

# BARK BEETLES

BIOLOGY AND ECOLOGY OF NATIVE AND INVASIVE SPECIES

Edited by **Fernando E. Vega** and **Richard W. Hofstetter**



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## Biology and Ecology of Native and Invasive Species

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# Natural History and Ecology of Bark Beetles

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## 1. INTRODUCTION

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are a highly diverse subfamily of weevils that spend most of their life histories within plants. They occur in all regions of the world, and are associated with most major groups of terrestrial plants, almost all plant parts, and a broad array of invertebrate and microbial symbionts. Bark beetles have served as some of the most prominent model systems for studies of chemical ecology, symbiosis, sexual selection, population dynamics, disturbance ecology, and coevolution.

Bark beetles play key roles in the structure of natural plant communities and large-scale biomes. They contribute to nutrient cycling, canopy thinning, gap dynamics, biodiversity, soil structure, hydrology, disturbance regimes, and successional pathways. Several species in particular can genuinely be designated “landscape engineers,” in that they exert stand-replacing cross-scale interactions.

In addition to their ecological roles, some bark beetles compete with humans for valued plants and plant products, and so are significant forest and agricultural pests. These species cause substantial socioeconomic losses, and at times necessitate management responses. Bark beetles and humans are both in the business of converting trees into homes, so our overlapping economies make some conflict of interest inevitable.

Anthropogenic activities are altering the environmental and genetic background on which bark beetles, their host plants, and symbionts interact. Factors that have already been shown to alter these relationships include transport of bark beetles and/or microbial associates, habitat manipulations in ways that homogenize or fragment plant communities, and climate change that raises temperatures and increases drought. These factors often lead to higher plant mortality or injury.

This chapter is intended to introduce, summarize, and highlight the major elements of bark beetle life history and ecology, for subsequent in-depth development in the following chapters. The enormous diversity of Scolytinae

makes it impossible to address each of these elements for all permutations of their life histories. Only relatively few species (1) exert documented selective pressures on their host species and have major roles in landscape-scale processes, (2) pose significant challenges to natural resource management, and (3) provide the majority of our basic biological knowledge. These are disproportionately concentrated within species that colonize the main stems of conifers. We therefore place particular emphasis on that guild.

## 2. DIVERSITY OF LIFESTYLES AND ECOLOGICAL RELATIONSHIPS

The Scolytinae have a long evolutionary history (Cognato and Grimaldi, 2009). They are a subfamily within the Curculionidae, the weevils or snout beetles. They are distinct in having reduced snouts as an adaptation to spending much of their adult life within host plant tissues. These beetles are roughly cylindrical in shape, with short legs and antennae, suitable for a life of tunneling. The head is armed with stout mandibles and many scolytines have morphological adaptations to their elytral declivity (e.g., *Ips* spp.), head (e.g., male *Trypodendron* spp.), or legs for removing plant fragments from their breeding galleries, packing wood shavings in older parts of their gallery (e.g., some *Dendroctonus* spp.), or blocking unwanted conspecifics, competitors or natural enemies from galleries (S. L. Wood, 1982). Beyond those general traits, scolytine beetles are highly variable. While the common name “bark beetle” is sometimes applied to the entire subfamily, many are not associated with bark at all, but rather utilize a variety of plant tissues, both for reproduction and feeding. Many scolytine species are ambrosia beetles, which establish breeding galleries in wood, but feed on symbiotic fungi rather than directly on plant tissues. In this chapter, we focus on bark beetles *sensu stricto*, i.e., those species that breed in the inner bark of their host, but where appropriate we will reference other feeding guilds as well.



## 2.1 General Life Cycle

For the purpose of this chapter, we will emphasize well-studied species to illustrate a general bark beetle life cycle. There are many variations, but most species emerge from their brood galleries in spring or summer, and seek a mate and a new host. The effective dispersal flight is often no more than a few hundred meters (Salom and McLean, 1989; Zumr, 1992) where most successful attacks tend to occur (Wichmann and Ravn, 2001), but the potential to actively fly many kilometers has been demonstrated in laboratory flight mill (Forsse and Solbreck, 1985; Jactel, 1993) and field (Jactel, 1991; Yan *et al.*, 2005) studies. Dispersal distances vary markedly among species, and within species with beetle condition, distribution of susceptible hosts, and environment (Franklin *et al.*, 1999, 2000). Long-range, wind-aided dispersal can extend for hundreds of kilometers (Nilssen, 1984; Jackson *et al.*, 2008; Ainslie and Jackson, 2011; de la Giroday *et al.*, 2011; Samarasekera *et al.*, 2012). Prior to colonizing new hosts, beetles may engage in maturation feeding, often in their brood gallery prior to dispersal. Some species disperse to a specific maturation feeding site, usually a live tree, prior to seeking a breeding site (Stoszek and Rudinsky, 1967; Långström, 1983; McNee *et al.*, 2000). In several species, this behavior can result in vectoring of important pathogens, such as *Verticicladiella wagneri* W. B. Kendr. (Witcosky *et al.*, 1986b) and *Ophiostoma novo-ulmi* Brasier (Webber, 1990).

Bark beetle reproductive strategies can be roughly divided into three types, depending on when and where mating occurs, and the gender initiating gallery construction. In *monogamous* species, females initiate the attack and are joined by a single male. Mating normally takes place on the bark or in the gallery, depending on species, but a small percentage of females may arrive at a host already mated (Bleiker *et al.*, 2013). In *polygamous* species, the male initiates attacks, generally by excavating a nuptial chamber where he mates with several females. A few species are *solitary*, with mated females attacking weakened but living hosts. These species are parasitic on trees, and rarely kill their host, which would perhaps be maladaptive because of the protection host resin provides from predators and parasites. Females of solitary beetles often mate in their brood gallery, with either a brother or, possibly, an unrelated male.

Eggs are laid singly in niches excavated along a narrow gallery (tunnel), in groups on alternating sides, or sometimes grouped along one side of the gallery. In some species, a chamber is excavated in which the eggs are deposited. After hatching, larvae feed on phloem tissue in individual niches or galleries radiating away from the maternal gallery. The lengths of larval mines vary widely among species, ranging from an expansion of the original egg niche to accommodate growing ambrosia beetle larvae,

to extensive galleries 10–15 cm long in species that derive most of their nutrients directly from host tissue (S. L. Wood, 1982). In some species, larvae spend only a brief time in the inner bark, after which they migrate to the nutrient-poor outer bark. This is possibly an avoidance mechanism, as cerambycid larvae may both destroy the phloem and consume bark beetle larvae (Flamm *et al.*, 1993; Schroeder and Weslien, 1994; Dodds *et al.*, 2001). Larvae develop through 3–5 instars, after which they pupate. Metamorphosis is completed in 5–10 days in many species, and the adult beetle ecloses as a callow or teneral adult. These young adults are lightly colored due to incomplete sclerotization of the exoskeleton. After maturation feeding, adults exit through an emergence hole, which they excavate through the bark or were formed by an earlier emerging beetle, or in the case of ambrosia beetles through the entrance hole to the maternal gallery.

## 2.2 Variations to the Generalized Life Cycle

### 2.2.1 Feeding Substrate

Bark and wood are relatively poor nutritional substrates, so most bark beetles feed on the slightly more nutritious inner bark, or phloem. A considerable number of species exploit the ability of fungi to concentrate nitrogen, by consuming either fungus-infected phloem, or fungi (Ayres *et al.*, 2000; Bleiker and Six, 2007). Associations between bark beetles and fungi range from facultative to obligatory symbioses. Bark beetles inoculate their fungal associates by carrying spores either on their exoskeleton, or by actively transporting and nurturing them. In evolutionarily advanced associations, the complexity and variety of specialized pockets (*mycangia*) that harbor symbionts suggest these symbioses have evolved independently multiple times (Six and Klepzig, 2004; Harrington, 2005). Ambrosia beetles represent the most advanced of such associations, and this specialization has allowed them to escape to the three-dimensional xylem from the essentially two-dimensional inner bark niche, where competition with other phloeophagous organisms may be fierce (Lindgren and Raffa, 2013). Thus, scolytine ambrosia beetles can occur at extremely high densities relative to bark beetles. Not surprisingly, ambrosia beetles have been extremely successful, particularly in the tropics, and another subfamily of the Curculionidae, the Platypodinae, have evolved to occupy a similar niche.

Many scolytine beetles have a relatively narrow host range, ranging from mono- to oligophagous. Some species may be associated with only one species of host tree, whereas others may be able to utilize most species within a genus, and on occasion other genera (Huber *et al.*, 2009). Among bark beetles *sensu stricto* that colonize live trees, most have evolved adaptations to exploit Pinaceae

despite formidable defenses that these trees can mount (Franceschi *et al.*, 2005). Many scolytines breed in angiosperms (Wood and Bright, 1992), but most of those are saprophages (Ohmart, 1989). Ambrosia beetles are often less constrained in their host range than phloem feeding bark beetles, and some are known to colonize many tree species (Hulcr *et al.*, 2007). This may be because the deciding factor is whether the tree can support the ambrosia fungus. For example, *Trypodendron lineatum* (Olivier), an economically important species in western North America and Europe, breeds in numerous Pinaceae genera, but also in at least four genera from three families of angiosperms (Lindgren, 1986).

In addition to species that utilize the trunk, a number of species breed in roots, twigs, or branches. Many scolytine beetles also utilize other plant parts, e.g., cone beetles in the genus *Conophthorus* breed in the cone axis of several species of conifers (Chapter 12), and *Hypothenemus hampei* (Ferrari), breeds in the seeds of two *Coffea* species and possibly other species in the family Rubiaceae (Chapter 11). Similarly, *Coccotrypes dactyliperda* F., breeds in the stone of green, unripened date fruits (Blumberg and Kehat, 1982), and a number of scolytine species breed in the woody petioles of *Cecropia* spp. (Jordal and Kirkendall, 1998). Furthermore, some species conduct maturation feeding outside the maternal gallery, e.g., in shoots of their host tree, such as several species of *Tomicus* (Långström, 1983; Kirkendall *et al.*, 2008; Chapter 10) and *Pseudohylesinus* (Stoszek and Rudinsky, 1967; Chapter 12).

### 2.2.2 Gender Roles

Host selection and gallery initiation are typically performed by females in monogamous (one male with one female) species, and males in polygamous (one male with several females) species, a distinction that holds at the genus level. In monogamous species, females arrive at a tree, and initiate a gallery while releasing pheromones. Males arrive at and attempt to enter the gallery. Male entrance, and hence mate choice, in these genera is typically dictated by female assessment of their suitability (Ryker and Rudinsky, 1976). A small percentage of females mate before they emerge (Bleiker *et al.*, 2013), and may arrive at the host already fertile, allowing them to construct a gallery and produce offspring without another male. This is assumed to occur either with a male that entered a natal gallery, or a sibling. In some parasitic species, e.g., *Dendroctonus micans* (Kugelann) and *Dendroctonus punctatus* LeConte, females attack by themselves, so mating occurs pre-emergence, or at least pre-attack (Grégoire, 1988; Furniss, 1995), or possibly both, as there is evidence that multiple mating can occur in *D. micans* (Fraser *et al.*, 2014). Exceptions to females being the pioneering sex

among monogamous species occur in some genera, such as the ambrosia beetle genus *Gnathotrichus*, in which the male initiates attack and is joined by one female. This may indicate that monogamy is a derived state in these genera. In polygamous species, the male initiates gallery construction in the form of a nuptial chamber. Females will attempt to join the male, who may resist entrance, i.e., in polygamous species the male controls mate selection (Wilkinson *et al.*, 1967; Løyning and Kirkendall, 1996). Subsequent females encounter increasing resistance by the male. In some cases, a late-arriving female may enter a gallery by excavating her own entrance, i.e., thus circumventing male mate selection.

Some polygamous species include pseudogynous females, i.e., females that require mating, but produce offspring parthenogenetically without the use of male gametes (Stenseth *et al.*, 1985; Løyning and Kirkendall, 1996). In some scolytine beetles, notably a few genera in the bark beetle tribe Dryocoetini and all species of the ambrosia beetle tribe Xyleborini, sex determination is by haplo-diploidy, with unmated diploid females producing haploid dwarf males with which they may later mate (Normark *et al.*, 1999; Jordal *et al.*, 2000). Sib mating and fungal symbiosis are closely associated with this evolutionary path (Jordal *et al.*, 2000). A fascinating special case of sib mating occurs in the genus *Ozopemon*, where neoteny (sexual maturation of larvae) has evolved in males (Jordal *et al.*, 2002). Beetles with this haplo-diploid sex determination system are eminently well adapted for invading novel habitats, because even a single female is theoretically sufficient for establishment in a novel habitat (Jordal *et al.*, 2001; Zayed *et al.*, 2007; Hulcr and Dunn, 2011). Ambrosia beetles are particularly advantaged because host specificity is primarily determined by the ability of the ambrosia fungus to thrive in novel hosts. Consequently, ambrosia beetles are easily transported in dunnage or wood products, and many, e.g., *Xyleborinus saxeseni* (Ratzeburg), now have an almost worldwide distribution.

### 2.2.3 Symbiotic Associations

A wide diversity of symbionts has contributed to the success of bark and ambrosia beetles. Because parasitoids exert a form of delayed predation, we will not treat them as symbionts here. For most species, one or several symbionts play important roles. In many cases, the roles of symbionts are poorly understood, but recent findings have begun to shed light on the importance of some associations.

Most scolytine beetles appear to be closely associated with symbiotic fungi (Kirisits, 2004; Harrington, 2005). There are few exceptions, with *D. micans* currently considered an example (Lieutier *et al.*, 1992). The roles of fungi vary widely (Six, 2012). For some groups, i.e., ambrosia

beetles, fungi serve as the sole source of nutrition for both adults and larvae. These species typically have a close association with one or two specialized symbiont fungi (Batra, 1966). For other groups, the relationship between the host and symbiont is less clear. For example, the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, normally is associated with two or three species of fungi, but at least 12 (including yeasts) have been identified (Lee *et al.*, 2006). The roles of these symbionts can range from beneficial, e.g., as a source of food (Ayres *et al.*, 2000; Bleiker and Six, 2007) to detrimental (Harrington, 2005). A pervasive paradigm has been that fungi are necessary for, or at least contribute to, killing the host tree, as evidenced by inoculation experiments (Krokene and Solheim, 1998). Six and Wingfield (2011) argue against this premise, however. More recent studies suggest these fungi can contribute to overcoming tree defenses by metabolizing conifer phenolics and terpenes (see Section 3.4). Species associations vary markedly, with some relationships are facultative or even casual, rather than obligatory (Six, 2012).

Phoretic mites are frequently found on bark beetles (Hofstetter *et al.*, 2013; Knee *et al.*, 2013; Chapter 6). Large numbers of mite species from several families have been associated with the galleries of many bark beetle species (Lindquist, 1970). For example, *Dendroctonus frontalis* Zimmermann has at least 57 species of phoretic mites (Moser and Roton, 1971; Moser *et al.*, 1974; Moser and Macías-Sámamo, 2000). Similarly, 38 species of mites are associated with *Ips typographus* L. captured in pheromone-baited traps in Europe (Moser *et al.*, 1989), and an additional three species were found on *I. typographus japonicus* Nijjima (Moser *et al.*, 1997). The roles and impacts of mites are not well understood, but vary from detrimental (predatory on bark beetle larvae, parasitic on eggs) to beneficial (predators on nematodes, mycophagous) (Klepzig *et al.*, 2001; Lombardero *et al.*, 2003;

Kenis *et al.*, 2004). Some mites also contribute to the fungal diversity in bark beetle galleries by transporting spores in specialized sporothecae (Moser, 1985). Host specificity also varies, depending on the ecological role of the mite species (Lindquist, 1969, 1970).

