Chapter 6: Insects

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Introduction

Insects are essential components of forest ecosystems, representing most of the biological diversity and affecting virtually all ecological processes (Schowalter 1994). Most species are beneficial (Coulson and Witter 1984, Haack and Byler 1993), yet others periodically become so abundant that they threaten ecological, economic, social or aesthetic values at local to regional scales (tables 6.1 through 6.3). Insects influence forest ecosystem structure and function in complex and dynamic ways, for example, by regulating certain aspects of primary production; nutrient cycling; ecological succession; and the size, distribution and abundance of plants and other animals (Mattson 1977, Mattson and Addy 1975). Effects on forest vegetation range from being undetectable, to short-term reductions in crown cover, to modest increases in background levels of tree mortality, to extensive amounts of tree mortality observed at regional scales.

Table 6.1—Bark beetles regarded as primary disturbance agents in western coniferous forests

Common name	Scientific name	Common host(s)
California fivespined ips	*Ips paraconfusus*	*Pinus contorta, P. lambertiana, P. ponderosa*
Douglas-fir beetle	*Dendroctonus pseudotsugae*	*Pseudotsuga menziesii*
Fir engraver	*Scolytus ventralis*	*Abies concolor, A. grandis, A. magnifica*
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*
Mountain pine beetle	*Dendroctonus ponderosae*	*P. albicaulis, P. contorta, P. flexilis, P. lambertiana, P. monticola, P. ponderosa*
Northern spruce engraver	*Ips perturbatus*	*Picea glauca, Pi. × lutzii*
Pine engraver	*Ips pini*	*P. contorta, P. jeffreyi, P. lambertiana, P. ponderosa*
Pinyon ips	*Ips confusus*	*P. edulis, P. monophylla*
Spruce beetle	*Dendroctonus rufipennis*	*Pi. engelmannii, Pi. glauca, Pi. × lutzii*
Western balsam bark beetle	*Dryocoetes confusus*	*A. lasiocarpa*
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri, P. ponderosa*

Note: all insect species listed above are native to western North America.

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Interactions With Other Disturbances

Forest insects are directly and indirectly influenced by other biotic (e.g., forest insects and diseases), abiotic (e.g., weather, wildfires, avalanches and windstorms), and anthropogenic (e.g., management activities and land use patterns) disturbances; other disturbances are often influenced by forest insects. As an example, consider bark beetles and wildfire, the principal drivers of change in western coniferous forests. Bark beetles alter forest fuels by killing varying numbers of trees of specific age classes, size classes, and species with consequences to the frequency, intensity, and severity of subsequent wildfires (Jenkins et al. 2014a). Conversely, sublethal heating of critical tree tissues by low- to moderate-intensity wildfires predispose trees to successful colonization by bark beetles because of weakening of their defensive mechanisms (Parker et al. 2006). This, in turn, may cause localized increases in bark beetle populations that lead to additional levels of tree mortality, with feedback loops that further influence fire risk and severity (Jenkins et al. 2014a). Furthermore, some bark beetle epidemics have been so severe that they have converted forests from carbon sinks to carbon sources, further contributing to climate change (Kurz et al. 2008). Climate change and fire suppression activities, among other factors, have resulted in substantial changes in forest conditions over millions of hectares in the Western United States, expressed primarily as increases in the density of shade-tolerant and fire-intolerant trees (e.g., true firs, *Abies* spp.) (Stine et al. 2014), further exacerbating both disturbances (Fettig et al. 2007, 2013; Westerling et al. 2006). These interactions have sparked concerns about the sustainability of some western forests to maintain the numerous ecological goods and services on which human societies have come to rely (Morris et al. 2017, 2018), and have motivated increases in the pace and scale of treatments designed to increase forest resilience to these disturbances (Stephens et al. 2018).

Current and Projected Trends in the Activity and Impacts of Forest Insects

In the following sections, we review the ecology, recent impacts (2000–2016), and projected future impacts (based on the "2013–2027 National Insect and Disease Forest Risk Assessment") of forest insects. We limit discussion to what we consider the 22 most prominent species in the Western United States in three feeding guilds (tables 6.1 through 6.3) based on their impacts to forest structure and composition. Most are native to western North America, with a few notable exceptions (tables 6.2 and 6.3).

This chapter reviews the ecology and impacts of 22 prominent insect species in the Western United States.

Table 6.2—Defoliating insects regarded as primary disturbance agents in western coniferous forests

Common name	Scientific name	Common host(s)
Douglas-fir tussock moth	*Orgyia pseudotsugata*	*Pseudotsuga menziesii, Abies* spp., *Picea* spp.
Forest tent caterpillar	*Malacosoma disstria*	*Populus tremuloides,* other hardwoods
Larch casebearer	*Coleophora laricella*	*Larix occidentalis*
Pandora moth	*Coloradia pandora*	*Pinus contorta, P. ponderosa*
Pine butterfly	*Neophasia menapia*	*P. ponderosa*
Pine sawflies	*Neodipridon* spp., *Zadiprion* spp.	*P. ponderosa, P. contorta*
Western hemlock looper	*Lambdina fiscellaria lugubrosa*	*Tsuga heterophylla, Abies balsamea, Picea* spp.
Western spruce budworm	*Choristoneura freemani*	*Ps. menziesii, Abies* spp., *Picea* spp.
Western tent caterpillar	*Malacosoma californicum*	*Po. tremuloides,* other hardwoods

Note: *Malacosoma* spp. also occur in deciduous forests and shrublands. All insect species listed above are native to western North America except larch casebearer.

Table 6.3—Sap-feeding insects regarded as primary disturbance agents in western coniferous forests

Common name	Scientific name	Common hosts
Balsam woolly adelgid	*Adelges piceae*	*Abies* spp.
Spruce aphid	*Elatobium abietinum*	*Picea engelmanni, Pi. sitchensis*

Note: both species are invasive to western North America.

Bark Beetles

Trees of all species, ages, and size classes may be colonized and killed by bark beetles, with the greatest impacts observed in conifers (table 6.1). Each bark beetle species exhibits unique host preferences, life history traits, and impacts. Some cause extensive levels of tree mortality as demonstrated by mountain pine beetle (*Dendroctonus ponderosae*) in several pines (most notably lodgepole pine (*Pinus contorta* var. *latifolia*) (fig. 6.1); western pine beetle (*Dendroctonus brevicomis*) in ponderosa pine (*Pinus ponderosa*); Douglas-fir beetle (*Dendroctonus pseudotsugae*) in Douglas-fir (*Pseudotsuga menziesii*); and spruce beetle (*Dendroctonus rufipennis* Kirby) in spruce (*Picea* spp.). Others, such as several species in the genus *Ips* (Wood 1982), are secondary agents that usually colonize stressed, dead, or dying trees.

Bark beetles often inflict density-dependent mortality (i.e., population growth rates and associated levels of tree mortality are partially regulated by the density of suitable hosts) (fig. 6.2), and help maintain a diversity of tree species, ages, sizes, and spatial heterogeneity (Fettig 2012). At endemic populations, bark beetles create small gaps in the forest canopy by killing trees stressed by age, drought, defoliation, or other factors. In this context, few negative impacts are observed

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Figure 6.1—The mountain pine beetle is the most significant forest insect in North America. Most large-scale epidemics occur in lodgepole pine forests in a nearly contiguous pattern across extensive areas. British Columbia, Canada, 2005.

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Figure 6.2—Thinning has long been advocated as a preventive measure to alleviate or reduce the amount of ponderosa pine mortality attributed to bark beetles, Shasta County, California, 2005. Among other factors, thinning reduces host density; 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.

(Morris et al. 2017). This differs from the impacts associated with epidemics, which may negatively affect 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 others (Morris et al. 2018). During the last three decades, the amount of tree mortality attributed to bark beetles in the Western States has exceeded that of wildfire (Hicke et al. 2016), and several recent epidemics are recognized as being among the most severe in recorded history (Bentz et al. 2009). Because bark beetles are highly sensitive to thermal conditions conducive to population survival and growth (Bentz et al. 2010), and drought stress negatively affects host tree vigor (Kolb et al. 2016), epidemics have been correlated with recent shifts in temperature and precipitation attributed to climate change. Forest densification has exacerbated the effect (Fettig et al. 2007).

