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Bark Beetles

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Bark beetles are small, dark, cylindrical beetles, usually less than 7 mm long. As their name implies, they are usually associated with woody plants. Despite their small size and modest appearance, they have an intriguing assemblage of feeding and

breeding habits, some of which result in significant economic losses to forest and agricultural industries. This article reviews the taxonomy, life cycle, host–plant interactions, and ecosystem consequences of bark beetles, concluding with management options.

Taxonomy

Bark beetles have commonly been considered a family, Scolytidae, but recent taxonomy places them as a subfamily, Scolytinae, within the weevil family Curculionidae. Major characteristics that are shared with weevils include elbowed, clubbed antennae, larvae that feed within plant tissues, and the loss of the development of legs in larvae (**Figure 1**). The Scolytinae and closely related Platypodinae differ from typical weevils in their oviposition behavior: adults bore deeply into plant tissues to oviposit, while typical weevils use their elongated rostrum to create egg niches from the surface of the plant. Many of the Scolytinae do not actually breed in bark, as discussed below, but the common name ‘bark beetle’ is applied to this whole taxonomic group.

Bark beetles comprise approximately 6000 species, found worldwide. Their origin was in the Cretaceous, with an early association with the ancient conifer *Araucaria* distributed across Gondwana. Subsequent diversification into tribes and subtribes has occurred in North America, South America, Eurasia, and Africa. About 30% of extant genera are temperate in distribution.

Life Cycle

Upon arrival at a host plant, adults quickly begin to burrow into the plant to breed. Several species are known to histolyze their wing muscles upon arriving at breeding habitat. The sex that initiates a breeding site, the pioneer sex, differs among species. In many species, the beetle initially constructs a nuptial chamber where mating will occur (**Figure 2**). Many species emit pheromones at this stage that attract the opposite sex but also others of the same sex. When both sexes are attracted, the pheromones are called aggregation pheromones, and they result in a rapid colonization of the surrounding plant tissues. Such aggregation is a notable feature of bark beetles. Many pheromones are derived from precursors in the plant tissues, especially defensive compounds such as monoterpenes. However, the same pheromones can sometimes be synthesized *de novo*, or be produced by associated microbes. The link between plant defenses and pheromones means that pheromones can indicate the state of the tree to other beetles, which is especially important for those beetle species that



Figure 1 Douglas-fir beetle, *Dendroctonus pseudotsugae* (Hopkins): (A) adult; (B) Larvae. Courtesy of MM Furniss.

breed in live trees that they must kill. Aggregation pheromones diminish once an individual is established and mated. In some species, antiaggregation



Figure 2 Exposed egg galleries of pine engravers, *Ips pini* (Say), within the phloem of lodgepole pine, *Pinus contorta* var. *latifolia* Engelm. Typical of a polygynous species, several egg galleries radiate from a central nuptial chamber. Some larval galleries are visible extending perpendicularly from egg galleries. Courtesy of ML Reid.

pheromones are subsequently produced by one or both sexes.

Bark beetles have a fascinating diversity of breeding systems, including monogamy, polygyny, inbreeding polygyny (often associated with haplodiploidy), and parthenogenesis. Monogamy and polygyny are clearest when males initiate breeding sites, with a species-typical number of females sharing the same nuptial chamber. Males contribute by removing debris produced by tunneling females and guarding the entrance against predators. Males may remain for some or all of the oviposition and larval development periods. When females initiate the breeding site, there is generally only a single female per nuptial chamber (monogyny), but males generally depart early in oviposition and may mate again elsewhere. In these outbred systems, mating generally occurs after dispersal at the new breeding site. In inbreeding polygyny, mating occurs between brothers and sisters at the natal site. Here the sex ratio is female-biased, usually achieved with haplodiploidy, and males are dwarfed and flightless. These species commonly breed in xylem or seeds rather than phloem. Another variant of breeding system in bark beetles is pseudogamy, in which triploid females mate but only produce daughter clones.

Females tunnel through the tissue, and create orderly, characteristic egg galleries that generally extend linearly from the initial entry point, either parallel or perpendicular to the grain of the wood (Figure 2). In many genera, eggs are laid in individual niches along the sides of the egg galleries. Phloem-feeding larvae tunnel perpendicular to the egg galleries, while fungal-feeding larvae feed communally in chambers. Larvae progress through three to four instars before pupating, all within the host tissue.

