asia where it is native (Hazarika et al. 2009), but there are no reports of damage from non-agricultural habitats. Also in the invaded regions such as South Africa or Israel, the *E. fornicatus* infestation has been documented mostly in managed urban vegetation or managed settings (Mendel et al. 2012; Paap et al. 2018). The various stressors that may trigger colonization by *E. fornicatus*, or that may facilitate development of the infestation, may also include unapparent tree disease. Attacks on living trees that have been pre-infested by a pathogen have been well documented for *E. validus* and *E. interjectus* (Kajiji et al. 2013; Kasson et al. 2013).

The pattern in *Euwallacea* damage suggests a distinct role of tree stress as a predisposing factor (Wang et al. 2021). However, there are also cases where the invasive beetles cause damage in naturally growing native vegetation, including increasingly in South Florida (Owens et al. 2018) and South Africa (Paap et al. 2018). Therefore, it may be too early to estimate the full impact of the *Euwallacea* global invasion.

11.3.4 Ambrosia Beetle Colonization Is a Sign of Tree Disease, not Its Cause

Plant pathologists have long understood the tripartite balance between a pathogen, the host, and the well-being of the host as the so called “disease triangle”. In other words, for a disease to occur, the three elements must be in place: the pathogen has to be present in the susceptible host and the environment has to be conducive to disease development. In ambrosia beetle management, the role of the environment and the pre-existing conditions of the trees has not yet been broadly appreciated.

In ambrosia beetle systems where environment has been studied, it is often tree stress that determines the impact of these beetles (Ranger et al. 2010; Boland and Woodward 2019). Also, in the case of the closely related phloem-feeding bark beetles, tree stress is often required for the bark beetles to arrive and facilitate tree death (Wallace 1859; Stephenson et al. 2019). Therefore, we recommend that, when tree disease or death is being diagnosed and when ambrosia beetles are involved, the default assumption is that beetle colonization is a part of multiple interacting negative factors, unless the beetles are explicitly determined to be the primary cause of the problem. Correct determination of the cause of plant diseases is the basis of plant pathology, and the most effective path towards a solution (Leach 1940).

11.4 Questions for Further Research

11.4.1 *Defense Against Invasive Ambrosia Beetles*

Invasive exotic pests and diseases are causing increasing tree mortality around the world. In the past several decades, governments and agencies have been mobilizing a range of solutions to improve national biosecurity, which follow two types of approaches. One approach relies on closing pathways for all new invasions, such as certification of pest-free status of goods and packaging, inspections, and quarantine (Hulme 2009). The second approach is focused on early detection of, and rapid response to, specific exotic species that may cause harm (Kenis et al. 2018; Rabaglia et al. 2019). The two approaches are complementary. While pathway limitations are sometimes perceived to be more effective, their implementation is more likely to impede trade and are thus politically complex. A focus on responses to individual exotic species requires nimble action that is often difficult to mobilize but is much more acceptable to agencies that need to balance pressure from trade organizations and biosecurity, such as the USDA APHIS.

Both approaches are dependent on data. As knowledge about the ecology of individual bark and ambrosia beetle species is growing, we are increasingly able to predict pathways of introductions, and species that are likely to pose harm when introduced to new regions. Species that are likely to cause harm are characterized by two features: the ability to invade and thrive in new habitats, and a propensity for negative impacts on plant commodities.

In the case of ambrosia beetles, pre-invasion assessment is becoming feasible because the features predisposing some species to invasions as well as to damage are becoming increasingly understood (Li et al. 2022). Successful spread and establishment in new regions are facilitated by the fact that the majority of the life-cycle is spent in a concealed habitat and that many species are capable of inbreeding without reduced fitness (Jordal et al. 2001). The capacity for repeated inbreeding allows even minute populations to grow, while in most other outcrossing organisms, repeated inbreeding often leads to expression of recessive deleterious features. Predisposition to actual damage by ambrosia beetles is less clear, but it appears to be determined by specificity to the commodity in question, and the ability to colonize living tissues (Hulcr et al. 2017).

11.4.2 *Ecological Significance*

The sheer abundance of some ambrosia beetles, such as the various Platypodinae or *Xyleborus* in several regions of the world makes these beetles among the most common insects in the forest. To the best of our knowledge however, these numbers have never been quantified, and their impact on ecosystem processes such as ecosystem-scale wood decay remain unclear.