The impact of wood borers, a related group, pales in comparison to that of bark beetles, but there are a few species, such as the California flatheaded borer (*Phaenops californica*), and flatheaded fir borer (*Phaenops drummondi*), that can cause noticeable levels of tree mortality in western coniferous forests (Furniss and Carolin 1977). Wood borers commonly infest trees stressed or killed by other agents and serve a very important ecological function by helping to facilitate wood decomposition and nutrient cycling (fig. 6.3), but given their minor role as primary disturbances will not be considered further.

Mountain pine beetle, *Dendroctonus ponderosae*—

Mountain pine beetle is regarded as the most significant forest insect in North America, and colonizes 15 tree species, primarily lodgepole pine, ponderosa pine, sugar pine (*P. lambertiana*), limber pine (*P. flexilis*), western white pine (*P. monticola*) and whitebark pine (*P. albicaulis*) (Negrón and Fettig 2014). The geographic distribution generally reflects the range of its primary hosts, although lodgepole pine extends farther to the north and ponderosa pine and other pines farther to the south than where mountain pine beetle populations currently exist (Bentz et al. 2010). Historically, the range of mountain pine beetle was restricted by climatic conditions unfavorable to brood development, but is expanding as a result of climate change and other factors. Populations were detected in Nebraska in 2009 (Costello and Schaupp 2011); in Alberta, Canada, in 2003 (Cudmore et al. 2010); and in the Northwest Territories, Canada, in 2012 (Natural Resources Canada 2013). Scientists have expressed a concern that mountain pine beetle could expand farther eastward across the boreal forest of Canada and into the Eastern United States (Safranyik et al. 2010). However, Bentz et al. (2010) described the probability of such a range expansion as low during this century.

The range of mountain pine beetle, regarded as the most significant forest insect in North America, is expanding.


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Figure 6.3—Bark beetles serve as keystone species that facilitate colonization of trees by other organisms. Of note, subsequent colonization by wood borers helps expedite decomposition and nutrient cycling. Lassen National Forest, California, 2005.

With few notable exceptions (Hopkins 1905), most large-scale epidemics occur in lodgepole pine forests. Mountain pine beetle initially colonizes the largest lodgepole pine in a stand (e.g., >23 cm diameter at breast height [d.b.h.]), which provides a higher reproductive potential and probability of beetle survival (Graf et al. 2012), with progressively smaller trees being colonized over time (Klein et al. 1978). In ponderosa pine, the small- to mid-diameter classes (e.g., 20 to 40 cm d.b.h.) tend to be colonized most frequently (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 is observed in lodgepole pine forests (Fettig et al. 2014). There is usually one generation per year (Bentz et al. 2014).

Since 2000, ~10.3 million ha have been affected by mountain pine beetle (fig. 6.4), which represents almost half of the total area affected by all bark beetles combined in the Western States. Activity began to increase substantially in 2004, peaked in 2009 when 3 578 591 ha were affected, and has declined since then (fig. 6.5). Despite this, mountain pine beetle is still ranked the most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~65.8 million m^2 of basal area occurring between 2013 and 2027 (fig. 6.6). Historically, mountain pine beetle epidemics were not usual, but the magnitude and extent of recent events may have exceeded the range of historic variability in some cases (Bentz et al. 2009), and have occurred at high elevations where they formerly were uncommon (see “Impacts to Sustainability”).

Western pine beetle, *Dendroctonus brevicomis*—
Western pine beetle is a significant cause of ponderosa pine mortality. The only other primary host in the West is Coulter pine (*P. coulteri*), a species indigenous to the Transverse and Peninsular Ranges of southern California (Miller and Keen 1960). Western pine beetle generally exhibits a preference for larger diameter (>50 cm d.b.h.) trees, but under certain conditions, such as extended drought, may colonize and kill trees of all ages and size classes (Fettig 2016). There are usually two to four generations per year.

Since 2000, there have been only 3 years when <40 469 ha were affected by western pine beetle. In response to a severe, prolonged drought, activity recently increased in 2014 and peaked in 2016 when 892 041 ha were affected (fig. 6.5), mostly in California (846 580 ha) (fig. 6.7). In some areas of the central and southern Sierra Nevada, tree mortality has exceeded 90 percent, and type conversions have been observed (Fettig et al. 2019), prompting California Governor Jerry Brown to declare a state of emergency over concerns about public health and safety. This event may foreshadow future impacts of western pine beetle as the intensity and duration of droughts, important inciting factors (Kolb et al. 2016), and the distribution of ponderosa pine are expected to increase in the future (Rehfeldt et al. 2006). Western pine beetle is ranked the eighth most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~15.4 million m^2 of basal area (fig. 6.6).

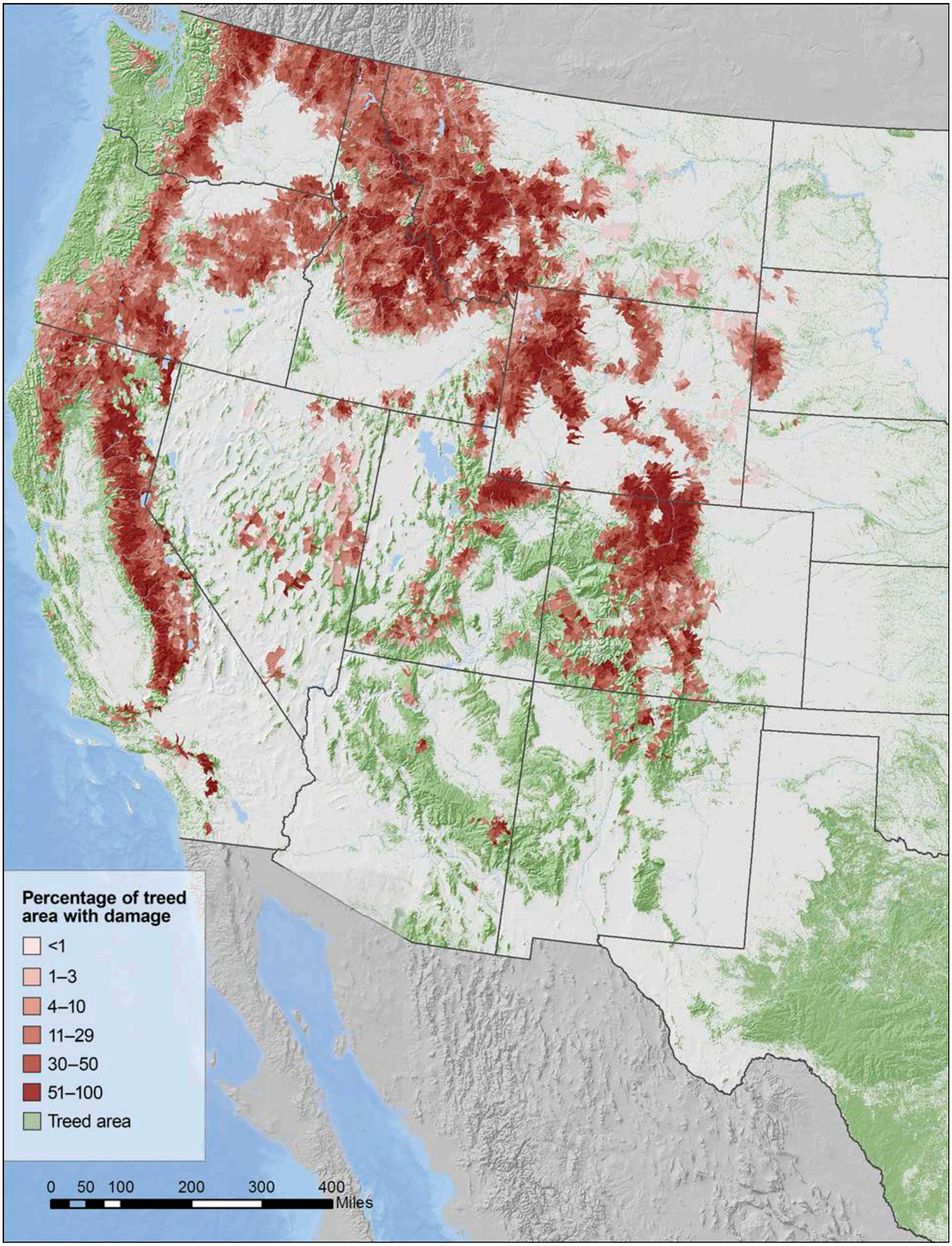

Figure 6.4—Area and severity of tree mortality attributed to mountain pine beetle, 2000–2016 (percentage of treed area by subwatersheds, 6th-level hydrologic unit codes). Data are from the U.S. Forest Service National Insect and Disease Survey database.