Generation times depend largely on temperature, though also on feeding substrate and body size. For example, within North America, the southern pine

beetle, *Dendroctonus frontalis*, a 3-mm beetle that breeds in the southeastern USA, may have eight generations a year. In contrast, the spruce beetle *D. rufipennis*, a 7-mm-long beetle breeding in northwestern Canada and Alaska, may take 2 or 4 years to complete a generation. Because the quality of the breeding substrate generally declines substantially over the course of offspring development, in part due to larval feeding, each generation typically disperses to a new breeding site. Parental adults may reemerge within a breeding season, after regenerating their wing muscles, and disperse to a new breeding site. The extent to which parent beetles successfully overwinter after breeding is unclear.

Host Plants

Evolutionarily, bark beetles appear to have originated in conifers, and many of the most conspicuous and economically important species breed in conifers. However, most bark beetle species (approximately 80%) breed in angiosperms.

As their name suggests, many bark beetles breed within the inner bark (phloem) of tree boles or branches. While these species are often the most important economically, phloem-feeding is characteristic of fewer than half of all bark beetle species. More commonly, bark beetles develop within tree xylem where they feed upon symbiotic fungi (xylomycetophagy). Such species are termed ambrosia beetles. Phloem-feeding species are characteristic of temperate environments (over 80% of temperate species), while ambrosia beetle species are numerically dominant in the humid tropics. Less common feeding and breeding substrates include the roots or stems of herbaceous plants, the pith of small stems, and seeds.

For species that breed within bark, host tree species are usually within a single genus. Ambrosia beetles often have a broader host range, likely because xylem is not as chemically distinctive as phloem, and because the beetles feed primarily on fungi rather than the tree itself.

Colonizing Host Plants

Bark beetles find their host trees primarily by chemical cues. These cues may come from trees themselves (tree kairomones), and may include both host volatiles to which beetles are attracted (primary attraction) and nonhost volatiles that deter beetles. The scale at which these cues operate is unclear. The proportion of host and nonhost volatiles may influence the distribution of bark beetles across the landscape (i.e., among stands). The problem of detecting an individual host tree that is suitable is

more difficult, requiring finer chemical and spatial resolution. Conifers of different genera share many volatiles, and odor plumes from individual trees may be readily mixed depending in part on stand density and wind. The visual acuity of bark beetles is relatively poor. As a consequence, the range of detection of an unoccupied, suitable tree may be at the scale of centimeters. While one species of bark beetle has been shown to recognize tree suitability in flight, it appears that beetles of other species must actually land on a tree, and even consume part of it, to determine its suitability. Such a search process may be very time- and energy-consuming, and many species of bark beetles also respond positively to volatiles produced by breeding conspecifics (pheromones). This is true for species that colonize either dead or living host trees.

Bark beetles have several strategies for coping with plant defenses against herbivory and disease. The most common strategy is to colonize trees that are poorly defended, often because the tree is dying or severed from its roots. Such beetles are termed secondary species, since they are not the primary cause of tree death (e.g., *Ips* spp. in North America). Population sizes of secondary species correspond to the availability of poorly defended trees, sometimes increasing to significant numbers following extensive drought or large windfall events. At high numbers, these species may attack healthy trees, but even here there is evidence that trees that are attacked have been growing more slowly than average.

Of greater economic significance are those bark beetle species, termed primary species, that regularly attack healthy trees. The best known of these feed on phloem in conifers. Two attributes are key to the success of primary feeders against a defended tree: mass attack and symbiotic fungi. Mass attack is the arrival of large numbers of beetles at a tree over a few days. The synchrony of attack is important because trees not only have constitutive defenses, present before any attack, but also induced defenses where additional monoterpenes and oleoresin are synthesized around the site of an attack to kill or deter a pioneer attacker. To overwhelm the tree's capacity for defense, high attack densities are required. Thus the optimal attack density (maximizing an individual's reproductive success) may range from 20 to over 240 attacks per square meter, depending on beetle species and presumably on the vigor of the host tree. In contrast, the optimal density for beetles breeding in undefended hosts may be one individual in an entire tree.

Symbiotic fungi may be important to successful colonization of live trees, especially conifers, but their role is not entirely clear. Their evolutionary

significance is indicated by special invaginations on the integument of adult beetles, called mycangia, in which particular species of fungi are carried. Among phloem-feeding beetle species, mycangia are most commonly found in species that kill trees. Interestingly, these mycangia occur at different places on different beetle species, including near the mandibles and in the thoracic pleural area. (Not surprisingly, many ambrosia beetles that feed on fungi also have mycangia.) In the temperate phloem-feeding bark beetles, the symbiotic fungi are usually ascomycetes within the genus *Ophiostoma*. Many, but not all, of these fungi stain the xylem blue, which diminishes the value of wood esthetically, though not structurally.

