Chapter 18
Native Bark Beetles and Wood Borers in Mediterranean Forests of California

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Abstract Several species of bark beetles (Coleoptera: Curculionidae, Scolytinae), and to a much lesser extent wood borers (primarily Coleoptera: Buprestidae and Cerambycidae), are capable of causing conifer mortality in Mediterranean forests of California, U.S. This mortality is an important part of the ecology of these ecosystems, but the economic and social implications can be significant when outbreaks occur. I review the ecology, impact and management of the more notable species, including western pine beetle, *Dendroctonus brevicomis* LeConte, mountain pine beetle, *D. ponderosae* Hopkins, Jeffrey pine beetle, *D. jeffreyi* Hopkins, red turpentine beetle, *D. valens* LeConte, California fivespined ips, *Ips paraconfusus* Lanier, pine engraver, *I. pini* (Say), pinyon ips, *I. confusus* LeConte, fir engraver, *Scolytus ventralis* LeConte, cedar bark beetles, *Phloeosinus* spp., and several wood borers.

18.1 Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae), a large and diverse group of insects consisting of >550 species in North America (Wood 1982b), are commonly recognized as important disturbance agents in conifer forests. While some 200 species are native to California (Wood 1982b), only a handful is capable of causing tree mortality in Mediterranean forests (Table 18.1). Trees of all species, ages and size classes may be colonized and killed, but each bark beetle species exhibits unique host preferences, life history traits, and impacts. For example, some species, such as *Ips*, are considered secondary agents that typically colonize stressed, dead or dying trees while others, such as the western pine beetle, *Dendroctonus ponderosae* LeConte, are capable of killing healthy trees (Furniss and Carolin 1977). In most cases, the resultant tree mortality goes unnoticed until a large infestation or outbreak occurs, which generally requires several years of favorable weather conducive to beetle survival and population growth, and an abundance of susceptible host trees (Bentz et al. 2010).

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Table 18.1 Notable conifer-infesting bark beetles and wood borers in Mediterranean forests of California

Common name	Scientific name	Primary host(s)
California fivespined ips	*Ips paraconfusus*	*Pinus coulteri*, *P. lambertiana*, *P. ponderosa*, *P. radiata*, *P. torreyana*
California flathead borer	*Phaenops californica*	*P. jeffreyi*, *P. lambertiana*, *P. ponderosa*
Cedar bark beetles	*Phloeosinus spp.*	*Calocedrus decurrens*, *Sequoia sempervirens*, *Sequoiadendron giganteum*
Fir engraver	*Scolytus ventralis*	*Abies concolor*
Flatheaded fir borer	*Phaenops drummondi*	*A. concolor*
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*
Mountain pine beetle	*Dendroctonus ponderosae*	*P. contorta*, *P. lambertiana*, *P. ponderosa*
Pine engraver	*Ips pini*	*P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*
Pinyon ips	*Ips confusus*	*P. monophylla*, *P. quadrifolia*
Red turpentine beetle	*Dendroctonus valens*	*P. jeffreyi*, *P. lambertiana*, *P. ponderosa*, *P. radiata*
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri*, *P. ponderosa*

Adult bark beetles maintain limited energy reserves (Atkins 1966), and are highly susceptible to predation, starvation and adverse weather conditions when searching for hosts. Therefore, it is important that bark beetles locate the correct habitat, correct tree species, and the most susceptible trees within these species with efficiency (Byers 1995; Borden 1997). The dominant theory for many species, such as the well-studied mountain pine beetle, *Dendroctonus ponderosae* Hopkins, suggests pioneering beetles (i.e., those that initiate host selection and colonization) use a combination of random landings and visual orientations followed by direct assessment of hosts based on olfactory and/or gustatory cues (Raffa and Berryman 1982, 1983). Given the cues received during these processes, the host is either rejected or accepted. If accepted, pioneering beetles bore through the outer bark and into the phloem where gallery construction occurs upon which many species release aggregation pheromones that enhance attraction of conspecifics to the target tree (Wood 1982a).

Successful host colonization requires overcoming tree defenses, which can only be accomplished by recruitment of a critical minimum number of beetles to *mass attack* vigorous hosts and overwhelm their defenses (i.e., the more "healthy" the tree the more beetles required to overcome tree defenses; Fettig et al. 2007a). Most conifers are capable of mobilizing large amounts of oleoresin following wounding, which constitutes their primary defense against colonization by bark beetles (Franceschi et al. 2005), although resin chemistry (Reid and Purcell 2011) and the development of hypersensitive responses are also important (Lieutier 2004). Bark beetles that initiate host selection are often killed by drowning or immobilization in

resin that collects at the entrance hole (*pitch tube*), which in combination with the presence of boring dust is commonly used to identify trees that have been recently attacked (Fig. 18.1). The number of pitch tubes and amount of boring dust is indicative of the number of beetles attacking the tree, while the size of pitch tubes indicates the vigor of the host at the time of attack. Vigorous hosts often produce large pitch tubes that are largely free of phloem material (Fig. 18.1, left), indicating the tree is likely to survive. Monoterpenes released from pitch tubes often enhance attraction to the host tree, however for most *aggressive* species (i.e., those capable of causing large amounts of tree mortality) attraction to host volatiles has not been demonstrated in the absence of aggregation pheromone components (e.g., Moeck et al. 1981). Following mating, eggs are laid in the phloem and larvae excavate feeding tunnels in this tissue and/or the outer bark (Furniss and Carolin 1977). Bark beetles carry a variety of phoretic organisms including bacteria, fungi, yeasts, mites, and nematodes. Relationships ranged from mutualistic to antagonistic. The best studied group are the symbiotic blue-stain fungal associates in the family Ophiostomataceae, which upon inoculation into the tree serve as important food sources for bark beetles, and may also negatively impact tree health (Paine et al. 1997; Six and Wingfield 2011), although tree mortality occurs primarily through girdling of the phloem and cambium tissues.