Bark and ambrosia beetles are often the first colonizers of dead and dying trees in most forest ecosystems, and as such, they are likely to play an important role in the recycling of the world's forest biomass and the release of carbon from decaying wood (Luyssaert et al. 2007; Le Quéré et al. 2013; Dossa et al. 2018). Living trees are the largest terrestrial sink for atmospheric carbon dioxide. After a tree dies, however, most of the carbon stored in its tissues is released to the soil and the atmosphere as the metabolic waste of fungal decomposers (Chambers et al. 2001). The rate of carbon release through wood decomposition is to a large degree determined by the identity, diversity, and sequence of fungal colonists (Fukami et al. 2010). Many of the saprotrophic fungi in wood, and in some cases most of the fungi, are introduced by bark and ambrosia beetles (Strid et al. 2014; Skelton et al. 2019b). Thus, by initiating fungal community assembly in recently dead wood, bark and ambrosia beetles are likely to have pervasive influence on wood decay rates, and that influence likely depends on the fungi they carry.

Contrary to the popular belief that they facilitate wood decomposition, new evidence suggests many ambrosia beetles could have the opposite effect. Relatively few fungi can degrade lignocellulose, the main structural component of wood. This process requires highly specialized enzymatic pathways. With the exception of the recently discovered ambrosial *Irpex* and perhaps the basidiomycete associates of some pine-infesting bark beetles [i.e. *Entomocorticium*; (Valiev et al. 2009), but see (Whitney et al. 1987)], no other fungi commonly associated with bark and ambrosia beetles are currently known to have this ability. Instead, most beetle associates depend on the scarcer but more labile resources present in fresh wood, such as sugars and nitrogenous compounds (Licht and Biedermann 2012; Huang et al. 2019).

Recent field and laboratory experiments have shown that some beetle-associated fungi exclude, or compete with, true wood-degrading fungi for labile resources, resulting in decreased decay rates during the early stages of decomposition (Skelton et al. 2019b, 2020). Thus, ambrosia beetles may actually slow carbon release from forest biomass by assembling saprotroph communities that do not decay wood, but instead compete with or exclude decay fungi. Whether these effects persist over the entire decomposition process and ultimately result in increased carbon burial in forest soils is currently unknown. The ecological impacts of widespread introductions and rapid increases in certain beetles that do vector aggressive decay fungi, and which displace native fungi, are also currently unknown and deserve future study (Hulcr et al. 2021; Jusino et al. 2020).

11.4.3 *Pests of the Future*

Eradicating established invasive ambrosia beetles is virtually impossible. Classical biological control has not yet been shown to work in ambrosia beetle pests. Likewise, the biology of the haplo-diploid and inbred ambrosia beetles precludes the effectiveness of some biotechnological applications such as gene drive. We see three options

as most promising for forest and tree health protection against invasive ambrosia pests.

First, preventing future invasions is key. While ambrosia beetles include many global “tourist” species (Gohli et al. 2016), rather few of them become true pests. Most of the damage attributed to invasive ambrosia beetles is actually caused by a few species, namely *X. glabratus*, *E. fornicatus*, and *Xylosandrus* spp. To allow agencies to focus on the pests that are likely to cause impact, and lessen focus on harmless species, it may be worth developing a formal pre-invasion assessment of the likely future pests.

Second, tree management needs to be adapted to the new pests. Fortunately, such adaptation may be within reach. In nurseries, defense against *Xylosandrus* stem borers may require not much more than more efficient water management (Ranger et al. 2016). In orchards affected by *E. fornicatus* and *E. kuroshio*, removal of the hyper-infested tree branches is sufficient to prevent escalation of the pest impact (Mendel et al. 2017).

Third, in cases where tree deaths result from a biotic interaction that is known and characterized, resistance breeding may be a valuable tool for tree protection. In laurel wilt-stricken *Persea*, for example, a certain percentage of the tree population survives, either via resistance to the pathogen or by being undetectable to the vector. Such resistance can be harnessed and resistant populations of these trees are now grown, composed of genotypes from multiple locations (Hughes et al. 2015). In highly valued species, resistance development by biotechnology is also plausible. For pathosystems involving fungi, such as the ambrosia beetle-fungus symbioses, known anti-fungal heritable defense can be deployed, such as has already been used in the protection of trees against invasive fungal diseases (Newhouse et al. 2014).

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