Mycangial fungi in tree-killing beetles species have been held responsible for early tree death that allows the beetles to breed, but this view has been disputed. The fungi penetrate and plug the vascular tissue, and their toxins may also adversely affect water relations and resin flow. However, mycangial fungi are found to be weakly pathogenic, and may spread into the vascular tissue after beetles are already established and breeding. Moreover, trees have been killed by primary bark beetles in the absence of these fungi. Thus it appears that the fungi may contribute to tree death, but high-density beetle attacks are also required. Additional benefits of fungi may be improved food quality, limitation of less beneficial fungi, and chemical communication. These latter benefits would also apply to secondary bark beetle species, but these species generally do not have mycangia.

Factors Limiting Population Growth

Although many bark beetles aggregate at breeding sites, individual reproductive success declines exponentially with breeding density in the absence of initial tree defenses. Part of this reduction can be attributed to changes in the oviposition behavior of females in response to density, such as by reducing egg density or the length of egg galleries. However, there is also competition where resources per larva are reduced by consumption of phloem or faster deterioration of heavily mined phloem. Cannibalism has also been reported. Offspring that do survive are usually smaller and have less fat when density is higher.

Mortality of bark beetles within their natal tree is often remarkably high, with fewer than 5% of eggs resulting in adult offspring (Table 1). As just mentioned, part of this mortality may be attributed to competition, but this is often difficult to identify directly. Host quality may significantly affect the survival of offspring from egg through to emergence.

Natural enemies are also an important source of mortality within the natal tree. Woodpeckers are an

obvious predator of bark beetles, but usually have a minor impact on bark beetle survival (Table 1). Insect predators and parasites can cause substantial mortality, based on studies using exclusion cages (Table 1). Parasitism, a distinguishable source of mortality, varies widely in intensity (Table 1). Predation by insects generally leaves a poorer record. Some species of clerid beetles (Cleridae) are bark beetle specialists that detect bark beetle pheromones, arriving in large numbers, along with bark beetle colonizing trees. Adult clerids consume adult bark beetles on the surface of the bark while their larvae consume larval bark beetles. Consumption by adults reduces the number of beetles successfully colonizing by as much as 50% under realistic experimental conditions. Clerid larvae consumed about 10% of *Ips pini* larvae in one experiment. Clerids may determine the dynamics as well as the size of beetle populations (Figure 3). For example, clerids have longer development times than their bark beetle hosts, potentially resulting in a lag effect that can result in cyclic population dynamics (see **Entomology: Population Dynamics of Forest Insects**). They may also disperse differently than their hosts, causing patchy spatial distributions of bark beetles.

Dispersal between natal trees and breeding sites is also a significant source of bark beetle mortality. As mentioned, the breeding habitat of many bark beetles is no longer suitable after one generation, requiring dispersal every generation. Suitable hosts are typically rare, particularly for those bark beetles species relying on trees lacking defenses but with undeteriorated tissues, such as windfalls. While dispersal mortality cannot be observed directly, estimates from equilibrium population models and changes in sex ratio between emerging and breeding beetles suggest that more than half of beetles die during dispersal (Table 1). This is despite the ability of many species to fly 40 km or more.

Abiotic factors can also severely affect the success of small ectotherms such as bark beetles. Of these, temperature is fundamentally important. At higher latitudes and altitudes, temperatures may drop to lethal values over winter despite the cold-hardiness of bark beetles in these environments. For example, protracted temperatures of $c. -40^{\circ}\text{C}$ at unseasonable times of the year are an important contributor to the collapse of mountain pine beetle (*D. ponderosae*) populations (Figure 3). Cold-hardened larvae experienced 80% mortality at -34°C , compared to 27% mortality at -12°C . Temperature also influences reproductive rates in many ways. Dispersal in many temperate species is limited to temperatures above 16°C and below 40°C . Oviposition and larval development are also temperature-dependent processes. The