Following pupation, adult beetles of the next generation tunnel outward through the bark and initiate flight in search of new hosts (Fig. 18.2). The time required to complete a generation (*voltinism*) varies among bark beetle species, among populations within a species, and among individuals within a population. For example,

Fig. 18.1 Bark beetles, such as this female *Dendroctonus brevicomis*, that initiate host colonization are often killed by drowning or immobilization in resin that collects at the entrance hole (*pitch tube*, *Left*), which in combination with the presence of boring frass (*Right*, in this case resulting from *D. ponderosae*) is commonly used to identify trees that have been recently colonized by bark beetles. Monoterpenes released from pitch tubes enhance attraction to the host tree, however for most *aggressive* bark beetle species attraction to host volatiles has not been demonstrated in the absence of aggregation pheromone components (Borden 1997) (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

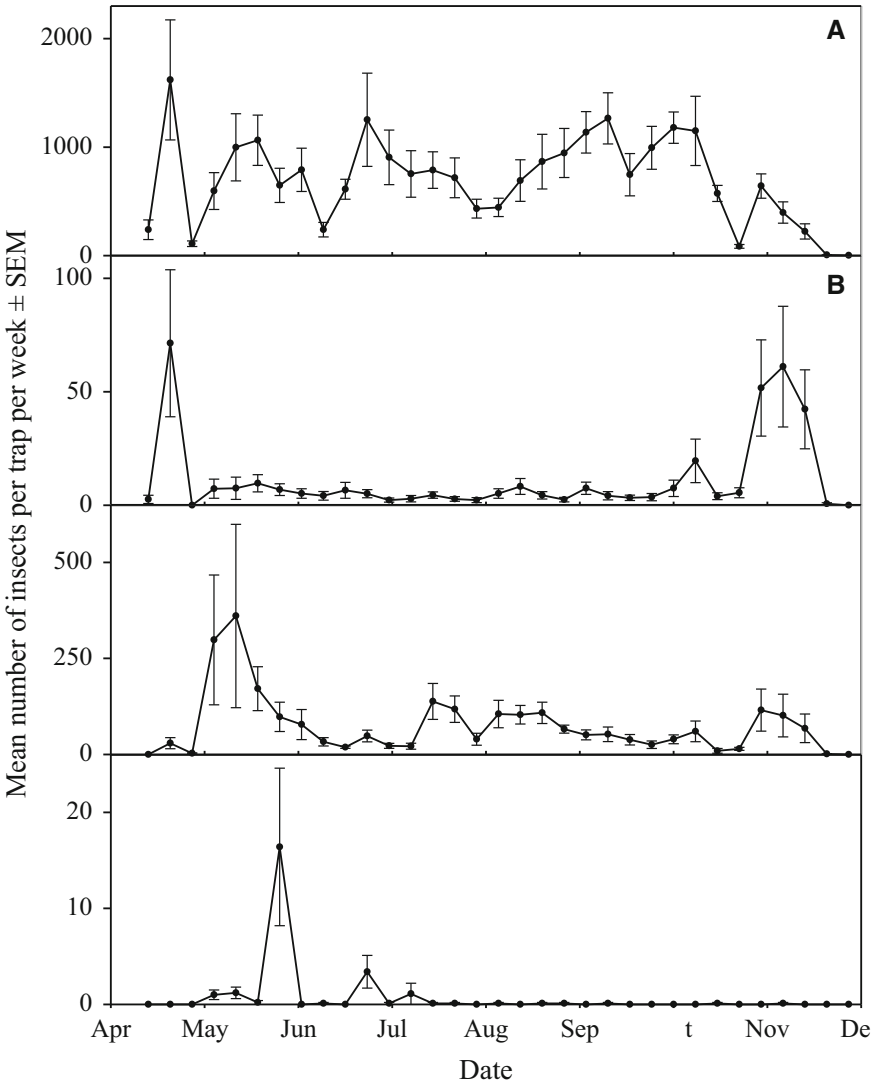

Fig. 18.2 The flight periodicity of (**A**) *Dendroctonus brevicomis*, (**B**) *D. ponderosae*, (**C**) *Ips paraconfusus*, and (**D**) *I. pini* at 823 m elevation, Georgetown Ranger District, Eldorado National Forest, California, 1992–1994 (Modified from Fettig et al. (2005a), and based on captures in baited, multiple-funnel traps)

species such as *D. brevicomis* may complete more than one generation per year, while others, such as the *D. ponderosae*, may take up to 3 years to complete a single generation depending on the temperature profile at a particular locale, among other factors. Because bark beetles are highly sensitive to thermal conditions conducive to population survival and growth, and drought stress influences host tree vigor,

recent outbreaks of several bark beetle species have been correlated with shifts in temperature and precipitation (Bentz et al. 2010). As such, many experts agree that anthropogenic-induced climate change will intensify the impacts of bark beetle outbreaks in the future (Fettig et al. 2013a). Hosts native to the Mediterranean forests of California are likely to be particularly vulnerable.

Substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of tree mortality attributed to bark beetles. *Direct control* involves short-term tactics designed to address current infestations by manipulating beetle populations, and often includes the use of insecticides, semiochemicals (i.e., chemicals released by one organism that elicit a response, usually behavior, in another organism), sanitation harvests that remove infested trees, or a combination of these treatments. Natural enemies, such as predators and parasitoids, are important in regulating bark beetle populations at endemic levels (Miller et al. 1987), but none have been successfully developed as biocontrol agents for bark beetles in western North America. Synthetic formulations of entomopathogenic microorganisms, such as fungi, are being developed for some species (Fettig and Hilszczański 2015). Often aerial surveys are conducted with helicopters and/or fixed-wing aircraft to identify and delineate infestations prior to more detailed ground surveys being conducted to determine if direct control measures are warranted. *Indirect control* is preventive, and designed to reduce the probability and severity of future bark beetle infestations by manipulating stand, forest and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and altering age classes and species compositions. Unlike direct control, the focus of indirect control is on the susceptibility of residual forest structure and composition to future infestations (Fettig and Hilszczański 2015), and represents an important component of proper forest management. In short, reducing tree competition improves tree growth and defensive mechanisms while often disrupting pheromone plumes, thus negatively affecting the beetle's ability to locate and successfully mass attack host trees (Fettig et al. 2007a). *Risk and hazard rating systems* have been developed for several species of bark beetles native to Mediterranean forests of California to provide land managers and others with a means of identifying stand conditions that are likely to foster initiation and/or spread of infestations (Fettig and Hilszczański 2015), but are rarely used.