Bark beetles are commonly associated with nematodes, most of which appear to be parasitic, phoretic, or commensal (Thong and Webster, 1983; Grucmanová and Holuša, 2013). Massey (1966) found 27 species of nematodes associated with *Dendroctonus adjunctus* (Blandford), and Grucmanová and Holuša (2013) list 11 phoretic, 12 endoparasitic, and eight species associated with frass of *Ips* spp. in central Europe. Cardoza *et al.* (2006b) found nematodes associated with special pockets, *nematangia*, on the hind wings of *Dendroctonus rufipennis* (Kirby). *Nematangia* have since been found on *Pityogenes bidentatus* (Herbst), containing the tree parasite *Bursaphelenchus pinophilus* Brzeski and Baujard (Nematoda: Parasitaphelenchinae) (Čermák *et al.*, 2012) and *Dryocoetes uniseriatus* Eggers, containing the insect parasite and nematode predator *Devibursaphelenchus* cf. *eproctatus* (Shimizu *et al.*, 2013).

Bacteria may play important roles in ensuring that the host environment remains hospitable, i.e., during initial attack when defense compounds may be high, and during later phases when contaminant antagonistic microorganisms could potentially harm the food supply or offspring. Scott *et al.* (2008) found that actinomycete bacteria associated with *D. frontalis* produce antibiotic compounds, a function similar to that of actinomycetes on leaf cutter ants, *Atta* spp. (Hymenoptera: Formicidae) (Currie *et al.*, 1999). Different bacteria vary in their tolerance of host terpenoids, and in particular bacteria associated with bark beetle species that breed in live resinous hosts are more tolerant than those that kill trees by mass attack (Figure 1.1A) (Adams *et al.*, 2011).



**FIGURE 1.1** Sample illustrations of bark beetle interactions with host plants. (A) *Dendroctonus micans* tunneling through resin. (B) Extensive competition to *D. ponderosae* (note vertical ovipositional gallery in center) caused by *Ips* (note extensive network of surrounding galleries) in a windthrown *P. contorta* in Wyoming. Reproduced with permission from Lindgren and Raffa (2013). Photos by (A): J.-C. Grégoire; (B): K. Raffa.



## 2.3 Variation in Ecological Impacts of Bark Beetles: from Decomposers to Landscape Engineers, and from Saprophages to Major Selective Agents on Tree Survival

Various bark beetle species are prominent members among the succession of organisms that occupy tree tissues from initial decline to decay (Lindgren and Raffa, 2013). The vast majority of bark beetles are saprophagous, strictly breeding in dead trees or tree parts. The primary ecological role of such species is to initiate or contribute to the breakdown of wood by feeding, vectoring symbiotic microorganisms, or providing access for decay microorganisms. Lindgren and Raffa (2013) subdivided this guild into late succession saprophages, which occupy the resource once most or all of the defensive compounds have been detoxified, and early succession saprophages, which can tolerate some defense compounds. In some cases, the latter species may serve as thinning agents by attacking and killing moribund or severely weakened host trees (Safranyik and Carroll, 2006). They may also facilitate the facultative predatory beetles (Smith *et al.*, 2011). Tree-killing bark beetles, while relatively few in number, can have profound ecological effects, including impacts on species composition, age structure, density, woody debris inputs, and even global carbon balance (Kurz *et al.*, 2008; Lindgren and Raffa, 2013).

## 2.4 Major Groups

Based on phylogenetic analyses, the bark and ambrosia beetles have recently been reassigned from the family Scolytidae to the subfamily Scolytinae within Curculionidae. Wood (1986) used morphological characteristics to divide Scolytidae into two subfamilies and 25 tribes. Alonso-Zarazaga and Lyal (2009) divided the Scolytinae into 29 tribes. Of the more than 6000 species of Scolytinae described to date, the vast majority are tropical or subtropical (Knížek and Beaver, 2004). Yet, most of our knowledge of bark beetles is based on a large number of studies on a relatively small number of environmentally and economically important species across a few tribes, and within the temperate regions of the northern hemisphere. In particular, studies have emphasized tree-killing species in the Hylesinini, Hylastini, Ipini, Scolytini, and Dryocoetini. Additional focus has been centered on the large tribe of haplo-diploid ambrosia beetles comprising the Xyleborini, because of both their interesting reproductive biology and their prominence as invasive species (Cognato *et al.*, 2010). Another ambrosia beetle tribe, the holarctic Xyloterini, is also relatively well studied, particularly the genus *Trypodendron*, and specifically *T. lineatum* because of its economic importance in northern Europe and western North America (Borden, 1988).

## 3. INTERACTIONS WITH HOST PLANTS

### 3.1 Host location and Selection

Most bark beetles deposit all or most of their clutch within a single tree, so the ability to locate and select suitable hosts is crucial for their reproductive success. Many species can only utilize a host for one, or perhaps a few, beetle generations, so each cohort must locate a suitable host to reproduce. The choice of a host tree is laden with trade-offs (Raffa, 2001; Lindgren and Raffa, 2013): trees that are already dead or whose defenses have been severely compromised by environmental or endogenous stress pose little risk during colonization. However, such trees are relatively rare, ephemeral in space and time, are occupied by a diversity of interspecific competitors (Figure 1.1B), and often provide a lower quality nutritional substrate. At the other end of this continuum, relatively unstressed trees are consistently plentiful, in some cases nutritionally superior because of the thicker phloem accompanying their vigorous growth, and only become available to competitors after the primary beetle kills them. However, these trees possess vigorous defenses that can kill potential colonizers that enter them. Making this decision even more daunting is the fact that bark beetle adults normally survive for only a few days (Pope *et al.*, 1980) to a few weeks (Byers and Löfqvist, 1989) outside the tree, and they are subject to rapid energy depletion and predation. Furthermore, the more time a beetle takes to find a tree that elicits its entry behavior, the more trees are eliminated from the available pool by competing conspecifics.

Adult bark beetles employ multiple and integrated modalities, including visual, olfactory, tactile, and gustatory, to perform the difficult tasks of host location and selection (Borg and Norris, 1969; Wood, 1972; Raffa and Berryman, 1982; Pureswaran *et al.*, 2006). Their responses to these signals are influenced by external cues, internal physiology, heredity, and gene by environment interactions (Wallin and Raffa, 2000, 2004; Wallin *et al.*, 2002).

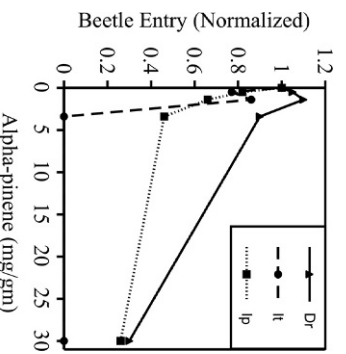
Initial landing is mediated by both visual and chemical cues (Saint-Germain *et al.*, 2007). Some species, such as *D. ponderosae*, show strong orientation to vertical silhouettes, which can be enhanced by coloration that provides greater contrast (Shepherd, 1966; Strom *et al.*, 1999). Chemical cues that elicit directed movement and landing can include host secondary compounds such as some monoterpenes, compounds indicative of stress such as ethanol, and compounds indicative of microbial infection or decay such as acetaldehyde. The extent to which initial attraction and landing in response to these compounds relates to ultimate host selection varies among species. In general, species that are solely associated with dead or highly stressed trees tend to respond to the latter groups of compounds and readily enter the hosts emitting these signals (Rudinsky, 1962). In contrast, species associated with less stressed or



healthy trees tend to land initially in response to visual cues and some monoterpenes, and then make subsequent decisions post-landing (Wood, 1972; Moeck *et al.*, 1981). In these species, landing rates tend to be much higher than entry rates (Hynum and Berryman, 1980; Raffa and Berryman, 1980; Anderbrant *et al.*, 1988; Paynter *et al.*, 1990).

Following landing, beetles locate potential entry sites under bark crevices, in response to microclimatic and thigmotactic stimuli. Borg and Norris (1969) demonstrated that pronotal stimulation is required for host compounds to elicit tunneling behavior, a finding routinely incorporated into subsequent bioassays evaluating chemical signals (Elkinton *et al.*, 1981; Raffa and Berryman, 1982; Sallé and Raffa, 2007). In nature, this scales up to beetle within-tree orientation toward bark crevices, so physical texture can play an important role in microsite selection (Paynter *et al.*, 1990). A beetle's decision on whether or not to enter is largely driven by concentrations of host compounds, especially monoterpenes. In addition to the variable attractiveness vs. repellency of different compounds, a common pattern is for low concentrations of a particular monoterpene to elicit tunneling behavior while higher concentrations deter entry or continued tunneling (Figure 1.2). Often, the eliciting concentrations are typical of those which occur in constitutive tissues, but the concentrations present in induced tissue are adequate to deter continued tunneling (Wallin and Raffa, 2000, 2004). The concentrations that elicit entry versus rejection behavior vary among beetle species.

Many bark beetle species can detect cues associated with stress physiology of their host plants. Higher entry rates have been observed in response to root infection, defoliation, fire injury, and other stresses (Lindgren and Raffa, 2013). In addition to external cues, internal cues can affect beetles' responses to host chemicals. For example, as their lipids are depleted, as occurs during flight and extended host searching, some beetles become more responsive to host cues (Kin *et al.*, 1994). Other internal cues that can increase a beetle's likelihood of entering a tree include age and the number of times it has already rejected putative



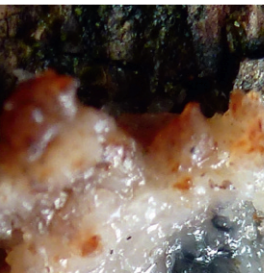
**FIGURE 1.2** Effects of host chemistry on entry or aversion behavior in bark beetles. Artificial media amended with synthetic  $\alpha$ -pinene for three species, *Dendroctonus rufipennis* (Dr), *Ips tridentis* (It), and *Ips pini* (Ip). From Wallin and Raffa (2000, 2004).

hosts, which likely relate to its dwindling likelihood of reproducing if it did not accept some host before dying (Wallin and Raffa, 2002). Beetle responses to host stimuli also show heritable variation. Laboratory experiments have demonstrated selection for “more discriminating” and “less discriminating” lines, based on the maximum monoterpene concentrations beetles will accept in amended media (Wallin *et al.*, 2002). In the field, *D. rufipennis* shows correlations between mothers and daughters in monoterpene concentrations that elicit entry, and these relationships persist for several generations. There are also differences among *D. rufipennis* from endemic vs. eruptive populations, with the latter showing a higher likelihood of entering high-terpene media when other beetles are present (Wallin and Raffa, 2004). Overall, there appears to be substantial plasticity in host selection among tree-killing bark beetles.

### 3.2 Host Defenses

Because phloem is essential to tree survival, conifers have evolved sophisticated defenses against bark beetle-microbial complexes. Five features of these defenses are particularly pertinent. First, they involve multiple modalities, including physical, histological, and biochemical components (Figure 1.3), and these modalities function in a highly integrated fashion (Raffa, 2001). Within each of these broad categories, there is further complexity and overlap. Chemical defense, for example, includes a variety of classes, and each class includes many different moieties of varying structure and chirality, and some chemical groups such as lignins and terpenoids contribute to physical barriers. Second, delivery of these toxins is augmented by physical structures such as resin canals and glands. Third, each of these physical, histological, and chemical components of defense include both constitutive defenses and rapidly induced defenses in response to attack (Reid *et al.*, 1967; Raffa and Berryman, 1983; Franceschi *et al.*, 2005; Bohmann and Gershenson, 2009). Fourth, these components of tree defense inhibit multiple aspects of both beetles' and microbial symbionts' life histories, such as host entry, pheromone signaling, survival, growth, and sporulation. Fifth, in addition to heritable features of host resistance, fully integrated functioning of these mechanisms is associated with vigorous whole-plant physiology, so a variety of acute and chronic stresses can impair the extent and rate of these defenses (Raffa *et al.*, 2005; Kane and Kolb, 2010).

Outer bark provides a tough physical barrier, which screens out all but those relatively few herbivores adapted for penetrating it with powerful mandibles, specially modified legs, and other body morphologies. As soon as a tunneling beetle encounters live tissue, trees exude a rapid flow of resin (Chapter 5). The quantity and importance of this resin vary greatly among conifer genera (Berryman, 1972), and even among species within a genus,



**FIGURE 1.3** Integrated physical, histological, and chemical defenses of conifers. (A) *D. micans* killed in resin during attempted colonization of *P. abies*; (B) *D. ponderosae* killed in hypersensitive response during attempted colonization of *P. contorta*; (C) profile of toxicity to *I. pini* adults (48 hours *in vitro* assays) of concentrations of  $\alpha$ -pinene present in constitutive and induced responses of *P. resinosa*. From Raffa and Smalley (1995). Photos by (A): J.-C. Grégoire; (B): K. Raffa.

as in *Pinus* (Matson and Hain, 1985). There is also substantial variation within species, and ontogenetic, phenological, and stress-mediated variation within individuals. Resin is stored in a variety of structures, such as specialized ducts and glands. This resin poses a significant physical barrier, and can entomb some beetles (Figure 1.3) (Raffa *et al.*, 2008). It also delays beetle progress, which can provide more time for histological and biochemical processes to achieve effective levels. Resin also contains various allelochemicals that can exert repellent and/or toxic effects. Tree-killing bark beetles, however, are often able to physiologically tolerate the concentrations present in constitutive resin.

As a bark beetle tunnels into a tree, inducible reactions begin rapidly. These include induced resinosis and traumatic resin duct formation, autonecrosis and associated alterations in polyphenolic parenchyma and stone cells, and biosynthesis of various compounds via a combination of mevalonic acid, 1-deoxy-D-xylose-5-phosphate, and shikimic acid pathways (Safaryik *et al.*, 1975; Raffa and Berryman, 1983; Popp *et al.*, 1991; Martin *et al.*, 2003; Franceschi *et al.*, 2005; Keeling and Bohlmann, 2006; Boone *et al.*, 2011). These inducible responses are mediated by signaling compounds such as jasmonic acid and salicylic acid, which are ubiquitous among plants.

As the name induced resinosis implies, resin flow from a wound, especially one accompanied with a biotic inciter such as a beetle or its fungal symbionts, increases rapidly. In addition to delaying the beetle's progress, a copious flow of resin can inhibit a beetle's ability to elicit the arrival of other beetles with pheromones. This likely occurs through a combination of gummy resins physically blocking the

emission of volatile pheromones from the entry site, and high ratios of volatile host terpenes to pheromones that either mask perception or inhibit attraction (Zhao *et al.*, 2011; Schiebe *et al.*, 2012). If mass attack is not elicited relatively quickly, the ratio of monoterpene to pheromones rises to such high levels that the likelihood of a tunneling beetle being joined by conspecifics becomes very low (Ehrlig *et al.*, 2003, 2006). While this is under way, the tree initiates an autonecrotic or "hypersensitive" reaction (Figure 1.3), in which rapidly progressing cell death forms a lesion that confines the attacking beetle and its symbionts. The nutritional value of this tissue is lost, and this reaction zone becomes the site of pronounced and rapid biochemical accumulation, apparently through both biosynthesis and translocation. Chemical changes include vastly increased concentrations of constitutive compounds, often from non-repellent to repellent, and non-lethal to lethal, doses, altered proportions of compounds present in constitutive synthesis, often with the more bioactive compounds undergoing disproportionately high increases, and production of new compounds that are not present (or at below detectable levels) in constitutive tissue (Raffa *et al.*, 2005). These abilities vary quantitatively among trees within a population. That is, all (or nearly all) trees are capable of this response, and fungal inoculation combined with mechanical wounding almost always elicits induced defenses. However, those trees that respond more extensively and rapidly are more likely to survive. For example, dose-dependent relationships between induced terpene accumulation and resistance to bark beetle attack in the field have been demonstrated in *Pinus* (Raffa and Berryman, 1983; Boone *et al.*, 2011), *Abies* (Raffa and Berryman, 1982), and *Picea* (Zhao *et al.*, 2011).