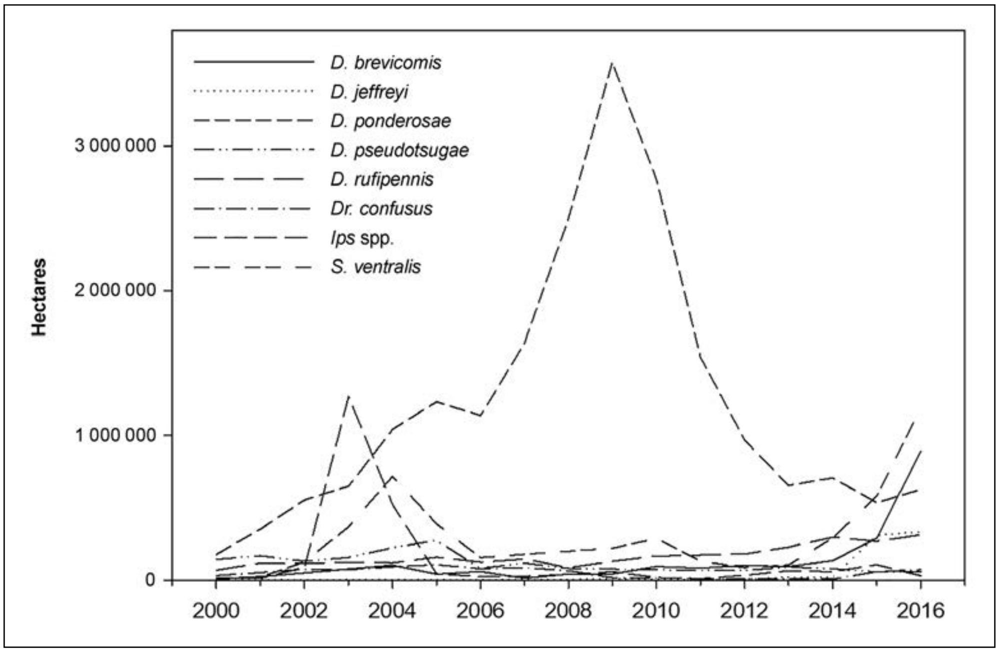

Figure 6.5—Area affected by year, 2000–2016. Values represent the impact observed each individual year and should not be summed across years (i.e., there may be overlap in areas affected from year to year). Data are from the U.S. Forest Service National Insect and Disease Survey database.

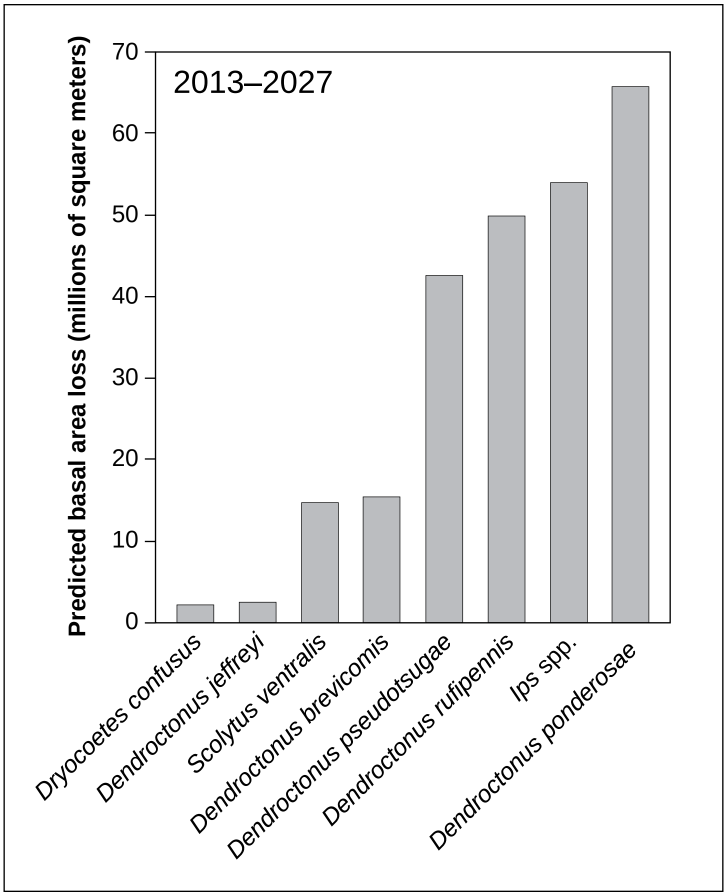

Figure 6.6—Projected losses, 2013–2027. *Ips* spp. including some species from the Eastern United States. Data are from the National Insect and Disease Forest Risk Assessment, 2013–2027 (Krist et al. 2014).