The impact of wood borers pales in comparison to that of bark beetles in most forests, but some species are capable of causing tree mortality. Eggs of most species are laid in slits created by females in the outer bark or within bark crevices. The larvae initially mine the cambium and phloem, and then extend their tunneling into the sapwood and occasionally the heartwood. The time required to complete a generation varies from months to years depending on the species and other factors. Two families are of significance. The Buprestidae compromise a large group of ~700 species in North America, many of them indigenous to the western U.S. (Furniss and Carolin 1977). The larvae have a flattened thorax (hence the common name, *flatheaded borers*) while the adults are often brightly-colored with a metallic-type luster (*metallic borers*). The Cerambycidae have a swollen thorax (*roundheaded borers*) while the adults have very long antennae (*longhorned beetles*). Some wood

borers pupate in the xylem, while others create a *chip cocoon* in the inner bark. Different species arrive at different times after a tree is stressed or killed, likely due to changes in the chemical composition of trees that influence host finding, selection and colonization behaviors (Kelsey and Joseph 2003). Wood borers serve a very important ecological function by helping to facilitate wood decomposition and nutrient cycling (Edmonds and Eglitis 1989).

Tree mortality resulting from colonization of native bark beetles and wood borers is an important part of the ecology of Mediterranean forests. Some level of tree mortality is desirable and often results in a mosaic of age classes and tree species compositions that increase resistance and resilience to multiple disturbances, including bark beetle infestations (Fettig 2012). This differs from the impacts associated with large infestations or outbreaks, which may negatively affect several ecological goods and services, including timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among many others. It is important to note that the ecology and impact of these insects is influenced by other biotic, abiotic, and anthropogenic (e.g., management activities and land use patterns) disturbances that also directly influence successional pathways.

In California, Mediterranean climates are distributed throughout much of the Coast Range, the Sacramento Valley, along the western slope of the Sierra Nevada, and in the Transverse and Peninsular Ranges of southern California (Kauffmann 2003). As such, I discuss the biology, ecology and management of bark beetles and wood borers native to conifer forests in these regions. Given the number of species involved, I focus exclusively on those that cause the majority of tree mortality (Table 18.1). In this context, many species are ignored that are also vital to the proper functioning of these ecosystems. Others, such as the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, are notable forest pests elsewhere in western North America (Furniss and Carolin 1977), but have limited and/or infrequent impacts in Mediterranean forests of California and are ignored.

18.2 Life History and Management of Bark Beetle and Wood Borers

18.2.1 estern Pine Beetle, Dendroctonus brevicomis

Dendroctonus brevicomis is recognized as a significant cause of *P. ponderosa* mortality in much of the western U.S., and particularly in Mediterranean forests of California. The only other host in California is Coulter pine, *P. coulteri* D. Don, a species indigenous to the Transverse and Peninsular Ranges of southern California. In the early and mid-twentieth century, substantial research was conducted on *D. brevicomis* due to its impacts in mature *P. ponderosa* stands in California, Oregon

and Washington, U.S. Much of the knowledge gained was published in a seminal work titled "Biology and Control of the Western Pine Beetle" by noted USDA Forest Service scientists J.M. Miller and F.P. Keen (1960), which I encourage the reader to review for more detailed information. Today, *D. brevicomis* continues to exert significant impacts on forests in California and elsewhere. For example, the mountain ranges of southern California experienced an outbreak of *D. brevicomis* in the early 2000s that resulted in 73.5 % and 78 % mortality of large-diameter (>43.2 cm diameter at breast height, dbh) *P. ponderosa* and *P. coulteri*, respectively (Walker et al. 2006). In some areas, tree mortality exceeded 80 % (Fig. 18.3).

Dendroctonus brevicomis generally exhibits a preference for larger diameter (>50 cm dbh) trees (Fig. 18.4), but under certain conditions may colonize and kill apparently-healthy trees of all ages and size classes. Female *D. brevicomis* initiate host colonization by tunneling through the outer bark and into the phloem and outer

Fig. 18.3 Tree mortality (bare and faded crowns) resulting from a notable *Dendroctonus brevicomis* outbreak in southern California. In 2000, *D. brevicomis* was first noticed colonizing *Pinus coulteri* at elevated levels in the San Jacinto Mountains on the San Bernardino National Forest (USDA Forest Service 2000). Activity peaked in 2002–2003 in both *P. coulteri* and *P. ponderosa*, and rapidly declined thereafter. Severe drought stress (i.e., precipitation was the lowest in recorded history during 2001–2002) was important in facilitating the outbreak, but elevated ozone and nitrogen deposition were likely predisposing factors (Jones et al. 2004). Estimates of commercial sawlogs and other fiber (all trees killed) salvaged (*above*) or harvested (e.g., during fuels reduction projects) ranged from 115,312 to 566,788 green metric tons (mt) per year during 2004–2008 (CJF, unpublished) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Fig. 18.4 A *Pinus ponderosa* snag that was killed by *Dendroctonus brevicomis* several years earlier (*Left*). Close examination of the lower bole, where the bark has sloughed, shows the characteristic "S"-shaped galleries produced by this species. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species. *Dendroctonus brevicomis* enters the bark during the second larval instar (there are four instars) and completes development within the mid-bark layer. Woodpeckers, especially the genus *Picoides* (Farris and Zack 2005), remove the outer bark of such trees to forage for larvae, pupae and adults (*Right*) (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

xylem where they rupture resin canals. As a result, oleoresin exudes and collects on the bark surface, as is commonly observed with other bark beetle species. During the early stages of attack, females release *exo*-brevicomin, which in combination with the host monoterpene myrcene released from pitch tubes is attractive to conspecifics (Bedard et al. 1969). Frontalin, produced by males (Kinzer et al. 1969), enhances attraction and mass attack ensues (Wood 1972; Bedard et al. 1985). These volatiles are commercially produced and effective attractants (Wood et al. 1976). Verbenone is produced during latter stages of the attack sequence by several pathways, and is thought to reduce intraspecific competition, and in some cases interspecific competition, by altering adult behavior to minimize overcrowding of developing brood within the host (Byers and Wood 1980; Byers et al. 1984). There are typically two to four generations per year (Furniss and Carolin 1977).