The major chemical groups that contribute to protection from bark beetle–microbial complexes include monoterpenes, diterpene acids, stilbene phenolics, and phenylpropanoids. These tend to have complementary activities (Raffa *et al.*, 2005). In general, high concentrations of monoterpenes are repellent, ovicidal, larvicidal, and adulticidal toward the beetles. Tolerance appears somewhat higher among the solitary-parasitic than gregarious-tree killing species. Monoterpenes moderately inhibit fungal germination and growth, and are likewise highly toxic to a broad range of bacteria associated with beetles. Phenolics tend to have relatively low activity against bark beetles, but have moderate activity against their fungal associates. Their activity against beetle-associated bacteria is unknown. Diterpene acids are the most toxic group to beetle-associated fungi, greatly inhibiting mycelial growth, conidiophore production, and germination (Boone *et al.*, 2013). In contrast, some beetle-associated bacteria are quite tolerant of diterpene acids. To date, no direct effects of diterpene acids against the beetles have been demonstrated. One phenylpropanoid, 4-allylanisole, is known to mediate conifer–bark beetle interactions by inhibiting the attraction of flying beetles to the pheromones emitted by a tunneling beetle (Hayes and Strom, 1994; Strom *et al.*, 1999; Kelsey *et al.*, 2001; Emerick *et al.*, 2008). This compound occurs in both subcortical and foliar tissues. We currently have little information on how various defense compounds interact, but a variety of effects, including synergism, seem likely. The overall pattern, however, is that no single chemical influences all components of beetle–microbial systems, but all components of beetle–microbial systems are influenced by one or more compounds.

In addition to the very rapid synthesis of defense compounds and autonecrosis of utilizable substrate at the attack site, there may also be some longer-term effects. For example, *Picea abies* (L.) H. Karst., that had been inoculated with the root fungus *Heterobasidium annosum* (Fr.) Bref. or the bark beetle-vectored fungus *Ceratocystis polonica* (Siemaszko) C. Moreau showed reduced symptoms to inoculation with *C. polonica* 4 weeks later (Krokene *et al.*, 2001). This appears to be primarily attributable to the induced formation of traumatic resin ducts, and the swelling and proliferation of polyphenolic parenchyma cells, a non-systemic response within the pretreated area (Krokene *et al.*, 2003, 2008). Similarly, persistent elevated terpene levels induced by application of methyl jasmonate were localized, i.e., within the treated but not untreated stem sections. This agrees with work on *Pinus resinosa* Aiton, in which inoculation with *Ophiostoma ips* (Rumbold) Nannf. did not cause systemic alterations in lesion formation or monoterpene accumulation in response to subsequent inoculations (Raffa and Smalley, 1988; Wallin and Raffa, 1999). The extent to which prior beetle attacks influence susceptibility to subsequent attacks under

natural conditions requires additional study. In the cases of the solitary *D. micans* and *Dendroctonus valens* LeConte, and the gregarious *Dendroctonus rufipennis* LeConte, previously attacked trees (*P. abies*, *P. resinosa*, and *Picea glauca* (Moench) Voss and *Picea engelmannii* Parry ex Engelm., respectively) were more likely to be attacked than unattacked trees (Gilbert *et al.*, 2001; Wallin and Raffa, 2004; Aukema *et al.*, 2010). These patterns are not consistent with priming or induced acquired resistance. However, they do not necessarily prove insect-induced susceptibility either, because subsequent cohorts of beetles could be responding to the same predisposing condition. Similar trends emerge from between-species, temporally spaced interactions. Prior sublethal infestation of the lower stems of *Pinus ponderosa* Douglas ex C. Lawson by *D. valens* and associated *Leptographium* is associated with increased subsequent attacks by *Dendroctonus brevicornis* LeConte (Owen *et al.*, 2005), prior colonization of *Pinus contorta* Douglas ex Loudon by *Pseudips mexicanus* (Hopkins) is associated with increased subsequent attacks by *D. ponderosae* (Safranyik and Carroll, 2006; Smith *et al.*, 2009, 2011; Boone *et al.*, 2011), and prior infestation of the lower stems of *Pinus resinosa* by *D. valens*, *Hylobius radialis* Buchanan, and associated *Leptographium* is associated with increased likelihood of subsequent attacks by *Ips pini* (Say) (Aukema *et al.*, 2010).

A fourth category of defenses, about which little is known, involves symbiotic associations. For example, endophytic bacteria in *P. contorta* can inhibit the growth of *Grosmannia clavigera* (Rob.-Jeffr. and R.W. Davidson), an important fungal symbiont of *D. ponderosae* (Adams *et al.*, 2008). We do not yet know what roles these relationships play in nature. In some plant–herbivore interactions, symbioses involving mycorrhizae and endophytes can be quite important, so this area requires more investigation.

### 3.3 Host Substrate Quality

The quality, or suitability, of a host as a substrate for developing brood is distinct from its susceptibility, i.e., the relative ease or difficulty with which it can be killed. Stem-colonizing bark beetles consume a resource that is spatially limited, and of relatively poor quality. The phloem is a relatively thin subcortical layer, and different beetle species are confined by different minimal requirements of phloem thickness, which in turn limits the sizes of trees and heights along the bole they can colonize. This limitation creates a true “carrying capacity,” in which the available resource per individual declines as the number of colonizing individuals increases (Coulson, 1979; Anderbrant, 1990). Hence, there are often direct relationships between phloem thickness and total beetle reproductive output, and between tree diameter and total beetle reproductive output (Amman, 1972).



Phloem tissue tends to be particularly low in nitrogen, which is often limiting to herbivorous insects (Mattson, 1980). Low nitrogen availability lengthens insect development times and reduces their fecundity. Bark beetles compensate for this resource deficiency with close associations with microbial symbionts, especially fungi and bacteria (Ayres *et al.*, 2000; Bleiker and Six, 2007; Morales-Jiménez *et al.*, 2009). The phloem resource also contains cellulose, but not in levels comparable to those in sapwood with which wood borers must contend, and so the cellulolytic capabilities of bacteria associated with bark beetles appear generally less than those of bacteria associated with cerambycids and siricids (Delalibera *et al.*, 2005; Adams *et al.*, 2011). Phloem tissue appears to have adequate concentrations of carbohydrates, sterols, and micronutrients for bark beetles, and there are no particular limitations in their availabilities.

Phenological changes in trees in temperate zones limit bark beetles to a relatively narrow window of resource availability. As the season proceeds, this tissue begins to harden, desiccate, and export resources. Once these changes begin, host quality declines. In multivoltine species such as *I. pini*, later-season development can be less productive, even though it may open periods of escape from predators (Redmer *et al.*, 2001). Host quality also deteriorates due to microbial exploitation following beetle colonization. The physical and chemical defenses that trees use against bark beetles also render this habitat unavailable to a diversity of saprophytic and antagonistic fungi. However, once the beetles have exhausted those defenses, the environment becomes available to competing organisms, which can exert substantial costs on beetle fitness.

Not much information is available on variation among host tree species in their resource quality for bark beetles, other than differences attributable to phloem thickness. In general, it appears that interspecific variation in substrate quality is mostly attributable to tree size and phloem thickness.

### 3.4 Roles of Symbionts in Host Plant Utilization

Symbionts play crucial roles in the life histories of bark beetles, especially in overcoming tree defense, utilizing host plant substrates, and protecting their resource. Numerous microbial taxa are associated with scolytines, and all scolytine species are associated with microorganisms.

Early work often depicted bark beetle-vectored fungi as virulent pathogens that killed the tree and thereby rendered it available for brood development. However, instances in which ophiostomatoid fungi directly kill trees appear limited to invasive species (such as *Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* in European and North

American *Ulmus* and *Leptographium procerum* (W. B. Kendr.) M. J. Wingf. in Chinese *Pinus*) (Gibbs, 1978; Brasier, 1991; Sun *et al.*, 2013), and a few species such as *C. polonica* (Krokene and Solheim, 1998) and certain strains of *G. clavigera* (Lee *et al.*, 2006; Plattner *et al.*, 2008; Alamouti *et al.*, 2011). Similarly, early researchers often envisioned these fungi as blocking the flow of resin to the point of attack, but subsequent experiments indicate that fungi probably do not grow quickly enough into tracheids to exert this effect (Hobson *et al.*, 1994).

More recent work indicates that microbial symbionts of bark beetles can metabolize host toxins. Specifically, *C. polonica* reduces concentrations of stilbene phenolics present in *Picea*, at least *in vitro* (Hammerbacher *et al.*, 2013). The fungus *G. clavigera* has genes that encode for terpene metabolism (DiGuistini *et al.*, 2011). Likewise, bacteria associated with *D. ponderosae* and their host trees have multiple genes encoding for detoxification of many terpenoids, and also greatly reduce concentrations on monoterpenes and diterpene acids *in vitro* (Adams *et al.*, 2013; Boone *et al.*, 2013). Furthermore, various bacteria species appear to have complementary metabolic activities, with different community members degrading specific compounds, but collectively all host chemicals being degraded by at least one bacterium. These relationships are dose dependent, as high concentrations of terpenes become toxic and negate bacterial activity. The tolerance of bacterial associates to host tree terpenes appears to vary with beetle life history strategy, with communities associated with species such as *D. valens* that often reproduce in live hosts being more tolerant than community members associated with mass-attacking species such as *D. ponderosae* (Adams *et al.*, 2011). In addition, yeasts can influence the composition of monoterpenes. When *Ogataea pini* (Holst) Y. Yamada, M. Matsuda, K. Maeda and Mikata from *D. brevicornis* mycangia was added to phloem disks of *P. ponderosae*, total monoterpenes were not reduced, but several individual components were higher or lower, relative to controls (Davis and Hofstetter, 2011). Overall, it appears that microbial associates function in concert with bark beetles to jointly overcome tree defenses, i.e., as cofactors (Klepzig *et al.*, 2009; Lieutier *et al.*, 2009). Further, microorganisms appear to detoxify tree chemicals in conjunction with, not in place of, detoxification by the beetles themselves, which are equipped with P-450 enzymes (Sandstrom *et al.*, 2006).

Microorganisms may also assist beetles in overcoming tree defense by contributing to biosynthesis of aggregation pheromones. For example, the bacterium *Bacillus cereus* converts  $\alpha$ -pinene into verbenol *in vitro* (Brand *et al.*, 1975). However, it is not clear whether this plays an important role in nature. There are also instances in which fungi reduce tree defenses indirectly and with a time lag. For example, vectoring of *Leptographium* fungi into roots and lower stems by various *Hylastes* and solitary



*Dendroctonus* species impairs defenses against subsequent lethal stem-colonizing attack bark beetles (Witcosky *et al.*, 1986a; Klepzig *et al.*, 1991; Eckhardt *et al.*, 2007). There may be important interactions among microorganisms in overcoming tree defenses. For example, *G. clavigera* and other ophiostomatoid fungi are highly susceptible to diterpene acids, but the bacteria associated with *D. ponderosae* greatly reduce concentrations of these compounds. Likewise, bacteria associated with *D. ponderosae* and *D. valens* can enhance mycelial growth and spore germination of various fungal symbionts. These interactions can be either enhanced or inhibited by host tree terpenes (Adams *et al.*, 2009).

Fungi play crucial roles in nutrient acquisition by bark beetles (Six, 2012). Almost all bark beetle species show close associations with fungi, and benefit both from fungal metabolism of the substrate into utilizable nutrients, and by directly consuming fungi. Basidiomycetes can be particularly important in this capacity. In addition, symbiotic bacteria may assist beetle larvae in obtaining nitrogen, through nitrogen fixation in the gut (Morales-Jiménez *et al.*, 2012).

The specific composition of various symbiotic species on or in a beetle can have strong effects on bark beetle success, and can be influenced by a number of environmental factors. For example, temperature affects the relative abundance of *G. clavigera* and *Ophiostoma montium* (Rumbold) Arx in galleries of *D. ponderosae* (Addison *et al.*, 2013). This has important ramifications to the beetle's population dynamics in different parts of its range, in different habitats, and implication in response to climate change. In *D. frontalis*, the relative abundances of the mycangial nutritional mutualists, and the antagonist *O. minus*, are strongly influenced by phoretic mites (Hofstetter *et al.*, 2006). The mites, in turn, have variable relationships with these fungi. The outcomes of these interactions are mediated by tree chemistry and temperature (Hofstetter *et al.*, 2007; Evans *et al.*, 2011; Hofstetter and Moser, 2014). The relative composition of various fungal symbionts can also vary spatially and temporally with beetle population density, as in *D. rufipennis* (Aukema *et al.*, 2005a). Likewise, bacterial communities can vary regionally within a beetle species (Adams *et al.*, 2010).

One of the challenges to the lifestyle of bark beetles that colonize live trees is that their mode of overcoming defense (i.e., mass attack) renders the host environment suitable to a broad array of competitors. This can be highly deleterious to developing brood. Bacterial symbionts can play important roles in reducing these losses. As female *D. rufipennis* excavate ovipositional galleries, they egest oral secretions that contain several species of bacteria (Cardoza *et al.*, 2006a). These bacteria are highly toxic to antagonistic fungi such as *Aspergillus* and *Trichoderma*. They are also partially selective, showing less toxicity to the symbiont *Leptographium abietinum* (Peck) Wingf. Likewise, *D. frontalis* carry symbiotic Actinomycetes that produce mycangimicin, which

selectively inhibits the antagonist *O. minus* but not the mutualistic *Entomocorticium* sp. (Scott *et al.*, 2008). Competitors also include conspecific beetles that arrive after a tree's defenses have been overcome. Many bark beetles reduce this form of exploitation by producing anti-aggregation pheromones during the later stages of host colonization, and some fungi, including yeasts, appear to contribute to production of these masking compounds (Brand *et al.*, 1976; Hunt and Borden, 1990).

The degree of association between bark beetles and microbes that contribute to host utilization varies extensively. Closely linked mutualists, such as some Basidiomycete fungi, are transported in specialized mycangia (Six and Klepzig, 2004). Other fungi reside on the exoskeleton. Some of the bacteria that degrade host compounds may be both conifer and beetle associates, such that the ability to degrade terpenes is a requirement for inhabiting phloem, and the attacking beetles become the indirect beneficiaries of that association when they enter (Adams *et al.*, 2013).

### 3.5 Resource Partitioning

Although conifer bark beetles compete for a common resource, phloem tissue, they have several mechanisms for partitioning this resource and thereby reducing direct competition. The first level of separation is geographic range, and several species with similar life histories and host ranges occupy distinct or at least partially distinct zones. Some examples include *D. ponderosae* and *Dendroctonus adjunctus* Blandford in the northern and southern ranges of *P. ponderosae*, and *Dendroctonus murrayanae* Hopkins and *D. valens* in the higher and lower elevations of *P. contorta*, respectively. A second level of resource partitioning occurs within a region, based on host range. This usually functions at the level of plant genus. Different species of bark beetles tend to be associated with a corresponding conifer genus, but can often colonize all the species within that genus within their geographic range (D. L. Wood, 1982). Some exceptions include *Dendroctonus jeffreyi* Hopkins that is closely associated with *Pinus jeffreyi* A. Murray, which in turn has unusual chemistry and is not attacked by most other scolytines. Also, *Pinus strobus* L. and *Pinus palustris* Mill. are not commonly attacked by *D. frontalis*, despite the high overlap with that insect's range. Although the most aggressive outbreak species are typically specialists on one genus, several of the moderately aggressive species, such as *Dendroctonus pseudotsugae* Hopkins, *Dryocoetes affaber* Mannerheim, and sometimes *I. pini*, utilize two genera, and the non-aggressive, often secondary, species such as *Orthotomicus caelatus* Eichhoff and *Dryocoetes autographus* (Ratzeburg) often colonize three or more genera.