Table 1 Estimates of mortality in natural populations of bark beetles

Source of mortality	Bark beetle species	Mortality (%)	Reference
Total mortality in natal tree	<i>Dendroctonus ponderosae</i>	96.3–99.5	Amman GD (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. <i>Environmental Entomology</i> 13: 184–191.
	<i>Dendroctonus ponderosae</i>	98.6–99.4	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. <i>Researches on Population Ecology</i> 23: 116–144.
	<i>Phloeosinus neotropicus</i>	88	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle <i>Phloeosinus neotropicus</i> in Jamaica. <i>Oikos</i> 37: 363–368.
	<i>Scolytus scolytus</i>	96	Beaver RA (1966) The development and expression of population tables for the bark beetle <i>Scolytus scolytus</i> (F.). <i>Journal of Animal Ecology</i> 35: 27–41.
Woodpeckers	<i>Dendroctonus ponderosae</i>	2–15	Amman GD (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. <i>Environmental Entomology</i> 13: 184–191.
	<i>Dendroctonus ponderosae</i>	2–5	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. <i>Researches on Population Ecology</i> 23: 116–144.
	<i>Dendroctonus frontalis</i>	4.5	Moore GE (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. <i>Environmental Entomology</i> 1: 58–65.
	<i>Scolytus scolytus</i>	1	Beaver RA (1966) The development and expression of population tables for the bark beetle <i>Scolytus scolytus</i> (F.). <i>Journal of Animal Ecology</i> 35: 27–41.
Insect natural enemies	<i>Ips calligraphus</i>	74–96	Miller MC (1984) Mortality contribution of insect natural enemies to successive generations of <i>Ips calligraphus</i> (Germar) (Coleoptera, Scolytidae) in loblolly pine. <i>Zeitschrift für angewandte Entomologie</i> 98: 495–500. Miller MC (1986) Survival of within-tree <i>Ips calligraphus</i> (Col.: Scolytidae): effect of insect associates. <i>Entomophaga</i> 31: 39–48.
	<i>Ips typographus</i>	83	Weslien J (1992) The arthropod complex associated with <i>Ips typographus</i> (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. <i>Entomologica Fennica</i> 3: 205–213.
	<i>Ips</i> spp.	31	Riley MA and Goyer RA (1986) Impact of beneficial insects on <i>Ips</i> spp (Coleoptera Scolytidae) bark beetles in felled loblolly and slash pines in Louisiana. <i>Environmental Entomology</i> 15: 1220–1224.
	<i>Dendroctonus frontalis</i>	24–28	Linit MJ and Stephen FM (1983) Parasite and predator component of within-tree southern pine beetle, <i>Dendroctonus frontalis</i> (Coleoptera: Scolytidae) mortality. <i>Canadian Entomologist</i> 115: 679–688.
Parasitism	<i>Dendroctonus ponderosae</i>	1–24	Reid RW (1963) Biology of the mountain pine beetle, <i>Dendroctonus monticolae</i> Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. <i>Canadian Entomologist</i> 95: 225–238.
	<i>Dendroctonus ponderosae</i>	3–6	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. <i>Research into Population Ecology</i> 23: 116–144.
	<i>Dendroctonus frontalis</i>	4	Moore GE (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. <i>Environmental Entomology</i> 1: 58–65.
	<i>Phloeosinus neotropicus</i>	10	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle <i>Phloeosinus neotropicus</i> in Jamaica. <i>Oikos</i> 37: 363–368.
	<i>Scolytus scolytus</i>	12	Beaver RA (1966) The development and expression of population tables for the bark beetle <i>Scolytus scolytus</i> (F.). <i>Journal of Animal Ecology</i> 35: 27–41.
	<i>Scolytus ventralis</i>	3–8	Stark RW and Borden JH (1965) Observations on mortality factors of the fir engraver beetle, <i>Scolytus ventralis</i> (Coleoptera: Scolytidae). <i>Journal of Economic Entomology</i> 58: 1162–1163.
	<i>Scolytus ventralis</i>	2	Ashraf M and Berryman AA (1969) Biology of <i>Scolytus ventralis</i> (Coleoptera: Scolytidae) attacking <i>Abies grandis</i> (Pinaceae) in northern Idaho. <i>Melanderia</i> 2: 1–22.
	<i>Ips paraconfusus</i>	0.2–70	Ball JC and Dahlsten DL (1973) Hymenopterous parasites of <i>Ips paraconfusus</i> (Coleoptera: Scolytidae) larvae and their contribution to mortality. I. Influence of host tree and tree diameter on parasitization. <i>Canadian Entomology</i> 105: 1453–1464.