Tactics for managing *D. brevicomis* infestations are limited to tree removals (thinning) that reduce stand density and host susceptibility (Fig. 18.5), sanitation harvests, and applications of insecticides to protect individual trees. Verbenone was the focus of early work designed to develop a semiochemical-based tool for mitigating undesirable levels of *P. ponderosa* mortality attributed to *D. brevicomis*, but alone is ineffective for protecting individual trees (Gillette et al. 2006) or forest

Fig. 18.5 Thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark beetle-caused tree mortality (Fettig et al. 2007a). Among other factors, thinning reduces host availability; reduces competition among trees for nutrients, water, and other resources thereby increasing vigor; and affects microclimate decreasing the effectiveness of chemical cues used in host finding, selection and colonization (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

stands (Fettig et al. 2009a). Based on early work by Paine and Hanlon (1991), Bertram and Paine (1994) found that applications of verbenone and ipsdienol significantly reduced both numbers of *D. brevicomis* landing on *P. ponderosa* and the densities of attacking beetles, but tree mortality rates were not determined. In more recent years, Fettig et al. (2008a, 2009b, 2012a, b) developed a four-component blend [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (−)-verbenone; Verbenone Plus] that has been demonstrated effective for protecting individual *P. ponderosa* and *P. ponderosa* stands from mortality attributed to *D. brevicomis*, but has yet to be commercialized.

18.2.2 Mountain Pine Beetle, Dendroctonus ponderosae

Dendroctonus ponderosae is the best studied of all bark beetles in North America, presumably a result of the significant impacts it exerts in several different hosts and forest types. The species colonizes at least 15 *Pinus* native to North America (Negrón and Fettig 2014), but in Mediterranean forests of California *P. ponderosa*,

Fig. 18.6 Like other *Dendroctonus*, female *D. ponderosae* initiate host colonization (*Left*). Notice the distinctive vertical galleries that often end in a "J"; the deceased adult (within *red circle*); and the presence of bluestain introduced upon colonization by the beetle (*Right*). Some studies have shown that fungi associated with *D. ponderosae* and other bark beetles are capable of directly causing mortality (e.g., on *P. ponderosa* seedlings, Owen et al. 1987), but others have failed to demonstrate such an effect (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

lodgepole pine, *Pinus contorta* Dougl. ex Loud. (Fig. 18.6), and sugar pine, *P. lambertiana* Dougl., are preferred hosts. At higher elevations in the Sierra Nevada, significant levels of mortality have been attributed to *D. ponderosae* in whitebark pine, *Pinus albicaulis* Engelm, a tree species of concern that has been considered for listing as a threatened and endangered species (Federal Register 2011). The lifecycle of *D. ponderosae* is generally considered univoltine, but a mixture of univoltine and semivoltine (i.e., less than univoltine) life cycles commonly occur (Bentz et al. 2014), even within the same tree. In southern California, three generations may be completed in 2 years (San Bernardino National Forest, 2100 m elevation; Bentz et al. 2014), but truly bivoltine populations (i.e., two generations per year) have not been documented.

Most large-scale infestations of *D. ponderosae* occur in *P. contorta* forests in a near contiguous pattern and often across extensive areas. To that end, recent outbreaks have been severe and long lasting, with >27 million hectares impacted in western North America (BC Ministry of Forests, Lands and Natural Resource Operations 2012; USDA Forest Service 2012). As a result, significant research has been executed on *D. ponderosae* in the last decade in both Canada and the U.S., much of which was recently reviewed in a special issue titled "Mountain Pine

Beetle, a Major Disturbance Agent in US Western Coniferous Forests: A Synthesis of the State of Knowledge" (Negrón and Fettig 2014). I encourage the reader to consult this publication for more detailed information on *D. ponderosae*.

In *P. contorta* forests, *D. ponderosae* tends to initially colonize the largest trees with progressively smaller trees being attacked over time (Klein et al. 1978). Larger-diameter *P. contorta* (e.g., >23 cm dbh) provide for a higher reproductive potential and probability of beetle survival (Reid and Purcell 2011; Graf et al. 2012) because of the greater quantity of phloem available on which larvae feed. Based on research conducted in Oregon, Mitchell and Preisler (1991) reported that small-diameter *P. contorta* were not colonized unless they were near currently-infested larger trees, and that larger trees (≥23 cm dbh) were colonized with greater frequency than could be accounted for by a random attack model. Working in British Columbia, Canada, Safranyik et al. (1974) reported that *P. contorta* ≤25 cm dbh serve as *D. ponderosae* sinks, whereas those >25 cm dbh serve as sources producing more beetles than required to overcome host defenses. Whitehead et al. (2004) and Whitehead and Russo (2005) showed thinning *P. contorta* stands to a uniform residual inter-tree spacing of at least 4 m or ~400–625 trees/ha is effective for mitigating levels of tree mortality attributed to *D. ponderosae*.