Beyond the coarser levels of geographic region and host genus or species, various bark beetle species partition the phloem resource at several finer scales. First, different

species are associated with different parts of a tree's stem (Coulson, 1979; Grünwald, 1986; Schlyter and Anderbrant, 1993; Flamm *et al.*, 1993). An example is the guild associated with southern pine beetle, in which the solitary or semi-solitary *Dendroctonus terebrans* Olivier colonizes the base, *D. frontalis* mass attacks the lower portion of the stem, *Ips grandicollis* Eichhoff often colonizes the portion above that, and *Ips calligraphus* (Germar) and *Ips avulsus* Eichhoff colonize both the main stem and lateral branches of the crown (Paine *et al.*, 1981). There are parallels within most systems. The degree of partitioning is typically partial rather than absolute when multiple species colonize a tree, and it is typically opportunistic rather than obligate, in that when one species is missing the others will extend into the zone the absent species normally occupies. Another level of partitioning can arise from seasonality, whereby one species tends to fly earlier, for a different length of time, or have different voltinism, than other species occupying the same host within a region. Finally, different species partition the resource based on host physiological condition (Rankin and Borden, 1991; Flechtmann *et al.*, 1999; Saint-Germain *et al.*, 2009). Many species only colonize dead trees or dead parts of trees. Others can colonize live trees, but only highly stressed individuals. Still other species can colonize healthy trees, but only during outbreaks. As with tree morphology, these relationships tend to be relative rather than strict. For example, beetle species that colonize healthy trees during outbreaks commonly rely on dead trees during lengthy endemic periods. Perhaps the species that comes most closely to relying solely on live trees is *D. frontalis*, which cannot be reared through its entire life cycle in dead logs. In general, those species that only colonize dead or severely stressed trees tend to be the most fit at competition, both when tree-killing species are limited to severely stressed trees, or when secondary beetles follow tree-killing species into healthy trees they overcome (Raffa and Berryman, 1987; Lindgren and Raffa, 2013).

In some cases, there is no apparent higher-level structuring to resource partitioning, but instead there initially appears to be scramble competition. However, in these cases there is often a secondary structuring mediated by pheromones (Lanier and Wood, 1975). That is, the first beetle to locate a susceptible stand or tree within a stand produces a species-specific pheromone that greatly biases local subsequent population ratios. For example, *I. pini* and *I. grandicollis* appear to interact much in this manner in the Great Lakes region of North America.

## 4. COMMUNICATION

Scolytine bark beetles are generally regarded as being largely subsocial (Wilson, 1971; Kirkendall *et al.*, 1997; Costa, 2006). Many species breed in aggregations on their

host plants, and most species provide some care for their offspring (Jordal *et al.*, 2011). Even in some solitary species, larvae often exhibit aggregation behavior (Grégoire *et al.*, 1982). The ambrosia beetle *X. saxeseni* exhibits high levels of sociality, including gallery, fungus, and brood care by both the adult and larval offspring of a single foundress (Biedermann and Taborsky, 2011). Aggregation behavior and other social interactions require efficient means of communication, and scolytine beetles have evolved several means by which they influence the behavior of conspecifics, including physiological and anatomical adaptations for the production, emission, and reception of chemical signals (Dickens and Payne, 1977; Blomquist *et al.*, 2010). However, there is a high noise to signal ratio in the complex environments where these beetles generally dwell, so their communication systems need to be flexible in order to convey a correct message that varies with context.

Bark beetles attacking live hosts have evolved behavioral and physiological traits to contend with the dynamic defenses of their hosts. Once the primary physical defense of the bark is breached, a plant will flood the area with a blend of defensive compounds in a more or less viscous liquid, e.g., terpene-rich oleoresins in conifers and latex or sap in angiosperms. A major function of this liquid is to physically flush the wound and thereby remove invading organisms. An additional function is to repel attackers by toxins, and thus many of the constituent compounds in these defensive liquids are general or specific toxins, the potency of which may depend on dose (Raffa, 2014). In the Pinaceae, these compounds are also volatile, which may partially explain why bark beetles are particularly prominent in this family of plants (Franceschi *et al.*, 2005; Lindgren and Raffa, 2013). Volatile toxins constitute a very effective defense, but a drawback is that they broadcast a distress signal, which is subject to interception by additional enemies that can then orient to a plant that is injured or under attack (Dixon and Payne, 1980; Erbilgin and Raffa, 2001; Raffa, 2001).

### 4.1 Functions and Roles

In order to reproduce successfully, a bark beetle must locate the resource, quickly occupy it, attract a mate, and ward off both inter- and intraspecific competitors (Lindgren and Raffa, 2013). Throughout this sequence of events, both inter- and intraspecific communication play important roles, first as a means of locating the host, then to attract conspecifics, including a mate, and finally to prevent overcrowding (Nilssen, 1978; Byers, 1984, 1992b). The predominant modality of communication is through chemicals via olfaction and gustation (Raffa, 2014), although acoustic communication is also important.

The function of a specific semiochemical is context dependent, having different functions depending on the circumstance (Table 1.1). So-called pioneer beetles, the first to arrive at a resource, must use a variety of host cues (Borden *et al.*, 1986). Pioneer beetles attacking live hosts may first use visually directed landing that is random relative to host susceptibility, and make subsequent selection decisions on the bark (Hynum and Berryman, 1980). Beetles joining an attack in progress are aided by both host volatiles and semiochemicals emitted by conspecifics in the process of occupying the host. Once they have successfully occupied and acquired

a resource, bark beetles can benefit from preventing additional beetles from arriving. This is accomplished by increased or decreased emissions of specific compounds, by special anti-aggregation or spacing pheromones, or by changes to the bouquet of host volatiles emitted because of cumulative biological and physical processes (Flechtmann *et al.*, 1999). Furthermore, bark beetles may use different cues for long-range and short-range orientation to a host (Saint-Germain *et al.*, 2007). Saprophages searching for dying, injured or fallen trees are guided by volatile emissions from the host (kairomones), such as monoterpenes and/or

**TABLE 1.1** Functional Terminology of Semiochemicals (Nordlund, 1981) with Examples Relevant to Bark Beetles. Note that the Same Compound can be Assigned Different Functions Depending on the Context

Functional Term	Effect		Intra- or Interspecific	Description	Examples	Selected References
	Emitter	Receiver				
<b>Pheromone</b>	+	+	Intra	<i>Aggregation pheromones</i> , attracts both male and female conspecifics to a breeding resource. <i>Epileictic (spacing) pheromones</i> , produced by breeding pair to prevent crowding detrimental to their offspring. <i>Anti-aggregation pheromones</i> , a type of epideictic pheromone that interrupts aggregation (and hence crowding) on a resource.	trans-Verbenol Ipsdienol Frontalin exo-Brevicommin Verbenone MCH	Pitman <i>et al.</i> , 1969 Young <i>et al.</i> , 1973 Pitman and Vité, 1970 Rudinsky <i>et al.</i> , 1974 Shore <i>et al.</i> , 1992 Lindgren and Miller, 2002a Furniss <i>et al.</i> , 1974 D. L. Wood, 1982
<b>Allomone</b>	+	–	Inter	Semiochemical emitted by a bark beetle that prevents occupation by other species of an already occupied resource, thus preventing detrimental effects for the emitter.	Ipsdienol	Birch <i>et al.</i> , 1980 D. L. Wood, 1982
<b>Kairomone</b>	–	+	Inter	Host volatiles emitted by a live host tree that attracts bark beetles. Semiochemicals that attract potential natural enemies.	Monoterpenes Ipsdienol	Byers, 1992a Sun <i>et al.</i> , 2004 Dahlsten <i>et al.</i> , 2003 Hulcr <i>et al.</i> , 2005
<b>Synomone</b>	+	+	Inter	Semiochemical emitted by a bark beetle that prevents aggregation of a second bark beetle to an occupied resource, therefore reducing competition.	Ipsenol Verbenone	Borden <i>et al.</i> , 1992 Hulcr <i>et al.</i> , 2005
<b>Apneumone</b>	0	+	Inter	Volatiles emitted from a dead organism that attracts a predator or parasite even in the absence of their host insect.	Ethanol	Schroeder and Weslien, 1994

ethanol (Byers, 1992a; Miller and Rabaglia, 2009). In all cases, predators and competitors eavesdrop on these signals, using them to orient to the same resource.

Communal feeding by larvae occurs in a number of scolytine species, particularly in parasitic species like *D. micans* and *D. punctatus* (Grégoire, 1988; Furniss and Johnson, 1989) where solitary, mated females establish their brood gallery on a live tree, as well as in a few other *Dendroctonus* species attacking trees that tend to have high levels of oleoresin (Pajares and Lanier, 1990). Larval aggregation in *D. micans* is mediated by chemical communication (Grégoire *et al.*, 1982).

## 4.2 Chemicals

Beetles that attack live trees must be able to avoid, tolerate or detoxify tree defense chemicals, or they and/or their offspring will be killed by the plant (Lindgren and Raffa, 2013). Metabolism of host compounds by beetles, such as hydroxylation of terpenes, can substantially reduce toxicity, and some of the resulting alcohols and ketones may be exploited by the insect for communication (D. L. Wood, 1982; Raffa and Berryman, 1983; Sandstrom *et al.*, 2006). For example, trans-verbenol, a female-produced aggregation pheromone of *D. ponderosae*, is derived through simple hydroxylation of the host monoterpene  $\alpha$ -pinene (Blomquist *et al.*, 2010). However, some bark beetles synthesize isoprenoid and monoterpenoid pheromones *de novo* (Ivarsson *et al.*, 1993; Seybold *et al.*, 1995; Blomquist *et al.*, 2010) through the mevalonate pathway, with specialized enzymes converting intermediates to pheromone components of the required stereochemistry (Blomquist *et al.*, 2010). Thus, *de novo* synthesis might be a predominant mode of pheromone production, at least among the Ipini, and for some semiochemicals used by members of Hylesinini. Lineatin, a complex tricyclic acetal that is an important aggregation pheromone or attractant for many *Trypodendron* species (Borden *et al.*, 1979; Schurig *et al.*, 1982; Lindgren *et al.*, 2000), is also synthesized *de novo*, as are exo- and endo-brevicomin, non-isoprenoid semiochemicals occurring widely in *Dendroctonus* (Blomquist *et al.*, 2010). In *Ips* and *Dendroctonus*, the most likely site of *de novo* pheromone production is the anterior midgut (Blomquist *et al.*, 2010).

Many bark beetle semiochemicals occur in more than one species and often in several tribes (Table 1.2). This supports the hypothesis that chemical communication has evolved primarily by exploitation of compounds that are naturally derived through commonly occurring, evolutionarily preserved biosynthetic processes. Significant overlap in aggregation pheromone blend components among species is common, e.g., frontalin is a primary component of the aggregation pheromone in a number of species in the genus *Dendroctonus* (Renwick and Vité, 1969;

Pitman and Vité, 1970; Dyer, 1975; Browne *et al.*, 1979), and ipsdienol and/or ipsenol are ubiquitous in the clade Ipini (Vité *et al.*, 1972; Phillips *et al.*, 1989) and also occur widely in the Dryocoetini (Klimetzek *et al.*, 1989). Many of these semiochemicals have also been found in non-insect taxa. For example, the aggregation pheromone of *Gnathotrichus sulcatus* (LeConte), sulcatol (Byrne *et al.*, 1974), has been identified in volatile extracts from various fungi (Vanhaelen *et al.*, 1978), and plants (Hüsni Can Başer *et al.*, 2001), and frontalin, a common aggregation pheromone in the genus *Dendroctonus*, has been found in Asian and African elephants (Rasmussen and Greenwood, 2003; Goodwin *et al.*, 2006) and in the bark of angiosperms (Huber *et al.*, 1999). Sulcatol and frontalin are both produced through the mevalonic pathway with sulcatone as an intermediate product (Blomquist *et al.*, 2010).

The relative ubiquity of specific semiochemicals across many species, genera, and tribes (Table 1.2) suggests that reproductive isolation is achieved through multiple, not single, modalities. Host species fidelity, within-host niche separation, temporal and geographic isolation, as well as behavioral and physiological incompatibility reduces the likelihood of hybridization (Flamm *et al.*, 1987; Schlyter and Anderbrant, 1993; Kelley and Farrell, 1998; Pureswaran and Borden, 2003). In addition, receptor specificity for different enantiomers, enantiomeric ratios, and semiochemical blends prevents cross attraction (Pitman *et al.*, 1969; Birch *et al.*, 1980; Borden *et al.*, 1980; Schlyter *et al.*, 1992).

## 4.3 Acoustics

Volatile semiochemicals constitute an efficient means of communication, but many bark beetles also use acoustic signaling in intraspecific communication on the host (Rudinsky and Michael, 1973). Males and/or females of many species have specialized stridulatory organs (Barr, 1969), which appear to be significant for mate choice and male competition (Wilkinson *et al.*, 1967; Ryker and Rudinsky, 1976). The location and structure of these stridulatory organs vary widely among Scolytinae. The functions of acoustic communication, and how they integrate with chemical, visual, and tactile signals, are just becoming more fully understood.

## 4.4 Intraspecific Variation

Bark beetle semiochemical blends may be highly variable, both quantitatively and qualitatively (Schlyter and Birgersson, 1989). The context in which a pheromone is produced and emitted affects how the receiver responds to it. A number of studies have established geographic variation in response to host volatiles and/or pheromones (Lanier *et al.*, 1972; Borden *et al.*, 1982; Miller *et al.*, 1989, 1997). The response by *I. pini* to pheromones has



**TABLE 1.2** Examples of Relative Ubiquity of Semiochemicals of the Scolytinae. Data from PheroBase (El-Sayed, 2012)

Semiochemical	Common Name	Presence in Tribes	No. of Species	Function*
2-methyl-6-methylene-7-octen-4-ol	Ipsenol	Dryocoetini	1	P
		Ipini	19	A2, P18
		Pityophthorini	1	A1
2-methyl-6-methylene-2,7-octadien-4-ol	Ipsdienol	Hylesinini	11	A10, P1
		Ipini	28	A16, P20
		Pityohtorini	1	A1
		Xyloterini	1	A1
1, 5-dimethyl-6,8-dioxabicyclo[3.2.1]octane	Frontalin	Hylesinini	11	A10, P7
		Cryphalini	1	A1
		Ipini	1	A1
		Pityophthorini	4	A4
		Scolytini	1	A1
		Xyloterini	1	K1
exo-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane	exo-Brevicomini	Hylesinini	10	A3, K1, P7
		Dryocoetini	3	P3
endo-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane		Hylesinini	3	P3
		Dryocoetini	3	P3
3,3,7-trimethyl-2,9-dioxatricyclo-[3.3. 1.0 4,7]nonane	Lineatin	Hylesinini	7	A7
		Cryphalini	1	A1
		Dryocoetini	1	A1
		Ipini	1	A1
		Xyleborini	1	A1
		Xyloterini	6+	A5, P1
6-methyl-5-hepten-2-ol	Sulcatol, Retusol‡	Corthylini	3	A1, P2
6-methyl-5-hepten-2-one	Sulcatone	Hylesinini	1	P1
2-(1-hydroxy-1-methylethyl)-5-methyltetrahydrofuran	Pityol	Pityophthorini	10	A3, K1, P7
(E)-2-methyl-6-methylene-octa-2,7-dienol	E-Myrcenol	Ipini	2	P2
cis-3-hydroxy-2,2,6-trimethyltetrahydropyran	Vittatol	Hylesinini	1	P1
2-methyl-3-buten-1-ol		Hylesinini	3	A2, P1
		Corthylini	1	A1
		Ipini	9	A7, P4
		Xyloterini	1	A1
2-methyl-3-buten-1-ol		Hylesinini	1	P1
		Ipini	1	P1
2-ethyl-1,6-dioxaspiro[4.4]nonane	Chalcogran	Ipini	3	A1, P3

Continued

**TABLE 1.2** Examples of Relative Ubiquity of Semiochemicals of the Scolytinae. Data from PheroBase (El-Sayed, 2012)—cont'd

Semiochemical	Common Name	Presence in Tribes	No. of Species	Function*
7-methyl-1,6-dioxaspiro[4.5]decane	Conophthorin	Hylesinini	1	A1
		Ipini	4	A4
		Pityophthorini	4	P4
		Scolytini	5	A5
5-ethyl-2,4-dimethyl-6,8-dioxabicyclo[3.2.1]octane	$\alpha$ -multistriatin	Scolytini	3	A1, P3
trans-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol	trans-Verbenol	Hylesinini	11	A4, 1A1, K1, P10
		Ipini	12	P12
cis-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol	cis-Verbenol	Hylesinini	9	A3, A11, P5
		Corthylini	1	A1
		Ipini	24	A10, P15
		Xyloterini	1	A1
4, 6, 6-trimethylbicyclo[3.1. 1]-hept-3-en-2-one	Verbenone	Hylesinini	11	A3, P10
		Ipini	6	A2, P4
4-methylene-6,6-dimethylbicyclo[3.1.1]hept-2-ene	Verbenene	Hylesinini	1	P1
		Ipini	1	P1
3-methylcyclohex-2-en-1-ol	Seudenol	Hylesinini	4	A3, P2
		Polygraphini	1	A1
		Ipini	2	A2
1-methylcyclohex-2-en-1-ol	MCOL	Hylesinini	2	A1, P1
3-methylcyclohex-2-en-1-one	MCH	Hylesinini	4	A11, P3

\*Functions: A= Attractant, A1= Allomone, K= Kairomone, P= Pheromone  
<sup>†</sup>Including two species from Lindgren et al. (2000)  
<sup>‡</sup>Combined as Retusol is the S-(+)-enantiomer of Sulcatol

been found to vary seasonally (Teale and Lanier, 1991; Steed and Wagner, 2008). Geographic variation in both chemical species and enantiomer composition, as well as seasonal variation in response to pheromones, may be due to a number of factors, such as interspecific competition (Lanier et al., 1972) and predator selection pressure (Raffa and Klepzig, 1989; Aukema and Raffa, 2000).