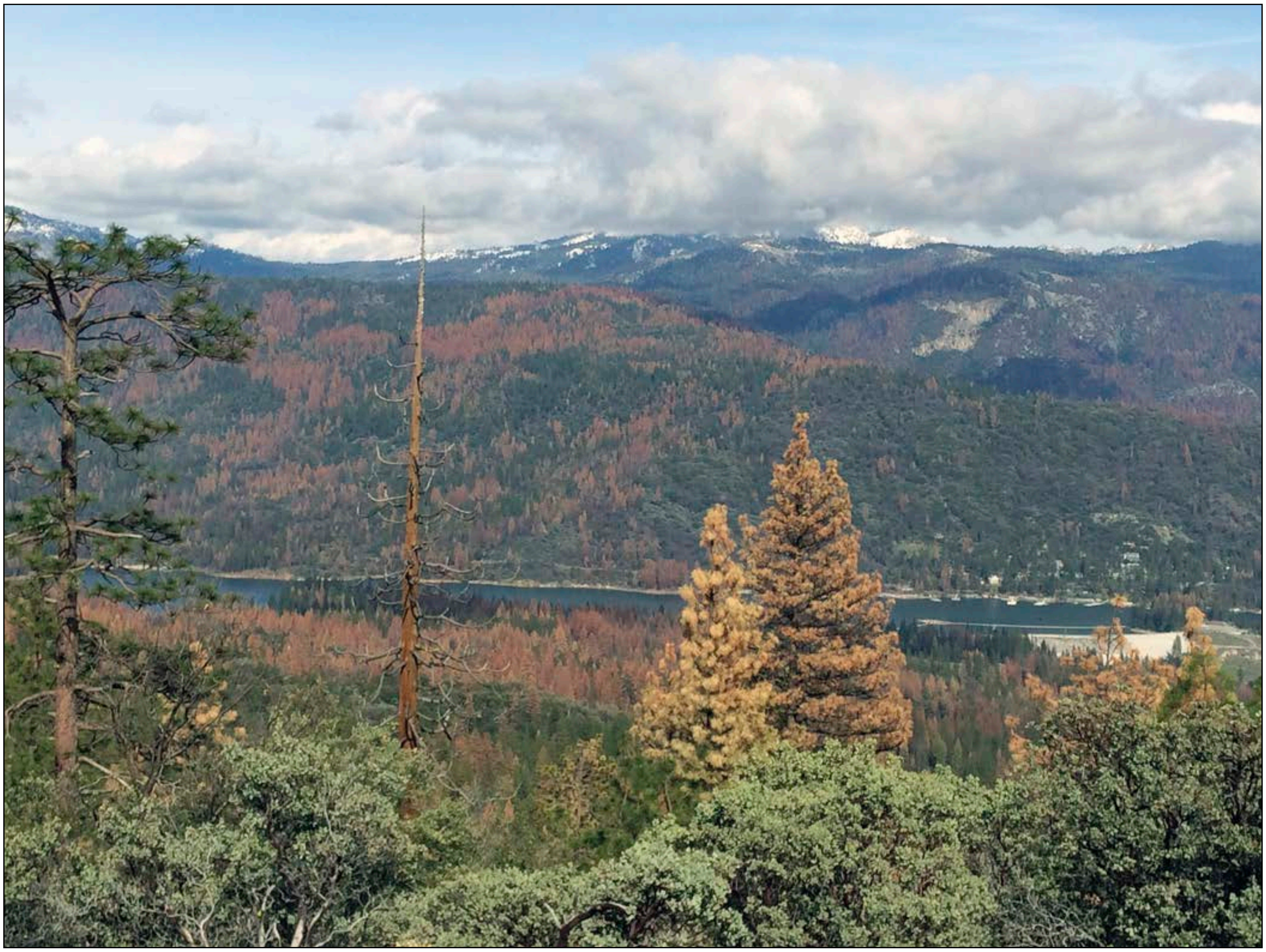

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Figure 6.7—Western pine beetle is a primary disturbance agent in ponderosa pine forests, Sierra National Forest. California, 2016. In 2016, 846 580 ha were affected by western pine beetle in California alone.

Jeffrey pine beetle, *Dendroctonus jeffreyi*—

Jeffrey pine beetle colonizes only Jeffrey pine (*P. jeffreyi*), a species that ranges from the Klamath Mountains in southwestern Oregon to throughout much of the Sierra Nevada and the Transverse and Peninsular Ranges in southern California, to the Sierra San Pedro Mártir in Baja California, Mexico. The species usually colonizes individual trees, and its activity often goes unnoticed, but during extended droughts large groups of trees may be killed (Fettig 2016). Although Jeffrey pine beetle is a significant source of disturbance in forests containing Jeffrey pine, the limited distribution and abundance of the host marginalizes the beetle's overall impact. There are one to two generations per year (Furniss and Carolin 1977). In most years, fewer than a few thousand hectares are affected (fig. 6.5), and consequently Jeffrey pine beetle is ranked the 15th most damaging forest insect in the

2013−2027 risk assessment (Krist et al. 2014), with a projected loss of ~2.6 million m^2 of basal area (fig. 6.6). Based on research focused on the Lake Tahoe Basin, California, Scheller et al. (2018) suggested that epidemics of Jeffrey pine beetle will increase in severity in the future.

Spruce beetle, *Dendroctonus rufipennis*—

Spruce beetle is the most significant mortality agent of mature spruce in the West and ranges throughout western North America, across the boreal forest of Canada, and into the Northeastern United States. Primary hosts include Engelmann spruce (*Picea engelmannii*) in the Intermountain West (fig. 6.8), and white spruce (*Pi. glauca*), Lutz spruce (*Pi.* × *lutzii*), Sitka spruce (*Pi. sitchensis*), and occasionally black spruce (*Pi. mariana*) in Alaska. Disturbances that produce an abundance of downed spruce, including timber harvests, blowdowns, landslides, and snow avalanches, have been implicated in the occurrence of most epidemics (Jenkins et al. 2014b). There are 0.3 to 1 generations per year (Furniss and Carolin 1977).

William M. Ciesla

Figure 6-8—Spruce beetle is the most significant mortality agent of mature spruce in the Western United States. Bridger-Teton National Forest, Wyoming, 2016.

Spruce beetle is the most significant mortality agent of mature spruce in western North America.

During the 1990s, a spruce beetle outbreak occurred on the Kenai Peninsula in south-central Alaska of a magnitude that had not been experienced in recorded history in North America for any bark beetle (Werner 1996), only to be surpassed by mountain pine beetle (fig. 6.5). At the peak, >485 000 ha were affected in a single year. In more recent years, activity increased in 2013 and peaked in 2016, when 313 260 ha were affected (fig. 6.5), mostly in Colorado (141 122 ha), south-central Alaska (76 096 ha), and Utah (50 292 ha). At the time of this writing, spruce beetle populations are undergoing a dramatic increase in Alaska.

Spruce beetle is ranked the fourth most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~49.8 million m^2 of basal area (fig. 6.6). High summer temperatures are correlated with an increase in the proportion of spruce beetle that complete a generation in a single year (Hansen and Bentz 2003), contributing to population growth and observed levels of tree mortality in some populations (Bentz et al. 2010, Berg et al. 2006). Overall, models suggest that future epidemics will be favored by increasing temperatures (Bentz et al. 2010), but projected reductions in the range of Engelmann spruce in the Intermountain West (Rehfeldt et al. 2006) could result in reduced impacts in that region.

Douglas-fir beetle, *Dendroctonus pseudotsugae*—
Douglas-fir beetle is the most important biotic disturbance affecting Douglas-fir forests in the Rocky Mountains (fig. 6.9). Occasionally western larch (*Larix occidentalis*) is colonized. When populations are at endemic levels, Douglas-fir beetle colonizes recently killed trees or trees weakened by defoliation, root disease, ice, fire, or wind. Under normal environmental conditions, small groups of trees are killed, but when large numbers of stressed trees occur, populations may increase in these trees and spread to adjacent healthy trees (Furniss et al. 1979, Furniss and Kegley 2014). The coastal Douglas-fir region, ranging from northern California to British Columbia, has sporadic epidemics of short duration that usually develop following extensive windthrow or large fires. There is one generation per year (Furniss and Carolin 1977). In most years, 80 000 to 100 000 ha are affected (fig. 6.5). In recent years, activity peaked in 2005 when 273 826 ha were affected (fig. 6.5). Douglas-fir beetle is ranked the fifth most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~42.5 million m^2 of basal area (fig. 6.6).

Western balsam bark beetle, *Dryocoetes confusus*—
Western balsam bark beetle is a significant source of disturbance in spruce-fir forests. Its range extends from British Columbia and Alberta south to Arizona and New Mexico (Wood 1982). This species primarily colonizes subalpine fir


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Figure 6.9—Douglas-fir beetle is a primary disturbance agent in Douglas-fir forests in the Western United States. Boise National Forest, Idaho, 2017.

(*Abies lasiocarpa*), although Pacific silver fir (*A. amabilis*), white fir (*A. concolor*), and Engelmann spruce are also hosts (Bright 1963). Western balsam bark beetle preferentially colonizes trees of reduced vigor, and blowdowns appear important in inciting epidemics (McMillin et al. 2003). There is 0.5 generation per year (Negrón and Popp 2009). Activity peaked in 2004 when 105 771 ha were affected (fig. 6.5), primarily in Montana (66 908 ha). Western balsam bark beetle is ranked the 18th most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~2.1 million m^2 of basal area (fig. 6.6).

Fir engraver, *Scolytus ventralis*—

Fir engraver colonizes true firs, particularly white fir. Trees of all sizes may be colonized and killed, but epidemics are typically associated with trees stressed by drought, defoliation (e.g., by Douglas-fir tussock moth (*Orgyia pseudotsugata*), root pathogens, or other factors (Berryman and Ferrell 1988, Ferrell et al. 1994). Large numbers of trees may be killed by fir engraver following prescribed fire (Fettig and McKelvey 2014). There is one generation per year throughout much of the range (Furniss and Carolin 1977). As was observed for western pine beetle, fir engraver activity increased in 2014 in response to a prolonged, severe drought, and peaked in 2016 when 1 186 737 ha were affected (fig. 6.5). Most of this activity occurred in

California (1 070 920 ha) (Fettig et al. 2019). Fir engraver is ranked the ninth most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~14.8 million m^2 of basal area (fig. 6.6).