In *P. ponderosa*, *D. ponderosae* tends to colonize trees in the small to mid-diameter classes (Olsen et al. 1996), but this may be an artifact of these forests being less dense, less continuous, and exhibiting a higher diversity of stand ages and tree sizes than *P. contorta* forests (Fettig et al. 2014). Working in the Colorado Front Range, U.S., Negrón and Popp (2004) reported the probability of *P. ponderosa* stands becoming infested by *D. ponderosae* is 0.71 when *P. ponderosa* basal area (cross-sectional area of trees at 1.37 m in height) is >17.1 m^2/ha and decreases to 0.21 when basal area is ≤17.1 m^2/ha. Interestingly, these values are similar to those reported by Larsson et al. (1983) for *P. ponderosa* forests in Oregon. In northeastern California, Egan et al. (2010) reported that higher levels of tree mortality occurred in unthinned *P. ponderosa* compared to pre-commercially thinned stands. Fiddler et al. (1989) showed that thinning significantly reduced the amount of *P. ponderosa* mortality caused by *D. ponderosae* in California. No tree mortality occurred in stands of <9 m^2/ha of basal area, which agrees with the optimal stocking level of 11 m^2/ha described by Oliver (1979, 1995). Mortality was reduced in thinned plots regardless of the level of thinning. In Mediterranean forests of California, where *D. brevicomis* and *D. ponderosae* often coexist in forests dominated by *P. ponderosa*, the role of *D. ponderosae* is usually secondary to that of *D. brevicomis*, particularly in larger-diameter trees (Fettig et al. 2010a). The two species occasionally colonize the same tree.

Progar et al. (2014) synthesized information related to the chemical ecology of *D. ponderosae*. In short, aggregation pheromones *trans*-verbenol and *cis*-verbenol are the primary compounds produced in the insect's hindgut (Miller and Lafontaine 1991). c*is*-Verbenol, produced by female *D. ponderosae*, increases the attraction of females to *exo*-brevicomin, but its effect is less than that of *trans*-verbenol (Miller and LaFontaine 1991). Attraction is enhanced by the presence of host volatiles α-pinene (Pitman et al. 1968) and myrcene (Borden et al. 1987), among others.

Male *D. ponderosae* release *exo*-brevicomin, which is a primary attractant of females, further augmenting mass attack (Amman and Lindgren 1995). Males also produce frontalin, which attracts females at low concentrations (Ryker and Libbey 1982). Several of these volatiles are commercially produced and effective attractants. During the latter stages of colonization, increasing amounts of verbenone are produced inhibiting additional *D. ponderosae* from infesting the target tree, thus limiting the number of infesting beetles to a density that increases the likelihood of brood survival (Amman and Lindgren 1995). Newly arriving *D. ponderosae* then reorient to adjacent trees where the cycle of colonization is repeated.

Fettig et al. (2014) analyzed the effectiveness of treatments for preventing and mitigating undesirable levels of tree mortality attributed to *D. ponderosae*. Tactics include silvicultural treatments that reduce stand density (thinning) and host susceptibility, sanitation harvests, applications of insecticides to protect individual trees (Fig. 18.7), and applications of semiochemicals including aggregation pheromones deployed in trap out or trap tree methods (i.e., where beetles are collected and later destroyed) and inhibitors used to disrupt colonization of individual trees or stands. Unlike *D. brevicomis*, verbenone is effective for reducing levels of tree mortality attributed to *D. ponderosae*, but efficacy varies (*see* Progar et al. 2014 for related factors), and studies indicate verbenone is ineffective for reducing levels of tree mortality attributed to *D. ponderosae* in *P. ponderosa* (Bentz et al. 1989; Gibson et al. 1991; Negrón et al. 2006). While several formulations of verbenone are registered in the U.S., pouches are most commonly used and stapled at maximum reach to individual trees (Fig. 18.8, left) or applied in a grid pattern when stand protection is the objective. Recently, a new biodegradable formulation of verbenone that is applied directly to the tree bole has been developed and demonstrated effective for protecting *P. contorta and P. lambertiana* from mortality attributed to *D. ponderosae* (Fettig et al. 2015) (Fig. 18.8, right).

18.2.3 effrey Pine Beetle, Dendroctonus jeffreyi

Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins, only colonizes Jeffrey pine, *P. jeffreyi* Grev. & Balf., a species that ranges from the Klamath Mountains in southwestern Oregon, throughout much of the Sierra Nevada and the Transverse and Peninsular Ranges in southern California, to the Sierra San Pedro Mártir of Baja California, Mexico. In Mediterranean forests of California, *D. jeffreyi* usually colonizes individual trees and its activity often goes unnoticed, but group kills of 20–30 trees are not uncommon (Smith et al. 2009). Large outbreaks may occur during periods of extended drought, but are typically associated with *P. jeffreyi* forests in other climatic zones. Paine et al. (1999) reported that 1–heptanol and n-heptane were attractive to *D. jeffreyi*, and a 5:95 blend is an effective trap lure (Strom et al. 2013). Frontalin, produced by males (Hall et al. 2002), reduces trap catches and

Fig. 18.7 A common method of protecting conifers from mortality attributed to bark beetles is to saturate all surfaces of the tree bole with an insecticide. Usually only high-value, individual trees growing in unique environments (e.g., campgrounds) or under unique circumstances are treated (Fettig et al. 2013b) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

may have utility for tree protection (Strom et al. 2013). There are one to two generations per year (Furniss and Carolin 1977).

Tactics for managing *D. jeffreyi* infestations are limited, and much of what is implemented is based on research executed in other bark beetle-host systems, typically *D. brevicomis* in *P. ponderosa*. Sanitation harvests and applications of insecticides to individual trees are commonly recommended (Smith et al. 2009). The USDA Forest Service is conducting a long-term study to determine the effectiveness of thinning for reducing stand susceptibility to *D. jeffreyi*, but results are thus far inconclusive due to few trees being colonized and killed by *D. jeffreyi* (Fettig et al. 2012c) (Fig. 18.9).