## 5. TRITROPHIC INTERACTIONS

Bark beetle-attacked trees provide abundant, though temporary, resources for hundreds of species of associated organisms. When attacked trees die, they provide a

succession of spatio-temporal niches exploited by various guilds of natural enemies, competitors, and inquilines living off other components of these resources (see Section 2.2.3). The links between bark beetles and their associates vary from clear predator/prey or parasitoid/host relationships to more complex interactions that may vary according to circumstances (see Boone et al., 2008a).

### 5.1 Major Predators, Parasitoids, Pathogens and their Life Histories

Natural enemies are discussed in detail in Chapter 7. Flies, beetles, wasps, mites, nematodes, and vertebrates (mostly

birds) are either predators, parasitoids, or true parasites of Scolytinae, which are also affected by a variety of pathogens that include viruses, bacteria, entomopathogenic fungi, protozoa, apicomplexa, and microsporidia. Several general reviews are available (Dahlsten, 1982; Mills, 1983; Kenis *et al.*, 2004; Wegensteiner, 2004). More specific reviews concern particular natural enemy taxa such as nematodes (Rühm, 1956), mites (Lindquist, 1964), chalcidoid parasitoids (Hedqvist, 1963), braconid parasitoids (Hedqvist, 1998), or microsporidia (Weiser, 1961). Other reviews focus on particular bark beetle species, e.g., *D. frontalis* (Berisford, 1980), *D. simplex* (Langor, 1991), or *Tomicus piniperda* (L.) (Hérard and Mercadier, 1996). In this section, we emphasize how the life history traits of these natural enemies are interwoven with those of the bark beetles

### 5.1.1 General Relationships with Bark Beetles

Some natural enemies arrive at the same time as the bark beetles on newly attacked trees. This is the case for phoretic mites, and for those nematodes and microorganisms that are attached to the beetles, either externally or internally. Lombardero *et al.* (2003) reported that more than 50 mite species and 40 species of fungi and bacteria are transported on *D. frontalis*; Knee *et al.* (2013) collected 33 mite species belonging to seven families on 18 bark beetle species in pheromone traps in Canada. The roles of these mites are highly diverse, including activities as predatory on various bark beetle stages, predatory on other associates, fungivorous, and saprophagous. Often these roles overlap, and in many cases they are unknown. Some coleopteran, dipteran, and hymenopteran predators and parasitoids also arrive early, in response to bark beetle pheromones. Clerid (*Thanasimus* spp. and *Enoclerus* spp.) and trogositid beetles (*Temnochila* spp.) feed on bark beetles landing on a new host (Vité and Williamson, 1970; Schroeder, 1999a, b; Zhou *et al.*, 2001), oviposit in bark cracks (Gauss, 1954; Schroeder, 1999a), and their larvae enter the prey galleries and feed on any organism they encounter inside, including their conspecifics. Colydiid beetles (*Lasconotus* spp.) and ostomids (*Nemosoma* spp.) enter the galleries and oviposit therein (Hackwell, 1973). Histerid adults (e.g., *Platysoma*) enter the galleries where they prey on adults and eggs, and oviposit. Their larvae feed on bark beetle larvae and pupae (Aukema *et al.*, 2004b). Staphylinidae also land early on attacked trees (Kennedy and McCullough, 2002). Dolichopodid predatory flies (e.g., *Medetera aldrichii* Wheeler) arrive early on attacked trees and oviposit near the prey galleries' entrance and ventilation holes (Fitzgerald and Nagel, 1972); the young larvae then enter the galleries. The larvae of *Medetera bistriata* Parent appear to paralyze their prey larvae with venom injected through their tentorial rods (Aukema *et al.*, 2004b). Egg-larval endoparasitoid

Hymenoptera (e.g., Eulophidae: *Entedon* spp.) oviposit in the eggs of the hosts and their larvae develop in the host larvae. They arrive early enough on the trees to enter the galleries of their hosts and parasitize their eggs, with *Entedon ergias* (Ratzeburg) attacking *Scolytus scolytus* F. (Beaver, 1966a). Finely tuned timing is also important for endoparasitic wasps attacking adult bark beetles (e.g., the pteromalids *Tomicobia* spp. and *Mesopolobus* spp.; the braconids *Cosmophorus* spp. and *Cryptoxilos* spp.), which land on attacked trees at the same time as their hosts (Faccoli, 2000).

A large group of natural enemies, such as the hymenopteran ectoparasitoids of bark beetle larvae (Braconidae, Pteromalidae, some Ichneumonidae) land on attacked trees after bark beetle aggregation has ceased (Stephen and Dahlsten, 1976), when at least some host larvae have already reached some degree of maturity. They either enter the galleries to paralyze their hosts directly and oviposit on their bodies ("cryptoparasitoids," e.g., *Roptrocercus xylophagorum* (Ratzeburg) (Samson, 1984)) or locate hosts through the bark, drilling with their ovipositor to paralyze the host and oviposit (e.g., *Coeloides* spp.; Ryan and Rudinsky, 1962; Hougardy and Grégoire, 2003). Among the monotomid beetles, *Rhizophagus grandis* Gyll. colonizes prey broods at any stage from eggs to pre-emergent adults (Grégoire, 1988; Grégoire *et al.*, 1992) and *Rhizophagus depressus* F. feeds mainly on the eggs of *T. piniperda* (Hérard and Mercadier, 1996), suggesting it arrives early in the tree colonization process.

Vertebrate predators show responses that are more diffuse. In a 15-year study in British Columbia, population densities of six woodpecker species increased in response to *D. ponderosae* epidemics, even though individual fecundity was not affected (Edworthy *et al.*, 2011). Another study in South Dakota (Bonnot *et al.*, 2009) focused on the black-backed woodpecker (*Picoides arcticus* (Swainson)), and showed that within 250 m of nests, nest location was best explained by densities of current *D. ponderosae*-infested trees. For those bark beetles that overwinter at least partly in the forest litter, insectivore mammals and rodents have probably some impact but, to our knowledge, this has never been measured.

### 5.1.2 Monoterpene Toxicity

In conifers, freshly attacked trees retain at least partly their own chemical and physical defenses, particularly when they survive attacks by parasitic bark beetles. After tree death, however, much larger communities are able to settle with the bark beetles with little or no exposure to toxic monoterpenes. *Rhizophagus grandis*, a specific predator of the parasitic bark beetle *D. micans*, has developed relatively high tolerance to monoterpene toxicity, which allows it to follow its prey in living, still fully defended, host trees. Tolerance

to monoterpenes also provides an almost exclusive niche to this predator, as potential competitors, such as *Rhizophagus dispar* (Paykull), do not possess the same level of resistance (Everaerts *et al.*, 1988).

### 5.1.3 Limited Resources for Associates of Bark Beetles in a Confined Environment

Many of the bark beetle-associated organisms (e.g., insect larvae, mites, nematodes) cannot leave the trees on their own, and must therefore optimize use of available food. For example, predators can adjust oviposition to the available resources. *Rhizophagus grandis* regulates its egg production according to both the presence of conspecific females (Baisier and Grégoire, 1988) and the larval density of *D. micans* as perceived through oviposition stimuli present in the frass (Baisier *et al.*, 1988; Grégoire *et al.*, 1991). The density of *Thanasimus formicarius* L. larvae in bolts infested with *I. typographus* seemed to stabilize, by either egg-laying regulation or cannibalism, whether four or eight pairs of predators had been enclosed with the bolts (Weslien and Regnander, 1992).

Natural enemies may also develop various opportunistic strategies, or strategies for reducing intra- or interspecific competition to compensate for prey or host scarcity. They can attack a flexible range of host developmental stages, as does *Cephalonomia stephanoderis* Betrem parasitizing *H. hampei* (Lauzière *et al.*, 2000), or they can turn to alternative prey. The mite *Pyemotes parviscolyti* Cross and Moser is phoretic and predaceous on *Pityophthorus bisulcatus* Eichhoff, but preys on other scolytine larvae when their galleries cross those of *P. bisulcatus* (Moser *et al.*, 1971). Occasional fungivory (Hackwell, 1973; Hérard and Mercadier, 1996; Merlin *et al.*, 1986), facultative hyperparasitism, and intraguild predation are sometimes compensatory solutions to local host scarcity. For example, the primary parasitoid of *I. typographus*, *Dinotiscus eupterus* (Walk.), has been observed hyperparasitizing the other primary parasitoid *Dendrosoter middendorffii* Ratzeburg (Sachtleben, 1952); *T. formicarius* larvae were reported feeding on *Medetera* larvae (Nuorteva, 1959); xylophagous larvae of the longhorn *Monochamus* spp. prey on bark beetles (Dodds *et al.*, 2001; Schoeller *et al.*, 2012); and larvae of *Temnochila chlorodia* (Mannerheim) attack larvae of *Enoclerus lecontei* (Wolcott) (Boone *et al.*, 2008a).

Facultative cleptoparasitism may be a response to interspecific competition. Mills (1991) reported female *Cheiro-pachus quadrum* (F.) and *Eurytoma morio* Boheman (primary parasitoids of various bark beetles) stealing *Leperisinus varius* (F.) larvae from *Coeloides filiformis* Ratzeburg; Hougardy and Grégoire (2003) observed a similar behavior in *Rhopalicus tutela* (Walker) displacing *Coeloides bostrichorum* Giraud after the latter located

*I. typographus* larvae through the bark. Finally, when prey density is low relative to the predator population, contest competition in the form of cannibalism is regularly observed, for example among *Medetera* sp. larvae in galleries of *S. scolytus* (Beaver, 1966b), *R. grandis* larvae in brood systems of *D. micans* (Baisier *et al.*, 1984), larvae of *T. formicarius* in galleries of *I. typographus* (Hui and Bakke, 1997), and *T. dubius* in galleries of *I. pini* (Aukema and Raffa, 2002).

### 5.1.4 Shifting Prey: an Adaptation to Long Life Cycles or to Fluctuating Prey?

Many natural enemies have life cycles shorter than, or adjusted to, that of their prey or host. Some species, however, live longer than the bark beetles they exploit, a feature that could generate a shortage of resources. *Thanasimus formicarius* has a 2-year generation time (Schroeder, 1999b) and has a long flight period of more than 4 months, which begins at the same time as the flights of the first bark beetles in the season, i.e., *T. piniperda*, *T. lineatum*, and *Hylurgops palliatus* Gyll. (Gauss, 1954). Likewise, *T. dubius* can develop over 2 years (Reeve, 2000). Attacking many different prey may benefit predators that are partially asynchronous with prey. *Thanasimus formicarius* is recorded to attack at least 27 different prey species (Gauss, 1954; Mills, 1983; Tømmerås, 1988), with overlapping phenologies during a season. *Thanasimus dubius* is also described as a generalist (Costa and Reeve, 2011). One of its major prey, *D. frontalis*, has three to nine overlapping generations per year in the southern portion of its range (Wagner *et al.*, 1984), but its major prey in northern regions, *I. pini*, *I. grandicollis*, and *D. rufipennis*, are univoltine. Costa and Reeve (2011) also show that a predator could be conditioned by a previous exposure to respond preferentially to a particular prey.

### 5.1.5 Habitat Characteristics and Natural Enemies

At the tree level, height and orientation on the trees, as well as bark thickness, are important factors influencing the performances of larval parasitoids that oviposit through the bark (Dahlsten, 1982). Goyer and Finger (1980) found that all parasitoids of *D. frontalis* were negatively influenced by bark thickness, except for *Roptrocerus eccoptogastri* Ratzeburg, which enters the galleries. However, Gargiullo and Berisford (1981) found that *Roptrocerus xylophagorum* Ratzeburg was influenced by bark thickness. Understanding such relationships is confounded by underlying relationships of host beetle density with bark thickness. Studying the natural enemies of *Scolytus multistriatus* (Marsham), *S. scolytus*, and *Scolytus pygmaeus* (F.), Merlin (1984) found general trends very similar to those of Goyer and Finger's (1980), with bark thickness influencing all



parasitoids except the cryptoparasitoid *Entedon leucogramma* (Ratzeburg). Bark thickness is also a limiting factor for *T. formicarius*. When the outer bark is too thin for the last instar larvae to create a pupal niche, they exit the tree (Warzée *et al.*, 2006). The relatively thicker outer bark of pine may explain why *T. formicarius* often has higher reproductive success on pine than spruce.

At the landscape scale, natural enemy performances are linked to several factors, such as stand composition and management history, and insect dispersal. Schroeder (1999a) found that *R. depressus* populations were higher in stands with high *T. piniperda* populations due to stumps and slash left after a thinning operation, than in unthinned stands, but *T. formicarius* showed little difference, suggesting that these predators had not moved preferentially into stands with high bark beetle densities. Schroeder (2007) confirmed the low mobility of natural enemies (including *T. formicarius*, *Medetera* spp., and parasitoids) between stands with high (left unmanaged since the 1995 storm) and low (windthrows removed) *I. typographus* densities, finding higher impact of the natural enemies in the managed stands two summers after the storm. Similarly, Ryall and Fahrig (2005) showed that ratios of predators (*T. dubius*, *Enoclerus nigripes* Say, and *Platysoma* sp.) to prey (*I. pini*) were significantly lower in isolated stands of *P. resinosa* than in contiguous forests, suggesting that the predators are less likely to exit habitat patches. This was further confirmed by Costa *et al.* (2013), who found that although *T. dubius* had a dispersal capacity 12 times higher than *I. grandicollis* (median: 1.54 km), it was less likely to disperse across fragmented landscapes. Their estimated dispersal distances strongly paralleled those of Cronin *et al.* (2000), who observed a median dispersal of 1.25 km in *T. dubius*, with 5% dispersing further than 5 km, and lower dispersal by the prey *D. frontalis*, with 95% of the predators flying as far as 5.1 km, and 95% of the prey reaching a maximum of 2.3 km.

Forest composition can significantly influence the abundance of polyphagous predators. Warzée *et al.* (2006) found that ratios of *T. formicarius* to *I. typographus* were higher in mixed spruce-pine stands than in pure spruce stands, presumably because the predators were more successful in pupating in pine. Abundant prey in the vicinity may also arrest dispersal of natural enemies. One year after releases of *R. grandis* for biological control of *D. micans* in France and England, this predator was recovered up to 200 m from the release sites (Grégoire *et al.*, 1985; Fielding *et al.*, 1991), although field observations suggest dispersal capacities up to at least 4 km (Fielding *et al.*, 1991). An additional but poorly understood aspect linked to stand composition is the need for synovigenic adult parasitoids to feed in order to reconstitute their egg load. However, plants producing pollen and nectar are frequent, including in even-aged, monospecific forest stands, and aphids in the tree crowns

produce fair amounts of honeydew (Hougardy and Grégoire, 2000; VanLaerhoven and Stephen, 2008).