Engraver beetles, *Ips* spp.—

There are about 25 species of *Ips* in the Western United States (Furniss and Carolin 1977). In most years, fewer than 40 000 ha are affected, but activity peaked in 2003 when 1 271 139 ha were affected in the West (by all *Ips* species) (fig. 6.5) owing largely to pinyon ips (*I. confusus*) in the Southwest. Collectively, *Ips* spp. are ranked the third most damaging forest insect(s) in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~53.9 million m^2 of basal area (fig. 6.6). However, this figure also includes contributions of several species from the Eastern United States.

In the Western States, most notable is the pine engraver (*I. pini*), which has a transcontinental distribution and is one of the most common bark beetles in North America (Kegley et al. 1997). Like most *Ips*, this species usually infests slash, saplings, and weakened trees (table 6.1). Top killing of ponderosa pine is common, and often facilitates colonization by western pine beetle or mountain pine beetle. Colonization rates are negatively correlated with tree diameter in ponderosa pine (Kolb et al. 2006), and trees 5 to 20 cm d.b.h. are most frequently colonized. Infestations of pine engraver are often short lived but may increase in scale and duration when suitable host material is plentiful and populations grow to sufficient numbers to kill apparently healthy trees. There are one to two generations per year (Furniss and Carolin 1977).

The distribution of the northern spruce engraver (*I. perturbatus*), generally coincides with that of its primary host, white spruce. Other hosts include Engelmann spruce, Lutz spruce, and black spruce. Although populations have been recorded in Idaho, Maine, Michigan, Minnesota, Montana, Washington, and nearly all the Canadian provinces, northern spruce engraver exerts its greatest impacts in Alaska (Burnside et al. 2011). In most years, endemic populations infest forest debris, widely scattered individual trees, or small groups of trees. However, natural (e.g., flooding, wildfire, and windstorms) and anthropogenic (e.g., road building, construction of utility rights-of-way, and logging) disturbances may produce large quantities of stressed, dead, and dying spruce that serve as ideal hosts for northern spruce engraver. Spring drought conditions led to epidemics on the Kenai Peninsula in the 1990s (Holsten 1998). Increased use of mechanical fuel reduction treatments and low-cost wood energy systems, and elevated summer temperatures, have been implicated in epidemics in Interior Alaska (Fettig et al. 2013a). Furthermore, the mean temperature in interior Alaska is projected to increase an additional 3 to 7 °C by the end of this century (Walsh et al. 2008) with only modest increases in precipitation that likely will be insufficient to offset increases in evapotranspiration. As a result, levels of drought stress in white spruce are expected to increase (Wolken et al. 2011) enhancing conditions favorable to northern spruce engraver. There is one generation per year (Burnside et al. 2011).

California fivespined ips (*I. 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) (fig. 6.10). Recently, populations were recorded in Washington (Murray et al. 2013). All pines occurring within the range

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Figure 6.10—Like most *Ips* spp., California fivespined ips readily colonizes logging slash where populations may rapidly increase and then emerge to colonize adjacent trees. Tahoe National Forest, California, 2004.

of California fivespined ips are susceptible to colonization, especially ponderosa pine. Like other *Ips*, endemic populations infest forest debris, widely scattered individual trees or small groups of trees. Occasionally, epidemics result in mortality of large numbers of trees but are usually associated with improper slash management or drought. California fivespined ips is also a vector of the fungus *Fusarium circinatum*, which causes pitch canker disease in Monterey pine (*P. radiata*) in California and other pines worldwide (Wingfield et al. 2008). There are two to five generations per year (Furniss and Carolin 1977). In most years, a few thousand hectares are affected. Activity peaked in 2008, when 24 130 ha were affected.

Pinyon ips (*I. confusus*) is a major cause of mortality in pinyon pine (*P. edulis* and *P. monophylla*) (Furniss and Carolin 1977). Epidemics frequently occur in the Great Basin and Southwestern United States and are usually associated with forest densification and drought (Kleinman et al. 2012, Negrón and Wilson 2003, Shaw et al. 2005). There are two to four generations per year (Furniss and Carolin 1977). In most years, fewer than 20 235 ha are affected, but activity peaked in 2003 when 1 188 785 ha were affected. These numbers likely under report the amount of activity as aerial detection surveys typically do not cover most of the pinyon-juniper woodlands.

Defoliators

Forest defoliators consume, mine, or skeletonize the foliage of trees, but their impacts pale in comparison to bark beetles. In most cases, eggs are laid on the buds, foliage, branches or boles of trees. Larval feeding may result in tree mortality depending on the timing, frequency, and extent of feeding (table 6.2). Most frequently defoliation retards growth, decreases tree vigor, and increases the amount of light reaching the forest floor, influencing understory and mid-story dynamics. Trees of all species, ages, and size classes may be defoliated, but each defoliator exhibits unique host preferences, life history traits, and impacts. Only two species, western spruce budworm (*Choristoneura freemani*) (also *C. occidentalis*) (see Gilligan and Brown 2014) and Douglas-fir tussock moth cause extensive levels of tree mortality. Predators and parasitoids have a strong regulatory effect on their populations, resulting in long time lags between epidemics.

Unlike the case of bark beetles, there appear to be few consistent trends among factors that incite forest defoliators. The cyclic nature of epidemics has prompted the formulation of a number of hypotheses that attempt to explain associated mechanisms, including genetic variation, qualitative variation, climatic release, food (host) quality deterioration or improvement, and diseases (parasitoids and pathogens), among others (Berryman 1996, Myers 1988). Drought has been implicated as an inciting factor (Mattson and Haack 1987), but a recent synthesis concluded that defoliators exhibit no consistent response to drought (Kolb et al. 2016). The projected future impacts of some notable species (e.g., pine butterfly [*Neophasia menapia*]) were not considered in the 2013–2027 risk assessment (Krist et al. 2014), and thus are absent in the discussion below.

Western spruce budworm, *Choristoneura freemani*—
Western spruce budworm is the most important defoliator in western North America (Brookes et al. 1987) (fig. 6.11). The species feeds on Douglas-fir, true firs, and occasionally spruce and western larch (Furniss and Carolin 1977). Its geographic range coincides with these hosts from British Columbia and Alberta south to Arizona and New Mexico and east to Colorado. Budworm populations erupt episodically over large regions. Defoliation continues for several years to more than a decade, then the insect becomes relatively rare for years to decades (Swetnam and Lynch 1993). This synchrony seems to be associated with favorable weather conditions, warm dry summers in conjunction with synchrony of larval emergence and bud flush, and the influences of natural enemies (Peltonen et al. 2002, Thomson et al. 2012). In mature stands, the most common impact is reduced growth, although repeated defoliation sometimes results in top kill and tree mortality. Severely defoliated trees are often colonized and killed by Douglas-fir beetle and fir engraver.

Outbreaks of western spruce budworm, the most important defoliator in western North America, are episodic.

L. Spiegel, USDA Forest Service Forest Health Protection

Figure 6.11—Western spruce budworm larvae are important defoliators of true firs and Douglas-fir.

Larvae also feed on staminate flowers and developing cones affecting regeneration. There is one generation per year (Furniss and Carolin 1977).