Fig. 18.8 The antiaggregant verbenone has been evaluated as a tool for mitigating tree mortality attributed to bark beetles for several decades. The most common application method includes the use of pouch release devices stapled at maximum reach to individual trees prior to beetle flight (*Left*), or applied in a grid pattern to achieve uniform coverage when stand protection is the objective. Bead, flake and sprayable formulations have also been evaluated, but are not widely used. Fettig et al. (2015) recently developed a novel formulation of verbenone (SPLAT® Verb, ISCA Technologies Inc., Riverside, CA) that has shown a high degree of efficacy for protecting *P. contorta* from *D. ponderosae*. Rather than a single release device, SPLAT® Verb is an amorphous, flowable controlled-release emulsion that is also biodegradable (*Right*), which allows for significant labor cost savings by not having to retrieve release devices from the field after use (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Fig. 18.9 The USDA Forest Service is conducting several studies to determine the effectiveness of different silvicultural treatments to reduce the susceptibility of forests to bark beetle infestations, the results of which are used to inform practitioners of proper management techniques. The study above was initiated in 1997. Treatments include thinning from below (i.e., initiating in the smallest diameter classes) to a residual target basal area of 18.4 m^2/ha, 27.6 m^2/ha or 41.3 m^2/ha, and an untreated control (*see* Fettig et al. 2012c) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

18.2.4 Red urpentine Beetle, Dendroctonus valens

Red turpentine beetle, *Dendroctonus valens* LeConte, is a common bark beetle species found throughout much of North America. This species colonizes all *Pinus* within its native range, and perhaps several other tree species (Furniss and Carolin 1977). Attacks are usually confined to basal portions of stressed, weakened, or dead and dying trees, and rarely cause mortality of healthy trees (Fig. 18.10). *Dendroctonus valens* was accidentally introduced into China from North America in the 1980s, and has caused significant levels of tree mortality in Chinese red pine, *P. tabuliformis* Carr. (Yan et al. 2005). There is concern that genetic changes in the fungus associated with *D. valens*, which likely contributed to the invasive success of the beetle–fungal complex in China, could pose an increased threat to North American forests if *D. valens* was re-introduced back into North America from China (Lu et al. 2011). The lifecycle is univoltine throughout much of the range including mid-elevations of the Sierra Nevada, but two to three generations per year may occur in warmer areas (Furniss and Carolin 1977).

Fig. 18.10 A robber fly (Diptera: Asilidae) predating upon *Dendroctonus valens* on the bark of *Pinus ponderosa* in California. *Dendroctonus valens* is the largest bark beetle in North America. Attacks are usually confined to the basal portions of stressed, weakened, or dead and dying trees (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Hobson et al. (1993) reported significant increases in *D. valens* trap catch attributable to 3-carene and α-pinene when added to β-pinene. Combinations of these three kairomones comprise an effective bait. More recently, it was demonstrated that female *D. valens* produce frontalin (Zhang and Sun 2006), which likely functions as both a sex and aggregation pheromone (Liu et al. 2013). Verbenone is present in the frass (Grégoire et al. 1991) and hindgut of *D. valens* (Yan et al. 2004), and has been demonstrated to reduce numbers of attacks on individual trees (Sun et al. 2003; Gillette et al. 2006; Fettig et al. 2008a). Working in the central Sierra Nevada, Fettig et al. (2006a) showed that California five-spined ips, *I. paraconfusus* LeConte, attack densities in logging slash were inversely related to *D. valens* attacks on adjacent freshly-cut stumps, and later demonstrated that components of the *I. paraconfusus* aggregation pheromone were inhibitory to *D. valens* (Fettig et al. 2005b). Levels of inhibition were increased with the addition of verbenone (Fettig et al. 2007b). However, due to the species limited pest status in North America, efforts there to develop a semiochemical-based tool for tree protection have been limited.

Management strategies are rarely implemented for *D. valens* in North America. Care should be taken to avoid damaging residual trees during harvest operations (Fig. 18.11), which may produce populations that attack nearby healthy trees, as

Fig. 18.11 During harvest operations, care should be taken to avoid damaging residual trees as populations of *Dendroctonus valens* may buildup in these hosts and then colonizing adjacent healthy trees. This can facilitate colonization by more aggressive species, such as *Dendroctonus brevicomis* (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

trees weakened by *D. valens* are more likely to be colonized and killed by more aggressive species (Furniss and Carolin 1977). The impact of *D. valens* in Mediterranean forests of California may become more significant due to the increased use of prescribed fire, which makes trees more susceptible to colonization by *D. valens* (Fettig et al. 2008b).

18.2.5 California Fivespined Ips, Ips paraconfusus

Ips paraconfusus was synonymous with pinyon ips, *Ips confusus* LeConte, until 1970 (Lanier 1970). As such, the reader must exert caution when consulting the early literature concerning these species. *Ips paraconfusus* occurs from southern Oregon to southern California and east to the crest of the Sierra Nevada and Cascade mountain ranges (Furniss and Carolin 1977). Recently, populations were recorded in Washington (Murray et al. 2013). All *Pinus* occurring within the range of *I. paraconfusus* are susceptible to colonization, especially *P. ponderosa*. Like other *Ips*, endemic populations of *I. paraconfusus* infest forest debris, widely scattered individual trees or small groups of trees. Top-killing of *P. ponderosa* is common, and often followed by *D. brevicomis* colonization of the main stem (Furniss and Carolin 1977). Occasionally, outbreaks result in mortality of large numbers of trees, but are usually associated with improper slash management (Fig. 18.12) or drought. *Ips paraconfusus* is also a vector of the fungus *Fusarium circinatum* Nirenberg & O'Donnell (Fox et al. 1991) that causes pitch canker disease in Monterey pine, *P. radiata* D. Don., and other *Pinus*, and represents a serious threat to *Pinus* production in Mediterranean forests worldwide (Wingfield et al. 2008). Male *I. paraconfusus* construct a nuptial chamber in the phloem and attract multiple females, typically three, yielding the classic "Y-shaped" gallery pattern. Males produce three aggregation pheromone components, ipsenol, ipsdienol, and *cis*-verbenol, which comprised the first pheromone to be fully described for any bark beetle species (Silverstein et al. 1966). There are two to five generations per year (Furniss and Carolin 1977).