## 5.2 Relative Importance of Natural Enemies to Bark Beetle Ecology

### 5.2.1 Impact of Natural Enemies on Bark Beetles

The impacts of natural enemies on bark beetles have been measured through a variety of approaches, including laboratory assays, field sampling, and modeling. In the laboratory, direct observations (Aukema and Raffa, 2004b) and experiments (Barson, 1977; Senger and Roitberg, 1992; Schroeder, 1996; Reeve, 1997; Aukema and Raffa, 2002) typically focus on singular cases under controlled conditions, with both the advantages and disadvantages of omitting the more complex influences operating at the landscape level. Short-term field observations (Mills, 1985; Schroeder, 1996, 1999a; Erbilgin *et al.*, 2002; Wermelinger *et al.*, 2013) and experiments (Weslien and Regnander, 1992; Schroeder, 2007) provide further information on how different local conditions mediate the impact of natural enemies. However, a more complete picture may appear at a larger scale (Raffa *et al.*, 2008; Kausrud *et al.*, 2011a) and in this respect, recent modeling approaches shed a particularly interesting light on global relationships. In particular, they can suggest how different global bottom-up or top-down influences characterize different bark beetle systems, and delineate how and when natural enemies exert significant influences on the dynamics of these systems. Marini *et al.* (2013) analyzed demographic time series data of *I. typographus* and *T. formicarius* in Sweden from 1995 to 2011, and showed that the provision of breeding material by storms was the principal trigger of outbreaks, with intraspecific competition as a density-dependent negative feedback. There was no clear influence of *T. formicarius* on the bark beetles' demography. In contrast, Turchin *et al.* (1999) provided a time series analysis of fluctuations in *D. frontalis*, which suggested that a delayed density-dependent factor dominates beetle dynamics. With a long-term predator-exclusion experiment, they explored the hypothesis that *T. dubius* could act as such a delayed density-dependent factor, and detected a delayed impact (possibly due to the often longer life cycles of predators than bark beetles), suggesting a significant role of *T. dubius* in the population dynamics of *D. frontalis*. The different results between these studies are striking, and may highlight two systems with quite different drivers. That is, *I. typographus* is strongly driven by a bottom-up force, i.e., the availability of suitable hosts (windfelled trees) when at an endemic level. In contrast, it is less clear whether bottom-up forces other than lightning-struck trees exert significant influences on

*D. frontalis* (Hodges and Pickard, 1971; Coulson *et al.*, 1983). However, Friedenberg *et al.* (2008) and Martinson *et al.* (2013) have questioned Turchin *et al.*'s (1999) model. Another large-scale study is provided by Aukema *et al.* (2005b), who modeled populations of *T. dubius*, *Platysoma cylindrica* (Paykull), and *I. pini* in *P. resinosa* plantations during 2 years, and found evidence that predation exerts some density-dependent feedback.

### 5.2.2 Bark Beetle Behavior and Impact Mitigation of Natural Enemies

Several behavioral aspects of bark beetles may reduce the impact of natural enemies. Prolonged male residence in the galleries of *I. pini* can partly protect the eggs from predation (Reid and Roitberg, 1994). Increased *I. pini* densities can reduce the proportional impact of predation by *T. dubius* and *P. cylindrica*, suggesting that aggregation dilutes predation (Aukema and Raffa, 2004a). These findings indicate that predator dilution may be a viable benefit to aggregation. Additionally, *T. dubius* may attack disproportionately more responding males pioneer than responding males, and more males than females, suggesting that predators may stabilize bark beetle communication systems by selecting against cheating (only responding to pheromones rather than engaging in host searching) (Aukema and Raffa, 2004c).

### 5.2.3 Applications

Natural enemies have been used with limited or sometimes no success in a number of classical, augmentative or conservative biological control programs (reviewed in Kenis *et al.*, 2004). European natural enemies were introduced in North America against *S. multistriatus*, vector of Dutch elm disease, in New Zealand against *Hylastes ater* Payk., and in South Africa against *Orthotomicus erosus* (Wollaston). The only example of an entirely successful classical biological control program involves the mass production and release of *R. grandis* against *D. micans* in the Caucasus mountains of Georgia (Kobakhidze, 1965), France (Grégoire *et al.*, 1985), Great Britain (Fielding *et al.*, 1991), and Turkey (Alkan and Aksu, 1990).

## 5.3 Competitors

Many organisms compete with bark beetles for resources. Cerambycids such as *Monochamus* spp. also act as intra-guild predators (Dodds *et al.*, 2001; Schoeller *et al.*, 2012), and exploit bark beetle semiochemicals as kairomones (Allison *et al.*, 2001). Sometimes, interspecific competitors can exert multiple effects. For example, *Ips* spp. are attracted to trees attacked by *Dendroctonus* and can both compete for resources and benefit predators that consume *Dendroctonus* (Boone *et al.*, 2008a; Martinson *et al.*, 2013).

## 5.4 Tritrophic Signaling

Natural enemies that arrive early in the colonization process of a newly attacked tree, including many predators, egg-larval parasitoids, and adult parasitoids, exploit bark beetle aggregation pheromones. This can exert a strong pressure on the bark beetles, which may sometimes modify their own communication system to obtain partial escape. For example, *I. pini* prefers stereospecific ratios of ipsdienol that differ from stereospecific preferences of local predators attracted to ipsdienol (Raffa and Dahlsten, 1995). Furthermore, *I. pini* produces and responds to lanierone in the Great Lakes region, to which the predators are non-responsive, even though predators in California, where *I. pini* does not produce lanierone, respond to this compound (Raffa *et al.*, 2007). These patterns suggest highly dynamic interactions.

Predators attacking multiple bark beetle prey have antennal receptor cells keyed to many pheromones produced by different prey. For example, *T. formicarius* has sensillae keyed to 22 bark beetle pheromone and conifer volatiles: (+) and (–)-ipsdienol; (*S*) and (*R*)-*cis-verbenol*; 2-methyl-3-buten-2-ol; (–) and (+)-ipsenol; (–) and (+)-verbenone; (–) and (+)-*trans-verbenol*; amitinol; exo- and endobrevicomin; frontalin; (+)-lineatin; phenylethanol; (–) and (+)- $\alpha$ -pinene; myrcene; camphor; and pino-camphone (Tømmerås, 1985). Although receptive to many signals, some predators can learn to respond to one particular signal after exposure (Costa and Reeve, 2011). Early arrivers are also sensitive to signals indicating that mass attack has reached its end. *Thanasimus undatulus* (Say), *Enoclerus spehegeus* F., *E. lecontei*, and *Lasconotus* sp. are repelled by verbenone (Lindgren and Miller, 2002b). Late arrivers (larval ectoparasitoids) respond to odors produced by microbial symbionts (Sullivan and Berisford, 2004; Boone *et al.*, 2008b).

## 6. POPULATION DYNAMICS

### 6.1 Diversity in Bark Beetle Population Dynamics

Like most insects, bark beetles have high reproductive potentials that provide the capability to undergo rapid, exponential population increase (Coulson, 1979; Økland and Bjørnstad, 2006; Marini *et al.*, 2013). However, also like most insects, their realized rates of reproductive increase are usually far below that potential. Despite the enormous diversity in bark beetle population dynamics among species, three overlapping groups can be distinguished (Raffa *et al.*, 1993; Lindgren and Raffa, 2013). In the first group, most species exhibit relatively stable population dynamics, with local densities rising and falling with resource availability, temperature, and other features

of environmental quality. The range of these numerical fluctuations can be orders of magnitude, but the populations do not become self-driving. A second smaller group can exert some positive feedback, such that once populations have risen in response to a resource pulse or more favorable environment, positive density dependence can contribute to numerical increases while conditions remain highly favorable. Finally, a third and much smaller group undergoes dramatic shifts in its relationships with host plants after a critical stand-level population threshold has been surpassed. Once this threshold, below which population growth is constrained by host defenses, is surpassed, populations become “eruptive” and enter a new reactive norm. Populations only return to endemic dynamics after resource depletions, intolerable temperatures, or some combination thereof, reduces beetle numbers below the critical density threshold.

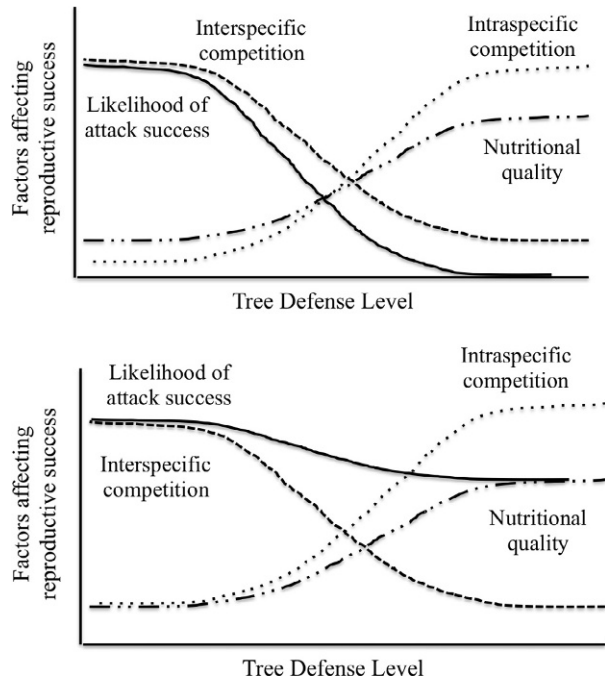
The first group is highly diverse, and includes species that feed on dead plants, dead parts of live plants, reproductive organs, roots, and lateral branches, among others. They also include insects that colonize the main stem, both gregarious species that are always associated with severely stressed plants, and solitary/parasitic species that colonize live but usually less vigorous hosts, most commonly on the basal stem. Solitary species can play important roles in maintaining populations of semi-eruptive and eruptive species (groups 2 and 3) during their endemic phases (Aukema *et al.*, 2010; Smith *et al.*, 2011). The second group includes gregarious species that colonize the main stems of both gymnosperms and angiosperms, and can kill stressed trees. These insects are broadly distributed worldwide, but overall, they show less diversity than the first group. This group includes a number of species that can be economically important pests when habitats are managed in fashions that stress or concentrate host trees. The third group, eruptive species, exerts the strongest effects on ecosystem processes. These insects can be considered true “ecosystem engineers” in that they exert major effects on forest structure, biodiversity, successional pathways, nutrient cycling, and geophysical processes (Romme *et al.*, 1986; Kurz *et al.*, 2008; Griffin *et al.*, 2011; Kaiser *et al.*, 2012). The widespread tree mortality over large spatial scales caused by eruptive bark beetles also exerts major feedbacks to other bark beetle species (i.e., groups 1 and 2), by providing large resource pulses that facilitate their reproduction (Flamm *et al.*, 1989). Eruptive bark beetles show the lowest diversity, being gregarious colonizers of the main stems of conifers, restricted to the northern hemisphere, and mostly concentrated within North America. An important consideration in evaluating their population dynamics is that both positive and negative sources of feedback are always present, and thus net feedbacks are crucial.

## 6.2 Factors Affecting Survival, Development, and Reproduction: Sources of Positive and Negative Feedback behind Bimodality

Because the majority of research on bark beetles has been conducted during the eruptive phase of species capable of undergoing spatially synchronized outbreaks, it is easy to visualize a forest as one big salad bar. In fact, nothing could be further from the truth. Individual trees within a species show enormous variation in their resistance levels, even within a single age category and local population (Safranyik *et al.*, 1975; Ruel *et al.*, 1998; Rosner and Hanrup, 2004). Heterogeneity in tree defensive capacity arises from genetic, environmental, gene by environment, phenological, and ontogenetic contributions (Safranyik *et al.*, 1975; Sturgeon and Mitton, 1986; Raffa *et al.*, 2005; Roberds and Strom, 2006; Ott *et al.*, 2011). The importance of this diversity becomes obscured during outbreaks (Boone *et al.*, 2011), so models that are heavily informed by those relatively rare events must pool host type into a relatively homogeneous construct. Thus, generalized treatments of host availability and suitability have limited utility for understanding the more persistent condition of endemic population dynamics, or for understanding mechanisms by which populations transition from endemic to eruptive dynamics (Raffa *et al.*, 2008; Björklund *et al.*, 2009; Bleiker *et al.*, 2014).

For purposes of analysis, it is common to compartmentalize the different factors affecting an insect’s replacement rate. But in the case of bark beetles, some of the most important drivers, such as food availability, plant defense, intraspecific competition, and interspecific competition, are so tightly interwoven that it is more useful to emphasize their interactions and linkages (Lindgren and Raffa, 2013; Marini *et al.*, 2013). A conceptual illustration of how these factors interact at the tree level is presented in Figure 1.4.

Beetle populations are most commonly at low, endemic population densities (Figure 1.4 top). Trees that are highly defended pose a high risk of attack failure to host-seeking beetles (solid line), due to the multifaceted defense mechanisms described above (Section 3.2). Trees with low defense level pose little risk, so the likelihood of successful colonization is high. In trees that have already died from some other cause, host defenses become nearly zero. Such undefended trees, however, are also available to a wide diversity of other phloeophagous and xylophagous species, including other Scolytinae (Figure 1.1B), woodborers, and microorganisms (Stephen and Dahlsten, 1976; Safranyik *et al.*, 1996; Wermelinger *et al.*, 2002; Saint-Germain *et al.*, 2007). Saprophytic Scolytinae are typically better competitors than tree-killing species (Poland and Borden, 1998a, b; Smith *et al.*, 2011, Lindgren and Raffa, 2013)



**FIGURE 1.4** Opposing effects of tree defense level on multiple selective pressures on bark beetles. Top: Low population densities, which typify most generations of a species within an area. Trees with high defense pose a high risk of attack failure. However, trees with compromised defenses are available to other subcortical species that are superior competitors to tree-killing species. Stressed trees often have thinner phloem, and so are nutritionally inferior. When beetles colonize well-defended trees, they not only incur greater risk, but they experience greater intraspecific competition because the requisite mass attacks create crowding within a limited resource. Bottom: High population densities. The same general shapes of these relationships remain. However, the likelihood that attacks on well-defended trees will succeed is high. The within-tree intraspecific competition curve rises somewhat, but only partially because the beetles' antiaggregation system limits the number of attackers. The optimal choice for a beetle depends on stand-level population density.

and some of the cerambycid woodborers are both competitors and predators of bark beetles (Dodds *et al.*, 2001), while many of the saprogenic microorganisms are antagonistic to bark beetles (Paine *et al.*, 1997; Six and Klepzig, 2004; Cardoza *et al.*, 2006a). Consequently, interspecific competition tends to be very high in poorly defended trees, and comparatively lower when beetles attack well-defended trees (Figure 1.4 top, dashed line). Interspecific competition never totally disappears, because saprophages also exploit previously healthy hosts that are overcome by tree-killing bark beetles. In addition to harboring more interspecific competitors, highly stressed trees also tend to be less nutritionally suitable for the beetles' developing brood (Figure 1.4 top, dashed and dotted line). Trees experiencing drought, defoliation, age-related senescence, etc., often produce thinner phloem, i.e., the larval food base (Boone *et al.*, 2011; Powell *et al.*, 2012; Creeden *et al.*, 2014). When beetles attempt to attack well-defended trees,

on the other hand, they not only incur higher risk, but their mechanism of overcoming resistance, mass attack, incurs higher intraspecific competition (Figure 1.4 top, dotted line). A tree's phloem is a finite resource, so each additional attacker depletes the resource available for brood development (Coulson, 1979; Raffa and Berryman, 1983; Anderbrandt, 1990; Robins and Reid, 1997). Beetles can partially limit this cost by producing anti-aggregation pheromones and ceasing production of aggregation pheromones, once tree defenses are exhausted (D.L. Wood, 1982; Borden, 1985; Keeling *et al.*, 2013).