In recent years, western spruce budworm activity peaked in 2009 when 2 066 266 ha were affected (fig. 6.12), mostly in Idaho and Montana. The impact of western spruce budworm may be increasing in some areas (e.g., eastern Oregon) because of extensive logging of ponderosa pine, which favors Douglas-fir (Swetnam et al. 1995). Other research suggests that the duration and intensity of epidemics in western Montana have increased as a result of a decrease in the frequency of wildfires attributed to fire suppression efforts, causing increased host species abundance and multistoried stands (Anderson et al. 1987). Epidemics have also been linked to drought or synchrony of larval development with foliage phenology (Campbell et al. 2006, Williams and Liebhold 1995), although other studies have found that epidemics were associated with wetter conditions at the end of droughts that increase food

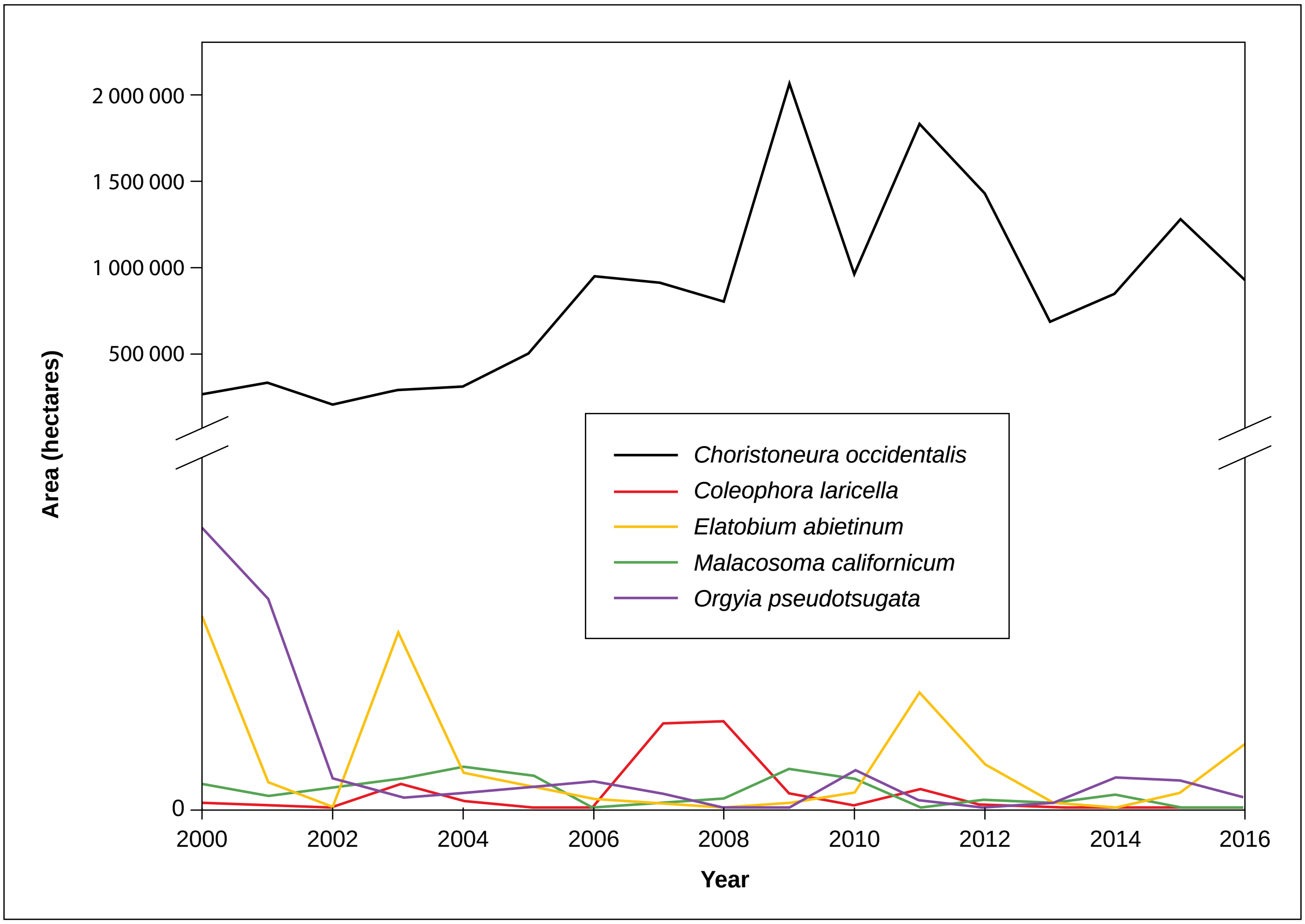

Figure 6.12—Area affected by year, 2000–2016. Values represent the impact observed each individual year and should not be summed across years (i.e., there may be overlap in areas affected from year to year). Data are from the USDA Forest Service National Insect and Disease Survey database. Several other species discussed in the text are not included owing to incomplete data.

resources (Flower et al. 2014, Ryerson et al. 2003, Swetnam and Lynch 1993). Western spruce budworm is ranked the 11th most damaging forest insect, second among native defoliators to eastern spruce budworm (*C. fumiferana*) in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~10.8 million m^2 of basal area. As observed for some bark beetles, western spruce budworm epidemics may increase fire risk and severity in affected stands (Hummel and Agee 2003, Ryerson et al. 2003, Schowalter 1986).

Douglas-fir tussock moth, *Orgyia pseudotsugata*—

Douglas-fir tussock moth is an important defoliator of true firs and Douglas-fir (fig. 6.13). The species consumes the foliage of several tree species (table 6.2), but only Douglas-fir, white fir, and grand fir (*A. grandis*) are considered primary hosts (Brooks et al. 1978). Epidemics develop quickly and then subside usually in 1 to 2 years, but some have persisted for longer periods (Schaupp et al. 2008). Defoliation by Douglas-fir tussock moth kills or top kills many trees, making them more susceptible to colonization by Douglas-fir beetle and fir engraver. There is one generation per year (Furniss and Carolin 1977).

T. Coleman, USDA Forest Service Forest Health Protection

Figure 6.13—Douglas-fir tussock moth is an important defoliator of true firs and Douglas-fir. Santa Fe National Forest, New Mexico, 2016.

Activity peaked in 2000 when 116 000 ha were affected (fig. 6.12), primarily in Idaho, Oregon, and Washington. Since 2001, the amount of defoliation attributed to Douglas-fir tussock moth has declined substantially, with the exception of 2011 and 2012 when 47 600 and 19 270 ha were affected, respectively. Historically, epidemics of Douglas-fir tussock moth in California were limited to the Sierra Nevada. However, an epidemic occurred in the Transverse Mountain Ranges of southern California in 2009 that was primarily attributed to fire suppression efforts resulting in significant increases in the density and continuity of white fir (Coleman et al. 2014). As a result, the potential for elevated impacts in southern California is of concern. Douglas-fir tussock moth is ranked the 16th most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~2.6 million m^2 of basal area.

Pine butterfly, *Neophasia menapia*—

Pine butterfly is a periodic defoliator of ponderosa pine in the Pacific Northwest (fig. 6.14) and Rocky Mountains, although Douglas-fir, western white pine, and lodgepole pine may also be colonized (Keen 1952). In most years, a few adults can be seen fluttering around the tops of pines in late summer and early fall, but evidence of defoliation from larval feeding is absent or inconspicuous. Repeated defoliation can reduce tree growth, making trees more susceptible to other disturbances, such as western pine beetle. Occasionally, severe (>75 percent) defoliation may result in tree mortality. There is one generation per year (Furniss and Carolin 1977). Historically, epidemics have been recorded in British Columbia, Idaho, Montana, Oregon, and Washington (Bousfield and Meyer 1972, Evenden 1926, Keen 1952). In recent years, activity peaked in 2011 when 101 343 ha were affected, mostly in Oregon.

Larch casebearer, *Coleophora laricella*—

Larch casebearer is native to Europe (Jagsch 1973), but was introduced into North America, likely on nursery stock. The species was first detected in Northampton, Massachusetts, in 1896, in Ottawa, Canada, in 1905 (Otvos and Quednau 1981), and in western North America near St. Maries, Idaho, in 1957 (Tunnock and Ryan 1983), and has since spread to Alberta, British Columbia, Montana, Oregon, and Washington. Larch casebearer feeds on the internal tissue of western larch needles, favoring younger trees growing in the open or along forest edges (Tunnock and Ryan 1983). Repeated defoliation can result in growth loss and tree mortality (Ryan et al. 1987). There is one generation per year (Furniss and Carolin 1977).

In eastern North America, larch casebearer was the subject of a very successful classical biological control program (i.e., the introduction of a natural enemy of

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Figure 6.14—Pine butterfly is a periodic defoliator of ponderosa pine in the Pacific Northwest and Intermountain West. Malheur National Forest, Oregon, 2010.

exotic origin to control an invasive species). As such, several nonnative parasitoids were released in the Western United States for control of larch casebearer starting in the 1960s (Ryan 1990). By the 1980s, two species, *Agathis pumila* and *Chrysocharis laricinellae*, were well established throughout the region, significantly reducing populations of larch casebearer (Ryan 1997). In recent years, activity peaked in 2008 when 36 130 ha were affected in the Western United States (fig. 6.12), but usually only 10 000 to 20 000 ha are affected annually.