continued

Table 1 Continued

Source of mortality	Bark beetle species	Mortality (%)	Reference
Dispersal	<i>Dendroctonus ponderosae</i>	10–85	Klein WH, Parker DL, and Jenson CE (1978) Attack, emergence and stand depletion of the mountain pine beetle, in a lodgepole pine stand during an outbreak. <i>Environmental Entomology</i> 7: 732–737.
	<i>Ips paraconfusus</i>	61	Cameron EA and Borden JH (1967) Emergence patterns of <i>Ips confusus</i> (Coleoptera: Scolytidae) from ponderosa pine. <i>Canadian Entomology</i> 99: 236–244.
	<i>Phloeosinus neotropicus</i>	73	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle <i>Phloeosinus neotropicus</i> in Jamaica. <i>Oikos</i> 37: 363–368.
	<i>Scolytus ventralis</i>	60	Berryman AA (1979) Dynamics of bark beetle populations: analysis of dispersal and redistribution. <i>Bulletin de la Société Entomologique Suisse</i> 52: 227–234.



Figure 3 Lodgepole pine forest in Alberta, Canada, recently affected by mountain pine beetle, *Dendroctonus ponderosae* Hopkins. Trees with red needles were killed the previous season, while the tree with yellow-green needles indicates a current year's attack. Courtesy of ML Reid.

size and fat content of adults are negatively related to temperature during development, presumably influencing future dispersal and reproductive success. Temperature also determines the rate of phloem desiccation and perhaps fungal growth, indirectly influencing bark beetles through food quality.

Ecosystem Processes

The contributions of bark beetles to community and ecosystem processes, such as succession, fire, and decomposition, have not been well quantified. Bark beetle species that kill large numbers of mature trees are likely to have the largest effects on many of these processes.

Fire

While a high density of dead trees, caused by bark beetles, would seem to increase the risk of forest fire, this relationship has not been well established

empirically. One study in Yellowstone National Park (Wyoming, USA) observed that severe pre-fire bark beetle damage was correlated with increased risk of crown fire, but the reverse was true when damage was moderate. Risk of fire will likely change with time after a beetle outbreak, because of changes in tree moisture, abundance of fine fuels, and responses of the understory plant community. It is possible that stands with large numbers of beetle-killed trees may actually have a reduced risk of fire. Once a fire has started, fallen trees killed by bark beetles may increase heat intensity around them, increasing consumption of organic matter in soil.

The effects of fire on bark beetles are better studied. For beetles already breeding in trees that are subsequently burned, reproductive success is reduced. However, because of the insulative properties of bark and the mass of the tree bole, and the occurrence of beetles over most of the tree bole, fires need to be intense to cause significant mortality. After a fire, burned trees may attract bark beetles both to the area and to particular trees, although the reverse has also been observed. The difference in response may be related to whether the bark beetle species are primary or secondary species. Successful attack of individual burned trees varies with tree species and the severity of burn. Resin response may either increase or decrease in burned pine trees, depending on species. Some species avoid scorched bark while others are limited to these areas.

Forest Succession

Because tree-killing bark beetle species attack dominant trees within one host genus, they have the potential of altering forest composition and the rate and routes of succession to the canopy. Not surprisingly, subcanopy trees show increased growth rates following a bark beetle outbreak. Whether this results in a change in the species composition in the canopy depends on the species composition in the

subcanopy and their relative responses. In one outbreak where half of the spruce trees were killed by bark beetles, there was no significant change in tree species composition.

Decomposition

Bark beetles are expected to hasten decomposition because they penetrate the wood material and are vectors for many species of fungi, but few studies have tested this. Douglas-fir beetles, *D. pseudotsugae*, had a small effect on log decomposition after 10 years, with wood borers contributing much more. Decomposition of spruce in Finland, as measured by percentage mass loss over 30 months, was positively correlated with the number of beetle attacks, although the difference in mass loss between logs with and without exposure to beetles was not large.

Management Options

Bark beetles that kill mature trees have many negative economic impacts. If the tree had been intended for timber, it remains usable for only a year or two after death before it becomes fractured. Discoloration by blue-stain fungi reduces the value of the wood for esthetic purposes. Penetration into sapwood by ambrosia beetles can reduce the structural and esthetic value of the affected area of wood. When outbreaks result in millions of trees being killed simultaneously, increased salvage harvesting may depress prices, and disrupt harvesting plans and expected future yield. The potential loss of individual trees valued by people also prompts management actions.

Management of bark beetles affecting trees includes three approaches. These are: (1) killing beetles directly; (2) manipulating beetle movement using semiochemicals (pheromones and kairomones); and (3) stand and landscape management to prevent increases in beetle populations.