Management strategies implemented for *I. paraconfusus* are similar to those recommended for other *Ips*. Early work by Buckhorn (1957) in Oregon demonstrated that tree mortality attributed to *Ips* was greatest when slash was generated between February and July. Conversely, the *safe period* for producing slash was August through December. During this time, host material declines in suitability over time as phloem moisture is reduced (Sartwell 1970). Most slash management treatments promote desiccation of slash and/or rendering slash unsuitable for colonization by chipping, cutting, lopping-and-scattering, or piling-and-burning (DeGomez et al. 2008). Slash that is infested by *I. paraconfusus* and related species can usually be successfully treated by solarization, a process that involves covering slash piles with clear plastic and securely anchoring the plastic to the ground. To be effective, solarization must result in temperatures that are high enough (>45 °C) to kill developing brood within slash prior to emergence. Insecticides may be applied to protect individual, high-value trees, but are rarely used. Shea and Neustein (1995) used baited

Fig. 18.12 Outbreaks of *Ips paraconfusus* are often associated with improper slash management (*Left*) or drought. Under most circumstances, slash should be treated to promote desiccation and/or to render it unsuitable for colonization by *Ips paraconfusus* and conspecifics by chipping, lopping-and-scattering (*Right*), burning or other treatments (DeGomez et al. 2008). If properly applied, this will reduce the risk of populations increasing in slash (i.e., where there is little or no host resistance) and then colonizing adjacent trees (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

traps to reduce the impact of *I. paraconfusus* in stands of Torrey pine, *Pinus torreyana* Parry ex Car., however, semiochemical-based tools for tree protection have not been commercialized for this species.

18.2.6 Pine Engraver, Ips pini

Pine engraver, *Ips pini* (Say), has a transcontinental distribution, and is one of the most common bark beetles in North America (Kegley et al. 1997). The species generally colonizes slash, saplings, and weakened trees. Top killing of *P. ponderosa* is common (Fig. 18.13, left), and often facilitates colonization by more aggressive bark beetles. Colonization rates are negatively correlated with tree diameter in *P. ponderosa* (Kolb et al. 2006), and trees 5–20 cm dbh are most frequently colonized. Infestations of *I. pini* are often short-lived, but may increase in scale and duration when suitable host material is plentiful and populations grow sufficient to kill apparently-healthy trees. Males construct a nuptial chamber in the phloem and produce ipsdienol and lanierone, which attracts multiple females (Fig. 18.13, right). These semiochemicals make an effective bait, but efficacy varies geographically (Lanier et al. 1972; Seybold et al. 1992, 1995). California populations are attracted to high ratios of (−)-ipsdienol, and lanierone has no effect on attraction (Miller et al. 1997). There are one to two generations per year (Furniss and Carolin 1977).

Fig. 18.13 Top killing of *Pinus ponderosa* by *Ips pini* is common (*Left*). Male *I. pini* construct a central nuptial chamber in the phloem and produce ipsdienol and lanierone, which attracts multiple females, typically 3–6. This results in a unique gallery pattern characteristic of the species (*Right*) (Photo credits: T. DeGomez, University of Arizona, with permission)

Similar to *I. paraconfusus*, guidelines for managing *I. pini* include separating slash production in time and space; generating slash during periods of beetle inactivity; limiting the size of treatment blocks; and treating slash through solarization, burning, chipping, lop-and-scattering and/or direct removal from the site (DeGomez et al. 2008). Insecticides may be applied to protect individual, high-value trees. While there is evidence that several semiochemicals are inhibitory to *I. pini* (Miller et al. 1995; Huber et al. 2001), none are used operationally for tree protection in California.

18.2.7 Pinyon Ips, Ips confusus

Notable outbreaks of *I. confusus* frequently occur in the Great Basin, U.S., and are usually associated with forest densification and drought (Kleinman et al. 2012). The species is mentioned here because although most of the mortality attributed to *I. confusus* in California occurs in other climatic zones, both single leaf pinyon, *P. monophylla* Torr. & Frem., and Parry pinyon, *P. quadrifolia* Parl. ex Sudw., grow to some degree in Mediterranean forests and are occasionally colonized and killed by *I. confusus* (Fig. 18.14). Males produce three aggregation pheromone components,

Fig. 18.14 *Pinus monophylla* killed (fading crowns) by *Ips confusus* (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

ipsenol, ipsdienol, and *cis*-verbenol (Young et al. 1973; Birch et al. 1977), which constitute an effective bait. In a somewhat unique adaptation, *I. confusus* adults overwinter in large numbers at the base of trees. There are two to four generations per year (Furniss and Carolin 1977).

Guidelines for managing *I. confusus* are similar those for other *Ips* (DeGomez et al. 2008). Insecticides may be applied to protect individual, high-value trees, but are rarely used (Fettig et al. 2006b), and caution should be exerted if harvesting of pinyon nuts is planned.

18.2.8 Fir Engraver, Scolytus ventralis

Fir engraver, *Scolytus ventralis* LeConte, frequently colonizes *Abies*, particularly white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., in Mediterranean forests of California. Trees of all sizes may be attacked and killed (Fig. 18.15), but outbreaks are typically associated with trees stressed by drought, defoliation (e.g., by Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough)), root pathogens or other factors (Berryman and Ferrell 1988; Ferrell et al. 1994). Large numbers of trees may be killed by *S. ventralis* following prescribed fire (Schwilk et al. 2006; Fettig and McKelvey 2014), particularly in the smaller-diameter classes (Table 18.2), but these treatments are usually implemented to promote *Pinus* over

Fig. 18.15 *Scolytus ventralis* frequently colonizes *Abies*, and produces a very distinctive gallery pattern that scores the sapwood. Infestations are typically associated with trees stressed by drought, defoliation, and/or root pathogens (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Abies and therefore this mortality may not interfere with management objectives. There is one generation per year throughout much of the range (Furniss and Carolin 1977). Our understanding of the chemical ecology of *S. ventralis* is poor. Macías-Sámano et al. (1998) hypothesized that both sexes of *S. ventralis* aggregate on a tree in response to odors emitted by the tree, which intensify when females bore into the bark further liberating host odors. The lack of identification of a strong attractant has, to some degree, limited other aspects of research on *S. ventralis*.