Western hemlock looper, *Lambdina fiscellaria lugubrosa*—
Western hemlock looper colonizes western hemlock (*Tsuga heterophylla*). Epidemics usually occur in coastal and interior wet belt regions of the Pacific Northwest in mature hemlock and hemlock-cedar stands. During an epidemic, western hemlock looper will feed on other tree species (table 6.2), and some broad-leaved trees and shrubs (Jardine 1969). Populations periodically increase and persist for 1 to 2 years, resulting in the death of large numbers of trees over limited but well-defined areas. There is one generation per year. Of note, 7571 ha were affected in Idaho in 2011.

Pine sawflies, *Neodiprion* spp.—
Pine sawflies are common defoliating insects of pines, consisting of 16 species in the Western States (Ciesla and Smith 2011, Ross 1955). Sawflies normally occur at low densities (e.g., a few individuals per tree); however, on occasion some species become epidemic, causing defoliation on a vast scale for one or more years (Furniss and Carolin 1977). Most species exhibit a preference for open-grown trees. For example, a study in Arizona showed that defoliation by *Neodiprion autumnalis*, the most widely distributed species that feeds on ponderosa pine, was limited to stands with <4.6 m^2/ha of basal area (McMillin et al. 1996). There is one generation per year. Although good records are not available on the impact of sawflies in the West, most recent activity is reported from Arizona and Colorado.

Pandora moth, *Coloradia pandora*—
Pandora moth larvae feed on the foliage of several pines, primarily ponderosa, lodgepole, and Jeffrey pines throughout much of the West (Furniss and Carolin 1977). Epidemics usually occur in mature stands and cause extensive defoliation, leading to growth loss and tree mortality. When tree mortality occurs, it is often associated with prolonged drought, dwarf mistletoe infection, or colonization by bark beetles (Wagner and Mathiasen 1985). Some epidemics encompass large areas but occur only where soils are loose enough for larvae to bury themselves where they pupate. Based on observations of 20th-century epidemics and interviews with American Indians who use the larvae and pupae as food, epidemics typically recur every 20 to 30 years and last about 6 to 8 years (Furniss and Carolin 1977). However, Clark et al. (2017) reconstructed epidemics from a 1,572-year (435 to 2006) ponderosa pine chronology in central Oregon and reported that epidemics occurred on average every 104 years. Pandora moth has 0.5 generation per year, with feeding and moth flight occurring in alternate years so that most of the defoliation occurs every other year. Although good records are not available on the impact of pandora moth, most recent activity is reported from Arizona.

Forest tent caterpillar, *Malacosoma disstria*, and western tent caterpillar, *Malacosoma californicum*—

Forest tent caterpillar is found throughout the United States and Canada, where preferred hosts include numerous broad-leaved trees (Batzer and Morris 1978). This species often defoliates extensive areas during epidemics, resulting in severe (>75 percent) growth loss, but tree morality is generally rare. Interestingly, analyses of historical data (1950–1984) from northern Ontario, Canada, indicate that host abundance such as that of aspen (*Populus tremuloides*) has no effect on the duration of epidemics (Roland 1993). Instead, the duration of epidemics was best predicted by the amount of forest edge per unit area (Roland 1993). Because forest tent caterpillar populations are regulated largely by parasitoids and pathogens (Witter and Kulman 1979), this suggests that forest fragmentation negatively affects interactions between these natural enemies and forest tent caterpillar (Roland and Kaupp 1995). If so, increased fragmentation of forests in the Western United States may exacerbate future epidemics. There is one generation per year (Batzer and Morris 1978). Forest tent caterpillar is ranked the 14th most damaging forest insect in the 2013–2027 risk assessment (Krist et al. 2014), with a projected loss of ~2.7 million m^2 of basal area nationwide. Among Western States, activity peaked in 2004 when 4938 ha were affected in Utah.

Like forest tent caterpillar, western forest tent caterpillar colonizes a wide range of tree and shrub species, but aspen is preferred (Furniss and Carolin 1977). Successive years of defoliation causes reduced growth and fruit production, branch dieback, top kill, and in rare cases, tree mortality. In Colorado, entire aspen stands across large areas have been defoliated. During epidemics, western forest tent caterpillar may only be one of several disturbance agents (including other insect defoliators and leaf diseases) that cause widespread defoliation of aspen. There is one generation per year. In recent years, activity peaked in 2003 when 16 828 ha were affected (fig. 6.12), mostly in New Mexico.

Sap-Sucking Insects

Aphids and adelgids comprise a large group of small (usually <4 mm in length), soft-bodied insects that are frequently found sucking sap from leaves and stems of plants. Most overwinter as eggs, which hatch in spring into females that reproduce parthenogenetically (asexually) and birth live young. This unique reproductive trait results in rapid changes in population densities over time (Minks and Harrewijn 1987). Sap-feeding insects are particularly susceptible to desiccation in drier climates. More mesic habitats are found to support higher populations (Progar and

Schowalter 2002), which are usually kept in check by numerous natural enemies and abiotic factors. Generally, feeding is manifested as needle stunting, needle chlorosis, and stem deformation. Several aphid species are also regarded as vectors of notable plant viruses (Minks and Harrewijn 1987). Aphids often go unnoticed in forests because of their small size and cryptic behavior. Adelgids are important pests of several conifers and are closely related to aphids (Havill and Foottit 2007).

Balsam woolly adelgid, *Adelges piceae*—
Balsam woolly adelgid is a nonnative, invasive insect that threatens true fir species throughout North America. The species was introduced into eastern North America from Europe before 1900 (Foottit and Mackauer 1980), and subsequently near San Francisco, California, in 1928 (Ragenovich and Mitchell 2006). In the Western States, it is now well established in Oregon and Washington, but continues to move eastward through Idaho and into Montana, threatening subalpine fir (fig. 6.15). A similar trend is observed in British Columbia (Zilahi-Balogh et al. 2016). In 2017, balsam woolly adelgid was detected for the first time in Utah, and now populations have been confirmed in several counties within the state (Alston et al. 2018). Hrinkevich et al. (2016) developed a climatic risk model for balsam woolly adelgid, and reported

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Figure 6.15—Balsam woolly adelgid is a nonnative, invasive insect that threatens fir species throughout North America. Feeding causes swelling or gouting on new growth. Wallowa-Whitman National Forest, Oregon, 2012.

climatic susceptibility decreases from the Olympic Peninsula in Washington and the Cascade Range in Oregon and Washington eastward, with the exception of some high-risk areas in northern Idaho and western Montana. There is also a pattern of decreasing climatic suitability from north to south in the Rocky Mountains.

In response to feeding by balsam woolly adelgid, the host produces a type of compression wood in the sapwood that inhibits waterflow within the tree, eventually leading to tree death. There are usually two generations per year (McMullen and Skovsgaard 1972). Balsam woolly adelgid is ranked the 10th most damaging forest insect, first among invasives in the Western United States in the 2013−2027 risk assessment (Krist et al. 2014), with a projected loss of ~11.3 million m^2 of basal area. In recent years, activity in the West peaked in 2010 when 79 757 ha were affected (fig. 6.12), mostly in Oregon. Balsam woolly adelgid is likely to become a more important disturbance agent in forests of Idaho, Montana, and Utah (Hrinkevich et al. 2016).

Spruce aphid, *Elatobium abietinum*—

Spruce aphid causes chlorosis, defoliation, and mortality of spruce (fig. 6.16) but has also been recorded infesting pine and Douglas-fir (Furniss and Carolin 1977). This insect, an exotic invasive from Europe, was first reported in British Columbia in 1916 (Carter and Halldórsson 1998), and has since spread throughout coastal British Columbia, southeast Alaska, Oregon, and Washington as well as several mountain ranges in Arizona and New Mexico (Lynch 2014). The highly dispersive nature of alates (winged individuals) allows populations to spread rapidly to the limits of its climatic tolerances (e.g., temperatures below -10 °C in maritime areas).