When beetle populations are high (Figure 1.4 bottom), the same qualitative relationships hold, but the coefficients change. Most importantly, the likelihood of successful attack becomes much higher, and much less sensitive to host defense. Because enough beetles are available to elicit (Erbilgin *et al.*, 2006) and conduct (Raffa and Berryman, 1983) mass attacks, colonization attempts are likely to succeed regardless of a tree's defensive capacity. The intraspecific competition curve can rise somewhat with increases in tree defense level, but this is again constrained by the beetle's sophisticated anti-aggregation pheromone system that nearly limits the number of attackers to that required to overcome defense. At some point, a tree can be so well defended that the number of beetles required to kill it is larger than the number of brood beetles that can develop in it. Beetles usually avoid such trees, but during the peak of intensive outbreaks and when these start to collapse, this relationship becomes apparent when beetles kill younger, smaller trees (Lindgren and Björklund, unpubl.).

The trade-offs between colonizing weak versus vigorous trees also have substantial higher-scale inputs. Trees undergoing acute stress due to lightning, root disease, and windthrow, for example, are relatively sparse in number across a landscape, yet are generally concentrated at highly localized spatial and temporal scales (Atkins, 1966; Coulson *et al.*, 1983; Smith *et al.*, 2011), which concentrates competition (Marini *et al.*, 2013). Further, tree-killing bark beetles can only utilize a host for one generation. Therefore, exploitable food resources are removed at each successful colonization event, which potentially leaves only healthier trees as an available, but not usually accessible, resource.

The importance of tree defense in bark beetle reproduction is somewhat of an enigma, in that its signature is mostly indirect. Although trees sometimes kill bark beetles directly (Figure 1.3), life tables usually show low within-tree mortality attributable to host resistance (Berryman, 1973; Coulson, 1979; Amman, 1984). This is somewhat expected, of course, because herbivores evolve sophisticated sensory apparatus and neuromuscular sequences for avoiding plants that would kill them and their brood. Additionally, pheromone-mediated mass attacks are not



analogous to human-wave assaults in which the first lines are slaughtered: such behavior would be highly maladaptive at the level of individual selection, and would require levels of kin selection that are highly unlikely to operate in the field (Raffa, 2001). When high populations succeed, the early arrivers experience only relatively minor costs (Raffa and Berryman, 1983; Pureswaran *et al.*, 2006; Latty and Reid, 2010). A better estimate of tree defense should incorporate the proportion of adults that emerge from brood trees, but do not encounter trees that elicit their entry behavior, before dying of other causes. When beetles are caged onto randomly selected trees within their host species and age range, for example, a sizable proportion will remain in their cage and die rather than enter (Raffa, 1988). Indeed, losses during host searching are high among bark beetles (Berryman, 1973, 1979; Pope *et al.*, 1980; Safranyik *et al.*, 2010). For example, Pope *et al.* (1980) estimated that even in the artificially homogeneous habitat structure of pine plantations, and even during outbreak conditions, 57% of emerging *D. frontalis* adults did not subsequently enter a new host, i.e., could not be accounted for by either new galleries or failed attacks. The proximate cause of death during host searching is not tree defense *per se* though, but rather is mostly energy depletion and predation (Rudinsky, 1962; Berryman, 1979; Gilbert and Grégoire, 2003).

Temperature is a major constraint and releaser on beetle populations (Régnière and Bentz, 2007; Trần *et al.*, 2007; Jönsson *et al.*, 2007; Powell and Bentz, 2009). Low winter temperatures can cause high mortality, and temperature is a major driver of beetle development rates (Bentz *et al.*, 1991). In multivoltine species such as *D. frontalis*, temperature strongly influences the number of generations per year, and in species such as *D. rufipennis* and *D. ponderosae*, temperature regimes determine whether local populations are univoltine or semivoltine. Temperature-driven survival and development rates translate directly into how closely bark beetles can approach their reproductive potential. Interactions between bark beetles and temperature are highly complex, and include multiple developmental and survival thresholds, often facultative diapause, and variable patterns of cold hardening (Bentz and Mullins, 1999; Lombardero *et al.*, 2000b; Hansen *et al.*, 2001; Hansen and Bentz, 2003; Košťál *et al.*, 2011; Inward *et al.*, 2012.). These multiple reaction norms overlay regionally genotypic variation (Mock *et al.*, 2007; Bentz *et al.*, 2011). The result of this complexity is that beetle responses are highly plastic, and a high diversity of outcomes can arise from variable inputs. A key feature of this plasticity is the linkage between bark beetle development and the need to overcome tree defense. Some bark beetle species exhibit relatively synchronous emergence despite a broad range of initial and developmental conditions, a relationship termed “adaptive

seasonality” (Bentz *et al.*, 1991; Logan and Bentz, 1999). In addition to affecting beetle development rates, temperature can influence the relative abundance of symbionts such as mites and fungi (Hofstetter *et al.*, 2007; Addison *et al.*, 2013), which feed back to beetle reproduction.

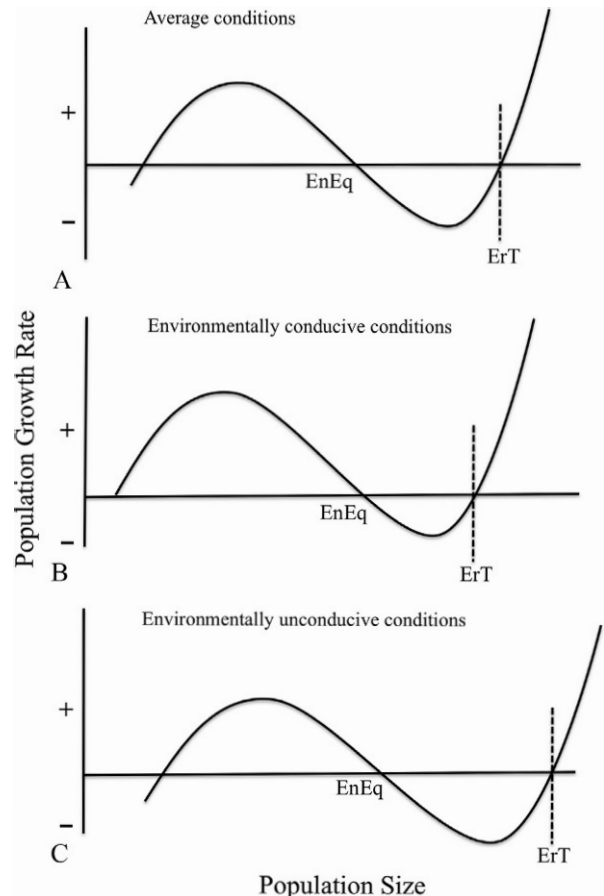
The importance of predators as mortality and potential regulating agents appears to vary among bark beetles. Predacious beetles and flies that feed on multiple life stages can be particularly important sources of mortality. These predators often exploit bark beetle aggregation pheromones, again creating linkages between bark beetles’ need to overcome tree defenses and other sources of mortality. Perhaps the strongest case for predatory regulating tree-killing bark beetle populations has been made for *D. frontalis* (Turchin *et al.*, 1999), but subsequent analyses have not supported such a role (Friedenberg *et al.*, 2008; Martinson *et al.*, 2013). Birds, especially woodpeckers, are likewise important and ubiquitous mortality agents (Fayt *et al.*, 2005). However, their roles are particularly difficult to quantify. A diversity of parasitoid species attack all stages of bark beetles (Linit and Stephen, 1983; Mills, 1991), and show sophisticated host location mechanisms, including responding to pheromones emitted by adults (Kudon and Berisford, 1981; Raffa *et al.*, 2007) and microbes associated with larvae (Sullivan and Berisford, 2004; Boone *et al.*, 2008b). Parasitoids can occasionally exert high mortality, but in general subcortical herbivores experience less parasitism than other insect guilds (Connor and Taverner, 1997). This presumably arises from the protection provided by the bark, and the energy and risk required to access hosts. Parasitism rates may be even further lowered in highly managed systems where nectar sources are reduced (Stephen and Browne, 2000). There is some evidence of density-dependent parasitism of some bark beetle species (Amman, 1984). However, to our knowledge, there are no bark beetles for which parasitoids have proven to be major population regulating agents.

Antagonistic microorganisms, including both pathogens and competitors, can likewise impose significant constraints on bark beetle reproduction. Gregarines and microsporidia can be among the most common pathogens, and can cause either mortality or sublethal effects such as reduced fecundity or dispersal ability. However, there is little evidence that they naturally exert enough mortality to be important regulating agents (Wegensteiner *et al.*, 2010). The fungus *O. minus* can be highly detrimental to several species of bark beetles, and substantially reduce brood survival. The mechanisms are not entirely understood, but appear to include competition for saccharides (Wang *et al.*, 2013) and reduction of immunocompetence (Shi *et al.*, 2012). Opportunistic fungi such as *Trichoderma* and *Aspergillus* can also reduce brood production (Fox *et al.*, 1992; Cardoza *et al.*, 2006b).

### 6.3 Transitions from Endemic to Eruptive Dynamics

The major consequence of the above positive and negative feedbacks is that some bark beetle species exhibit bimodal population dynamics. That is, their within-tree and within-stand replacement rates show strong relationships to stand-level population density, but these relationships vary both quantitatively and qualitatively between different population phases (Figure 1.5). Within the endemic phase, replacement rates can be represented using standard density-dependence curves: populations increase until they reach a stable, or endemic, equilibrium (EnEq), and when they exceed that density, negative feedbacks, such as depletion of the stressed-tree pool, prevail and the population declines. Over time, populations fluctuate with increasing or decreasing habitat favorability. In general, the beetles' within-tree reproductive gains are offset by within-tree and within-stand losses. In bimodal systems, however, if a population somehow reaches a critical eruptive threshold density (ErT), it then enters a new regime in which positive density-dependent feedback again prevails, and above that density, the population increases exponentially. Bimodal dynamics have been observed in diverse types of organisms, including locusts, Lepidoptera, sawflies, and fish among others, but the underlying bottom-up, lateral, and top-down mechanisms vary (Ricker, 1954; Southwood and Comins, 1976; Campbell and Sloan, 1977; Simpson *et al.*, 1999; Larsson *et al.*, 2000; Despland and Simpson, 2000, 2005; Dussutour *et al.*, 2008).

For a bimodal model to be both credible and useful to our understanding, it must satisfy two conditions. First, there must be some mechanism by which a population can increase from EnEq to ErT. The paradox is that, by definition, a population higher than EnEq will decline. Second, there must be a validated mechanism that drives continuous positive feedback above ErT. In the case of bark beetles, there is a substantial body of research informing both questions: (1) Bark beetle populations can rise quickly due to increased winter or summer temperatures, which improve overwintering survival and reduce development time (Bentz *et al.*, 1991; Safranyik and Carroll, 2006; Aukema *et al.*, 2008; Powell and Bentz, 2009; Preisler *et al.*, 2012; Régnière *et al.*, 2012), area-wide stresses that increase resource availability and within-stand replacement rates (Hicke *et al.*, 2006; Breshears *et al.*, 2009; McDowell *et al.*, 2011; Creeden *et al.*, 2014; Hart *et al.*, 2014), immigration that directly increases populations (Jackson *et al.*, 2008; Aukema *et al.*, 2008; Samarasekera *et al.*, 2012; Simard *et al.*, 2012). (2) Bark beetles have plastic host selection behaviors, which coupled with their ability to coordinate mass attacks, functionally expand their food supply in response to increasing beetle population density (Rudinsky, 1962; Berryman, 1981; Wallin and



**FIGURE 1.5** Conceptual model illustrating onset of self-perpetuating landscape-scale outbreaks based on underlying feedback structure.

A high intrinsic rate of increase, coupled with negative density-dependence feedback, generates a classic parabolic relationship between population growth rate and population size. Past the endemic equilibrium (EnEq), any population increase results in population decline. However, the cooperative host procurement behavior of bark beetles generates a second zone of net positive feedback. If a population rises to the eruptive threshold (ErT), the beetle's relationship with its host changes, and defense is no longer a significant constraint. Under most conditions, populations do not bridge this gap. However, increased temperatures that reduce mortality and shorten development time, immigration, or a sudden widespread pulse of stressed trees such as during drought can raise the level to ErT. Once populations breach this threshold, a return of external drivers to their initial condition may not halt an outbreak. (A) Average stand conditions; (B) conditions favorable to bark beetles, such as high temperature or homogeneous mature stands narrow this gap, making transitions more likely; (C) suboptimal environmental conditions, such as cold temperature or stand heterogeneity, make transitions unlikely. For most bark beetle species, the gap from EnEq to ErT is essentially infinite, because they show relatively little density-dependent plasticity in host selection behavior. Redrawn from Raffa and Berryman (1986).

Raffa, 2004; Kausrud *et al.*, 2011a). The selection pressures on choices made by individual beetles change between low- and high-density conditions. Moreover, the initial conditions required to increase the population from EnEq to ErT are not necessarily required to maintain the population

above ErT once that threshold has been breached (Raffa *et al.*, 2008; Creeden *et al.*, 2014)

Despite the potential of several single drivers to raise populations from EnEq to ErT, a combination of factors is more commonly required (Raffa *et al.*, in press). There are also many cases where outbreaks did not develop even when one or more of the above drivers were pronounced. The conditions most conducive to the development of outbreaks are a combination of: (1) amenable forest structure, specifically large, contiguous, relatively homogeneous, mature stands species; (2) high temperatures, which both benefit beetles directly and add to evapotranspiration stresses on trees; (3) region-wide stresses that reduce host defenses and cause a large number of trees to become abruptly and simultaneously accessible; and (4) reduced numbers of natural enemies, and an abundance of beneficial symbionts. An important feature of these constraints and drivers is how they interact. For example, a severe stress on trees can both make hosts available to an “eruptive” species, and also render them available to “secondary beetles” that can outcompete (conditions 3 and 4) the tree killers. Likewise, the rate at which populations increase in response to a temperature elevation (condition 2) or an environmental stress (condition 3) will be steeper in a more homogeneously than heterogeneously structured forest, and with larger than smaller trees. Similarly, the combination of symbiotic fungi (condition 4) varies with temperature (condition 2), and the local abundance of natural enemies (condition 4) varies with forest structure (condition 1). Overall, a rather uncommon set of conditions is required to facilitate the development of an outbreak at any particular time and place. However, at any one time, outbreaks are occurring somewhere in areas with suitable forest structure, composition, and weather.

The combination of these four conditions can be conceptualized as an “eruptive window” (Raffa *et al.*, in press), in which each coordinate expands or contracts, such that the area determines the distance from EnEq to ErT in Figure 1.5. The relative importance of these four coordinates in determining that area varies from system to system. The strength of the various underlying constraints that typically constrain bark beetle populations, relative to their population growth potential, can be also seen in the responses of historically non-eruptive species when anthropogenic activities relax or remove their actions. Some of the most dramatic examples have occurred when beetle–fungal complexes were introduced into areas in which native trees had not coevolved, and thus the important natural constraint of host resistance was lacking. These include instances of transport from Eurasia to North America and vice versa. Other examples include habitat manipulations that homogenize species and age composition, thus facilitating host finding, or that fragment patches in ways that reduce tracking by predators. More globally, elevated temperatures caused by climate change have resulted in outbreaks.

Several empirical examples demonstrate the importance of interactions among key drivers. Outbreaks by *D. rufipennis* in coastal Alaska can arise from warm temperatures that convert typically semivoltine to univoltine populations (Werner and Holsten, 1985; Berg *et al.*, 2006). However, in central Alaska, univoltine populations are the norm, yet populations rarely undergo outbreaks. This is probably due in part to drier conditions in central Alaska that yield drier phloem, which favors competitors (Werner *et al.*, 2006). Likewise, windstorms in Europe can release outbreaks by *I. typographus* (Marini *et al.*, 2013), but large windstorms in the midwestern US do not typically release outbreaks by *D. rufipennis*, probably because of the high tree species diversity and associated high predator and competitor abundances there (Gandhi *et al.*, 2009; Raffa *et al.*, in press). Furthermore, the effects of stress on tree defense can be complex, with severe water deficit reducing resistance, but moderate water stress resulting in increased constitutive but decreased induced levels (Lewinsohn *et al.*, 1993; Lombardero *et al.*, 2000a).