Killing bark beetles is difficult because most of their life cycle is spent within plant tissue. For individual beetle-infected trees, it is possible to kill beetle broods by applying insecticides that are conducted through the tree's vascular system to the developing broods (e.g., monosodium methanearsenate). An interesting biological approach is to attract less aggressive but faster-developing bark beetle competitors into trees colonized by pest species. However, these individual tree treatments are not practical on a large scale. Small groups of trees may be felled and either debarked or burned. Infested stands may be harvested or burned with prescribed fire although, as noted above, fire may not kill most

beetles. When stand removal is prescribed, beetles can be lured into the stand using semiochemicals to maximize the number of beetles removed. A difficulty with any plan to remove beetles in trees is that the presence of beetles may be hard to detect, as trees may not show obvious signs of attack until broods are well developed or already emerged. Consequently, experienced surveyors are required on the ground to assess beetle populations.

For some species of bark beetle, large numbers of beetles can be removed by using traps baited with semiochemicals, especially pheromones. To minimize the number of predators that are also captured, small discrepancies in the chemicals that are maximally attractive to bark beetles and their predators can be exploited. Mass-trapping is simple and inexpensive to implement once the baits have been developed, but it is difficult to assess how much the population is reduced, since many dispersing beetles fail to establish in trees anyway. In addition, the baits may attract high densities of beetles into a local area, increasing the risk that trees around the baited traps will be successfully attacked (spillover). Consequently, it is often recommended that the baited traps be placed far from host trees. An alternative approach is to use baited trees as traps (trap trees); these tend to be more attractive than baited traps initially, but then become unattractive once saturated with beetles, minimizing the risk of spillover. More effort is required to dispose of the trap tree to prevent beetle emergence than for pheromone traps.

Manipulation of beetle search behavior is an approach that takes advantage of bark beetles' reliance on chemical cues for host selection and mate finding. Beetles can be deterred from settling on trees, or even in stands, by conspecific antiaggregation pheromones, pheromones of competitor bark beetle species, or nonhost volatiles. For species that require high densities of beetles to overcome tree defenses, even some deterrence might allow trees to defend against beetle attacks.

A preventive approach to bark beetle control is to manage stands and landscapes to prevent the development of large beetle populations. However, by definition, pest species use trees that people want, so any plan to make host trees difficult for beetles to find will usually compromise the economy of harvest. Indeed, many bark beetle species have become pests because their host plants have been planted in monocultures, reducing dispersal mortality. It is possible to manage the risk of beetle attack by predicting when a stand is likely to be at risk, and taking action at that time. Risk and hazard rating systems are based on stand conditions (e.g., tree size, age, density, physiography) and on current beetle

population size. Beetle population size can be assessed by surveying the number of trees recently killed in the area, by assessing the success of broods, and by monitoring baited traps.

A preventive method widely used to control mountain pine beetles (*D. ponderosae*) is stand-thinning. The mechanisms by which this method works are unclear, but may include increased vigor of remaining trees and a less favorable microclimate of thinned stands (warmer and windier). Some studies of thinning, focusing on other bark beetle species, have found no effect or a positive effect of thinning on beetle populations. If thinning is conducted on mature stands, costs of this approach include increased tree damage due to wind sway and wind throw, as well as the requirement to enter the stand multiple times. Thinning is therefore not an approach to be implemented indiscriminately.

See also: **Entomology:** Population Dynamics of Forest Insects. **Health and Protection:** Integrated Pest Management Practices; Integrated Pest Management Principles. **Pathology:** Insect Associated Tree Diseases.

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Introduction and Definitions

There is considerable debate over definitions for the word ‘forest’ and even for ‘tree.’ Most vegetation types fall clearly into the categories of forest or nonforest, but there is dispute at the margins. The following are contentious questions:

- Does ‘forest’ apply to a type of land cover, or to a type of land use? (An apple orchard, for example,

may consist of a high density of trees but is not normally considered to be forest, whereas areas of bare land in the phase between clearfelling and replanting are normally included as forest.)

- At what height is a woody species classified as a tree? Does this vary with the age of the plant?
- At what proportion of ground cover do trees collectively form forests? (For example, do widely spaced trees in the African savannah or Australian outback constitute a forest? Do heavily tree-lined cities constitute forests?)

A similar debate rages over the classification of forests into natural and artificial types. On the one hand, we could say that totally natural forests do not