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Figure 6.16—Defoliation of Sitka spruce by spruce aphid in southeast Alaska, 2005.

High densities can lead to severe defoliation, but needle loss is generally restricted to 1-year-old and older needles in spring and summer. In the fall and winter, feeding occurs on current as well as older needles, and high populations at this time of year are capable of causing complete defoliation of the tree. Young trees that have been heavily defoliated during the winter often have terminal buds that fail to break the following spring (Carter 1977). Impacts are most significant in coastal southeast Alaska on Sitka spruce and in Arizona on Engelmann spruce. In 2003, 73 039 ha were affected (fig. 6.12), mostly in Arizona.

Host water stress is thought to positively influence sap-sucking insects through an increase in phloem nitrogen content (Kolb et al. 2016). Spruce aphid populations are higher when water stress is intermittent and lowest when water stress is continuous. Lynch (2003) reported that epidemics tend to occur after dry winter and spring conditions in high-elevation forests in Arizona, but do not seem to be influenced by the amount of moisture received during the summer monsoon. Given projected increases in temperature and the frequency of droughts in the West, spruce aphid will likely become a more significant disturbance agent.

Role of Management in Mitigating Impacts

Management to reduce the vulnerability of forests to insects has historically focused on suppression and prevention.

Several tactics are available to reduce the vulnerability of forests to insects, including those that help reduce atmospheric warming (through reductions in carbon dioxide and other greenhouse gas emissions), which increases drought stress and the probability that trees will succumb to colonization by insects (Kolb et al. 2016). Others facilitate transition of forest stands to tree species better adapted to future climates (Fettig et al. 2013b, Millar et al. 2007, Millar and Stephenson 2015). Historically, management has focused on suppression and prevention. Suppression involves short-term tactics designed to reduce current infestations by manipulating insect populations through the use of fire, pesticides (contact and systemic insecticides, microbials [bacteria, viruses, pathogens and nematodes]), insect growth regulators, soaps, and horticultural oils, semiochemicals (chemicals produced by one organism that elicits a response, usually behavioral, in another organisms, e.g., pheromones), sanitation harvests (harvesting currently infested material and destroying living life stages in that material before they emerge), or combinations of these treatments (Coulson and Witter 1984, Fettig and Hilszczański 2015). For suppression to be effective, accurate detection and survey methods are required to identify and delineate infestations prior to treatment. Prevention is designed to reduce the probability and severity of future infestations by manipulating forest conditions through thinning, prescribed burning, or alterations of age classes and species composition. There is considerable support for thinning of conifer forests to reduce the severity of bark beetle infestations (Fettig and Hilszczański 2015, Fettig et al. 2007, but see Six et al. 2014). In contrast, there is little consensus regarding the efficacy of thinning for reducing vulnerability to most forest defoliators (Muzika and Liebhold 2000). Given the diversity of ecologies and life histories displayed by forest insects, it should be no surprise that the application of many of these tactics must be tailored to specific insect-host associations (e.g., in regard to timing of treatments, use of specific semiochemicals, etc.).

When implementing prevention or suppression, there are opportunities for collaboration with other resource disciplines, allowing additional objectives to be met perhaps with little or no additional cost. For example, fuel reduction treatments are frequently applied in the Western States to reduce the quantity and continuity of forest fuels (Stephens et al. 2012). Although prescriptions generally differ between thinning implemented for fuels reduction and that for prevention of certain insects (e.g., bark beetles), there are opportunities to alter fuel reduction treatments without reducing their efficacy while increasing the effectiveness of these same treatments for reducing the vulnerability of forests to insects.

Impacts to Sustainability

The impacts of insects on forests extend beyond the levels of tree mortality caused and associated cascading ecological effects. For example, bark beetle epidemics may increase water yield yet diminish water quality because of pulses of concentrated nutrients and suspended sediment loads (Mikkelson et al. 2013), as well as degrade air quality by the release of volatile organic compounds and biogenic aerosols (Berg et al. 2013). Landscape aesthetics are important drivers of nature-based tourism and may be negatively affected (Morris et al. 2018). In the wildland-urban interface, concerns are often more practical and focused on property values, hazard trees, and fire risk (Cohen and other 2016). Interestingly, a notable western pine beetle outbreak in southern California affected how homes were advertised and sold (Fettig 2019).

Several recent assessments have concluded that western forests are increasingly vulnerable to mortality associated with the direct and indirect effects of climate change, and that substantial shifts in the geographic distributions of some tree species and forest ecosystems is likely (Fettig et al. 2013b, Williams et al. 2013). Rehfeldt et al. (2006) suggested that about 48 percent of the Western U.S. landscape is likely to experience climate profiles with no contemporary analog for the current coniferous vegetation by the end of this century. Projections show that distributions of grassland, chaparral, and montane forest are likely to increase at the expense of subalpine forest, tundra, and Great Basin woodland. Shifts are expected to be most

Several recent assessments have concluded that western forests are increasingly vulnerabile to mortality associated with the direct and indirect effects of climate change.

rapid along ecotones, particularly in semiarid landscapes (Allen and Breshears 1998). To that end, Krist et al. (2014) projected that most Western States have at least 10 percent of their forested landscapes at risk (defined as without remediation at least 25 percent of standing live basal area greater than 2.54 cm in diameter will be killed in the next 15 years) to forest insects and diseases epidemics. Most notable, in Idaho 28 percent of the forested landscape is considered at risk (Krist et al. 2014).

In the West, seven trees species are expected to suffer substantial levels of tree mortality in the near future, including whitebark pine (58 percent of total basal area), limber pine (44 percent), lodgepole pine (39 percent), ponderosa pine (28 percent), pinyon pine (27 percent), Jeffrey pine (26 percent), and grand fir (25 percent) (Krist et al. 2014). In particular, whitebark pine is of concern as it serves as a keystone species. Whitebark pine seed is a critical food source for birds, small mammals, and bears. Furthermore, the species quickly establishes after disturbance, and is important in maintaining snowpacks and reducing erosion of steep slopes. Significant levels of whitebark pine mortality have been attributed to mountain pine beetle (and its interactions with climate change and white pine blister rust), and the U.S. Fish and Wildlife Service first announced in 2011 that it determined whitebark pine to warrant protection under the Endangered Species Act, but that adding the species to the Federal List of Endangered and Threatened Wildlife and Plants was precluded by the need to address other listing actions of higher priority (Federal Register 2011). Some have questioned if the species can be saved (Neuenschwander et al. 1999).

Conclusions

Most forest insects are beneficial, but a few species periodically become so abundant that they threaten ecological, economic, social, or aesthetic values.

Most forest insects are beneficial (e.g., they help facilitate decomposition, nutrient cycling, and pollination), but a few species periodically become so abundant that they threaten ecological, economic, social, or aesthetic values. In the Western United States, chief among these are several species of bark beetles (table 6.1), most notably mountain pine beetle. Several defoliating and sap-sucking insects are also important (tables 6.2 and 6.3). These disturbance agents have interacted with others such as wildfire for millennia, shaping the structure and composition of forests over time. Unlike the Eastern United States, relatively few exotic insects are the source of important disturbance in western forests, but we expect an increase in their prevalence in the future owing to recent shifts in human populations and trade (Aukema et al. 2010, 2011), among other factors. Relatedly, the recent establishment of goldspotted oak borer (*Agrilus coxalis*) in California (Coleman and Seybold 2008) and emerald ash borer (*A. planipennis*) in Colorado (Berry et al. 2017) are cause for concern. The heterogeneity of western landscapes and the diversity of climates that occur in relatively small geographic areas (ranging from deserts to subarctic) do provide some buffer against invasion.

We expect that epidemics of the species described herein will occur with relatively predictable frequency and that basic host relationships will remain largely intact. However, with climate change, we expect the severity of most bark beetle epidemics to increase as long as susceptible hosts exist. Overall, the impact of climate change on defoliating and sap-sucking insects is less unclear. Finally, we agree with many experts who have argued to increase the pace and scale of treatments designed to increase forest resilience to insects and other disturbances exacerbated by climate change.

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