Comparisons among systems, locations, and seasons can be further developed within the conceptual model shown in Figure 1.5. When conditions for beetle reproduction are conducive (Figure 1.5A), the distance between the population size thresholds, EnEq and ErT, decreases (Figure 1.5B), and when they are less conducive this distance increases (Figure 1.5C). For example, at latitudes or elevations where temperatures are low, in forests that are sufficiently diverse, or in stands where the trees are too young to support high population densities, this gap becomes insurmountable. Similarly, many bark beetle species do not exhibit a high degree of plasticity in host selection behavior relative to defense physiology, so the distance between EnEq and ErT is essentially infinite. Some examples in which high initial populations increase in response to severe environmental stress but are not followed by sustained positive feedback include *Ips confusus* (LeConte) and *I. pini* following drought (Raffa *et al.*, 2008; Aukema *et al.*, 2010), and *I. grandicollis* following defoliation (Wallin and Raffa, 2001).

The support for bimodality of bark beetle populations arises from five complementary sources. The first is observation. Records by a number of early forest entomologists depict outbreak populations as being not only numerically but also dynamically different from endemic populations (Keen, 1938; Beal, 1939; Evenden *et al.*, 1943; Schwerdfeger, 1955; Zwölfer, 1957; Thalenhorst, 1958; Rudinsky, 1962; Atkins, 1966). Perhaps the most explicit statements of a link between individual- and population-level behavior are those of Keen (1938): “Endemic populations select weaker, less vigorous trees for attack, but no such selection is apparent during epidemic conditions,” and Beal (1939): “When the Black Hills beetle is not numerous it breeds in weakened trees or those injured by lightning or in some other way... During outbreaks

this insects attacks vigorous healthy trees...and shows a slight preference for the more vigorous, rapidly growing trees.” A second line of support comes from theoretical, first-principles arguments (Berryman, 1979, 1981), which adapted similar relationships from other outbreak species (Southwood and Comins, 1976; Campbell and Sloan, 1977), extinction principles (Allee, 1949), and sustainable resource models (Ricker, 1954). Third, simulation models founded on the underlying assumptions of threshold-based bimodality have generated behaviors consistent with field observations (Økland and Bjørnstad, 2006; Kausrud *et al.*, 2011b). Fourth, analyses of stand-level (Mawby *et al.*, 1989; MacQuarrie and Cooke, 2011; Martinson *et al.*, 2013), and within-tree (Berryman, 1974; Robins and Reid, 1997; Raffa, 2001) population replacement curves have demonstrated zones dominated by negative and positive density dependence, in agreement with historical data. Fifth, manipulative experiments testing the underlying mechanisms of positive feedback, the efficacy and individual benefit of cooperative attack, and the adaptive plasticity of host selection behavior have validated these processes (Raffa and Berryman, 1983; Lewis and Lindgren, 2002; Wallin and Raffa, 2004).

Two other features of the dynamic relationships illustrated in Figure 1.5 occur at the extremes. At very low population sizes, the within-tree Allee effect (Raffa and Berryman, 1983) can extend to stand-level extinction (Friedenberg *et al.*, 2007). At the other extreme, populations can collapse due to resource depletion, cold temperatures, or both (not shown).

Threshold-based relationships pose special challenges to research on bark beetles. First, the intervals between EnEq and ErT are transient, highly unstable states, so populations rapidly jump to either condition, and thus are difficult to measure. One might conceptualize them similarly as we envision short-lived free radicals in chemical reactions. Second, the key transitions occur at very low stand-level densities, which are below detection by aerial tree-mortality surveys (Boone *et al.*, 2011). Unfortunately, the available methods for studying such low-density populations are limited, costly, statistically challenging, and professionally risky. Third, key mechanisms that restrict populations at low densities may be unimportant at high densities. In systems characterized by thresholds at multiple levels of scale, there is often no correlation between key drivers and emergent patterns (Raffa *et al.*, 2008), which impedes *post-hoc* analyses.

## 7. ROLES IN ECOLOGICAL PROCESSES AND SOCIOECONOMIC IMPACTS

### 7.1 Ecological Processes

Progar *et al.* (2009) and Müller *et al.* (2008) describe bark beetle activity as vital at many scales. Bark beetles

influence forest regeneration by killing mature trees, thus creating gaps in the forest, which are beneficial to many species of wildlife. They also promote variability in tree sizes and ages, which increases forest and stand resiliency (Harvey *et al.*, 2013). In some cases, bark beetle outbreaks were found to increase forest fire risk (Bigler *et al.*, 2005), while in others they appear to lower fire risk (DeRose and Long, 2009) or have no measurable effect. Each of these processes is scale dependent.

The *D. ponderosae* outbreak in western North America provides a useful illustration of how profoundly bark beetles can affect forest ecosystem services. Costanza *et al.* (1997) list 17 ecosystem services provided by forests that could be affected by bark beetle outbreaks: gas regulation, climate regulation, disturbance regulation, water regulation, water supply, erosion control and sediment retention, soil formation, nutrient cycling, waste treatment, pollination, biological control, refugia, food production, raw materials, genetic resources, recreation and cultural services. Embrey *et al.* (2012) present a comprehensive review of ecosystem services that have been affected in the US and Canada by the *D. ponderosae* outbreak. Among these, the regulating and supporting services have been damaged, lowering the capacity of affected forests to regulate air and water quality and water flows, with increased water yields in the spring and shortage in the summer, because of a change in the capacity to receive snowmelt. Increased water runoff alters nutrient cycling and increases erosion, and water quality is threatened. The forest has also turned from a carbon sink to a source, at least prior to understory regeneration. Kurz *et al.* (2008) estimate that “the cumulative impact of the beetle outbreak in the affected region during 2000–2020 will be 270 megatonnes (Mt) carbon (or 36 g carbon m<sup>-2</sup> yr<sup>-1</sup> on average over 374,000 km<sup>2</sup> of forest).” In addition, the provisioning and cultural services, the commodities and immaterial services obtained from the forest are also jeopardized by insect damage. Products such as timber, firewood and pulp, and additional services such as cultural, aesthetic, and touristic values are being diminished. In the area of Davos, Switzerland, Bebi *et al.* (2012) examined the potential impact of natural disturbances such as fire or insect pests, and identified five ecosystem services that could be severely impacted: avalanche protection, recreation, CO<sub>2</sub> sequestration and storage, habitats of an endangered grouse (*Tetrao urogallus* L.), and timber production.

### 7.2 Socioeconomic Impacts

Socioeconomic impacts beyond lost timber values are difficult to calculate and require further attention. We provide below a brief summary of analyses addressing this topic. Costanza *et al.* (1997) estimated the value of annual ecosystem services offered by different biomes, including the temperate/boreal forests (Table 1.3). The global yearly



**TABLE 1.3** Ecosystem Services Provided by the Temperate/Boreal Forests (Data from Costanza *et al.*, 1997)

Ecosystem Services	Cost 1994 (US\$ ha <sup>-1</sup> yr <sup>-1</sup> )
Climate regulation	88
Water regulation	0
Soil formation	10
Waste treatment	87
Biological control	4
Food production	50
Raw materials	25
Recreation	36
Cultural	2
<b>Total value (ha<sup>-1</sup> yr<sup>-1</sup>)</b>	<b>302</b>

value of these services provided by temperate/boreal forests amounts to US\$63.6 billion. These figures were calculated based on the “willingness-to-pay” for each service. Krieger (2001) proposed an analysis of ecosystem services provided by the forests in each of the US regions. He proposed a summary description of the various local indicators used to calculate values, when possible and relevant, for watershed services (water quantity; water quality; soil stabilization; air quality; climate regulation and carbon sequestration; biological diversity); recreation (economic impact; wilderness recreation; hunting and fishing; non-timber products); and cultural values (aesthetic and passive use; endangered species; cultural heritage).

The economic impact of timber loss in British Columbia directly resulted in the loss of 27,000 jobs (Abbott *et al.*, 2008). Price *et al.* (2010) applied hedonic analysis to the assessment of changes in property value after the mountain pine beetle epidemics. They found that property values declined by \$648, \$43, and \$17, respectively, for every tree killed by mountain pine beetle infestations within a 0.1, 0.5, and 1.0 km buffer. Embrey *et al.* (2012) discussed the health impacts of the North American Rocky Mountain pine beetle outbreak. They included multiple factors, such as the direct and indirect effects of forest fire (although the extent to which bark beetle outbreaks predispose forests to fire is a matter of contention), quality losses in water supplies (also with possible long-range impact), consequences of property losses, and unemployment. Rittmaster *et al.* (2006) constructed an empirical air dispersion model to estimate the concentration of fine smoke particulate matter produced by a fire in Chisholm, Alberta, and used benefit transfer methods to estimate health impacts. The economic impacts

were high, second only to timber losses. Similarly, water quality is likely to be affected by insect damage, as deforestation-generated runoffs can translate into increased water turbidity, contamination with heavy metals, etc. Recent explosions in two sawmills in north-central British Columbia, which caused the death of four sawmill workers and severe injuries to many more, as well as the prolonged loss of work for other employees due to the destruction of the mills, was blamed in part on extremely dry sawdust generated from processing beetle-killed timber (Franck, 2012).

The management challenge to addressing bark beetles is essentially a matter of favoring the natural processes that promote their ecological services, while judiciously minimizing the socioeconomic costs they exert. For those species that can be locally damaging, either acutely or chronically, but do not undergo self-perpetuating outbreaks driven by positive feedback, desired results can often be attained by minimizing predisposing factors or reducing populations after environmental stresses raised them. For those species capable of landscape-scale outbreaks, management should emphasize keeping populations from surpassing the eruptive threshold. In all cases, however, it is essential to have clear and consistent management objectives. This poses a paradox, however: judicious human interactions with complex, large-scale, persistent systems such as forest biomes require consistency and integration over large scales of time and space, yet our sociopolitical institutions do the opposite (Chapter 15).

### 7.3 Invasive Species

The importance of effective plant defense can be readily seen during the initial stages of interaction between exotic organisms and novel hosts, i.e., new interactions where no co-evolutionary selection has been acting on the respective genomes. In such situations, large numbers of host trees may be killed by insects not known to cause mortality in their native range (Yan *et al.*, 2005; Poland and McCullough, 2006). For example, 5 years after *D. valens* was first detected in China, the beetle had spread over half a million hectares, killing 10 million *Pinus tabuliformis* Carrière (Yan *et al.*, 2005). Earlier, even more dramatic examples include *S. multistriatus* in North America. In some cases, introduced bark beetles may establish new associations with native phytopathogens, or introduced phytopathogens may establish new associations with native bark beetles. Similarly, high levels of mortality may result when native organisms encounter naïve hosts because of range expansion (Cudmore *et al.*, 2010). Extremely high populations of *D. ponderosae* in British Columbia have resulted in almost 100% mortality of lodgepole pine of susceptible host size class in many stands. In these examples, the population of the attacking insect increases rapidly, with dire consequences for the host plant populations and hence to local economies.

## 8 CONCLUSIONS

1. Bark beetles show a high diversity in their life histories. However, they also show some generalities arising from their reproduction within plant parts. These generalities include sophisticated host location systems, morphological adaptations facilitating tunneling, advanced communication systems, and close associations with microbial symbionts.
2. Life history strategies can be monogamous or polygamous with regard to mating, and solitary or gregarious with regard to intraspecific interactions. The gender responsible for host plant selection relates to mating strategy. The levels of parental care range from gallery maintenance in many tribes to eusociality in some ambrosia beetles.
3. Interactions with host plants vary markedly in terms of host species range, plant part, and physiological condition. Bark beetles are associated with a broad taxonomic range of plants, especially woody, perennial species. The tissues colonized by bark beetles are relatively poor in nutritional content for species that develop in roots, branches, and stems, and higher for species that develop in reproductive parts. The highest overall diversity of bark beetles is in tropical biomes.
4. Bark beetle species vary in the physiological condition of trees they colonize. Most species colonize dead plants or dead parts of plants. Some colonize trees that have been stressed by biotic or abiotic agents. A very few can colonize healthy trees. The last group exerts the strongest influences on ecosystem dynamics, and likewise poses the most serious challenges to natural resource management.
5. Bark beetles engage in sophisticated chemical signaling. Their pheromones serve to attract mates, and additional functions vary with their host–plant relationships. Some species use aggregation pheromones for cooperative resource procurement, by jointly overcoming tree defenses. Living trees pose formidable defenses that are multimodal, integrated, inducible, and capable of resisting attacks by individual or small numbers of beetles. Scolytine pheromones also incorporate plant chemicals, as precursors and/or synergists, into multicomponent signals.
6. A broad array of microbial symbionts, particularly fungi and bacteria, are associated with bark beetles. There is enormous diversity in their functional roles, including casual associations, antagonists, mycangial fungi transported in specialized structures, and ambrosia fungi that are actively gardened by the beetles. The fidelity of association ranges from incidental to obligatory, and in some cases there may be functional redundancy or substitutability. The benefits to beetles include assistance in procuring nutrients from phloem, a direct nutritional substrate, and assistance in overcoming tree defenses through detoxification of phytoalexins, among others. There are pronounced interactions among these symbionts, with outcomes mediated by host–plant chemistry, other phoretic organisms such as mites and nematodes, and temperature.
7. A wide diversity of predators, competitors, and parasites exploit bark beetles. Many of these exploit chemical signals associated with the beetles. Insect predators include several families of beetles and flies, and these, along with parasitoids of adult and egg stages, are often attracted to scolytine aggregation pheromones. Parasitoids of later stages are often attracted to volatiles emanating from the beetles' symbionts and deteriorating host plants. Despite the high diversity of predators and parasites affecting bark beetles, their habitat poses substantial physical protection that exerts substantial costs and challenges to organisms that exploit them. Thus, the effects of these natural enemies on bark beetle population dynamics are often limited.
8. Populations of most bark beetles in their native habitat tend to rise and fall with resource availability and weather. Because most species occupy a resource that is highly ephemeral in space and time, and can be utilized for only a limited duration, population increases incur substantial negative feedback. A few species, however, undergo intermittent landscape-scale population eruptions interspaced between much more extensive endemic periods. Populations of these species experience both the negative feedbacks of resource depletion, and also the positive feedbacks of increased resource availability driven by larger population size. The underlying mechanisms are driven by the cooperative behavior of mass attack and flexible, density-dependent host selection strategies. Critical thresholds, that operate at multiple levels of scale, and cross-scale interactions, govern these dynamics. Factors such as elevated temperature, drought, widespread environmental disturbance or immigration are needed for populations to surpass an eruptive threshold, and often multiple factors are required.
9. Bark beetles play important roles in ecosystem processing. These include nutrient cycling, decomposition, enhancing both animal and vegetative biodiversity, stand thinning, gap formation, and stand replacement depending on species. The eruptive species also have substantial influences on soil, hydrology, albedo, carbon sequestration, and other disturbance regimes. The landscape-transforming species are primarily associated with conifer biomes in northern temperate regions. These species exert substantial socioeconomic impacts.

10. Human activities have greatly magnified the reproductive success, and hence socioeconomic impacts of some bark beetles. These activities include transport of beetles and their symbionts to new regions, in which local trees have not evolved effective defenses; manipulation of the landscape in manners that reduce the heterogeneity of forest habitats or inhibit the success or dispersal of natural enemies; and climatic changes, specifically elevated temperatures that reduce overwintering mortality, accelerate beetle development and add to evapotranspiration stress on trees, and severe drought, which compromises tree defenses. Climate changes are resulting in both increased frequency and magnitude of outbreaks within historical ranges, and range expansions into new areas where trees lack coevolutionary adaptation.

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