Tactics for managing *S. ventralis* are limited to tree removals (thinning) that reduce stand density and presumably host susceptibility (although specific studies have not been conducted to determine the influence of thinning on *S. ventralis*), and sanitation harvests (Berryman and Ferrell 1988).

18.2.9 Cedar Bark Beetles, Phloeosinus *spp.*

The genus *Phloeosinus* contains some 25 species in North America, which generally colonize the twigs, branches and stems of trees weakened by drought or other

Table 18.2 Numbers of trees killed by bark beetles by diameter class (mid-point of 10 cm diameter classes) and treatment (*LoD* low structural diversity, *HiD* high structural diversity) in 12 experimental plots ranging in size from 77 to 144 ha 10 years following prescribed burns (*B*), California (From Fettig and McKelvey 2014)

Treatment	Dbh Class	*Dendroctonus brevicomis*	*Dendroctonus ponderosae*	*Dendroctonus jeffreyi*	*Ips* spp.	*Scolytus ventralis*	Total
HiD + B	24.1	190	448	7	129	1354	2128
	34.3	198	227	11	28	537	1001
	44.5	102	59	2	1	157	321
	54.7	66	10	2	2	27	107
	>59.7	250	28	2	1	14	295
	All	806	772	24	161	2089	3852
HiD	24.1	119	450	1	2	1071	1643
	34.3	89	175	1	0	626	891
	44.5	33	37	2	0	200	272
	54.7	27	10	0	0	29	66
	>59.7	100	13	0	0	17	130
	All	368	685	4	2	1943	3002
LoD + B	24.1	65	221	5	252	1151	1694
	34.3	86	104	3	60	549	802
	44.5	18	13	1	2	66	100
	54.7	0	4	0	0	*	4
	>59.7	*	*	0	*	0	0
	All	169	342	9	314	1766	2600
LoD	24.1	12	68	4	6	586	676
	34.3	27	30	1	1	381	440
	44.5	11	3	0	0	67	81
	54.7	1	0	0	0	*	1
	>59.7	0	2	0	0	1	3
	All	51	103	5	7	1035	1201
Total		1394	1902	42	484	6833	10,655

Asterisks denote the host was not present

factors (Furniss and Carolin 1977). Several hosts are colonized in Mediterranean forests of California, including coast redwood, *Sequoia sempervirens* (D. Don) Endl., giant sequoia, *Sequoiadendron giganteum* (Lindl.) J. Buchh., incense cedar, *Calocedrus decurrens* (Torr.) Florin, and Monterey cypress, *Cupressus macrocarpa* Hartw. While generally not considered an important cause of tree mortality, severe droughts in the Sierra Nevada during the 1980s and then again in the early 2000s resulted in significant branch flagging and some tree mortality attributed to the western cedar bark beetle, *Ph. punctatus* LeConte (USDA Forest Service 2003). In addition, some *Phloeosinus* spp. vector the fungus *Seiridium cardinal* (Wag.), which may result in cypress canker, a disease that is of increasing importance worldwide (Graniti 1998). Management strategies are rarely implemented for these species.

18.2.10 ood Borers

In Mediterranean forests of California, two wood-boring species, the California flatheaded borer, *Phaenops californica* (Van Dyke), and flatheaded fir borer, *Phaenops drummondi* (Kirby) (Coleoptera: Buprestidae), occasionally cause noticeable levels of tree mortality. *Phaenops californica* is native to western North America (Lyon 1970), but perhaps exerts its greatest impact in California where it colonizes *P. ponderosa* and *P. jeffreyi* in addition to other *Pinus*. Typically, stressed, dead or dying trees are colonized (Fig. 18.16). However, *Ph. californica* may colonize and kill apparently-healthy trees, and repeated attacks may facilitate those of more aggressive species, such as *D. brevicomis* or *I. pini*. The life cycle is quite variable, and

Fig. 18.16 In many cases, bark beetles serve as keystone species facilitating colonization of trees by other organisms. For example, Stephen and Dahlsten (1976) collected >100 species of insects on the bark surface of *Pinus ponderosa* shortly after being colonized by *Dendroctonus brevicomis*. In particular, wood borers help facilitate decomposition and nutrient cycling (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

may take from several months to several years to complete (Lyon 1970). *Phaenops drummondi* has a transcontinental distribution and colonizes a wide variety of hosts in Pinaceae. However, its impact is most significant in the western U.S. where it readily colonizes *A. concolor* and is often a common associate of *S. ventralis*. There is one generation per year (Furniss and Carolin 1977). Management strategies are rarely implemented for either species.

While wood borers may not be considered an important source of tree mortality overall, Fettig et al. (2008a) reported that wood borers were directly contributing to tree mortality in fire-injured *P. ponderosa* during the second year following prescribed fires in California, but similar effects were not observed in related studies (e.g., Fettig et al. 2010a, b). Lumber degrade and introduction of wood decay fungi may be of concern if salvage is planned. Some wood borers (e.g., *Monochamus* spp., Coleoptera: Cerambycidae) are vectors of a wilting disease caused by pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickel (Linit 1988). Infection affects water transport in susceptible (non-native) *Pinus*, often rapidly resulting in tree death.

18.3 Conclusions

In the Mediterranean forests of California, most (>90 %) bark beetle and wood borer species are beneficial while several others are capable of occasionally causing undesirable levels of tree mortality (Table 18.1). However, this mortality is essential to the proper functioning of these ecosystems and influences ecological succession, community structure, nutrient cycling, and habitat creation (Franklin et al. 1987). For example, snags created by the activity of bark beetles and wood borers provide critical habitat for insects and many other species of wildlife (Fig. 18.16), including amphibians, reptiles, birds and mammals (Bull et al. 1997). Furthermore, while infestations of some species may affect timber and fiber production, and indirectly a wide range of ecosystem goods and services, the mortality of individual or small groups of trees provides fine-scale spatial heterogeneity in composition and structure thereby increasing forest resilience and resistance to a multitude of disturbances (Fettig 2012). This differs from the negative impacts associated with large-scale infestations or outbreaks that homogenize the landscape and may merit intervention.

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