



# Fire and Insect Interactions in North American Forests

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## Abstract

**Purpose of Review** Fire and insects are major disturbances in North American forests. We reviewed literature on the effects of fire on bark beetles, defoliators, and pollinators, as well as on the effects of bark beetle and defoliator epidemics on fuels and wildfires.

**Recent Findings** Fire has direct and indirect effects on insects, but our understanding of these effects is confounded by several factors identified in this review. Direct effects are expressed through insect mortality due to exposure to fire, with few studies published on this topic. Indirect effects are expressed through changes in insect hosts and forest conditions, with bark beetle responses to fire-injured trees following prescribed fires and low-severity wildfires being the most studied. Although fire effects on pollinators are an emerging field of research, it is clear that fire can benefit pollinators by creating more open forest conditions, which, in turn, enhance floral resource availability. Bark beetle and defoliator epidemics can exert large effects on fuels, but their effects on wildfires are mixed. Differences in the severity, extent, and timing of epidemics, fire regimes, fire weather, topography, and the metrics and models used to assess wildfires, among other factors, confound our understanding of the effects of bark beetle and defoliator epidemics on wildfires.

**Summary** Fire has both positive and negative effects on insects. Bark beetle and defoliator epidemics have positive and negative effects on wildfires. Additional study of these relationships is warranted given the effects of climate change on forests and forest disturbances, recent declines in some pollinator species in North America, and interests in restoring fire-adapted forest ecosystems.

**Keywords** Bark beetles · Defoliators · Pollinators · Prescribed fire · Tree mortality · Wildfire

## Introduction

Fire is both a natural and anthropogenic disturbance affecting the distribution, structure, and function of forests. Patterns of wildfire and their effects on forests are governed by

complex interactions among climate, weather, fuels, vegetation, topography, and ignition patterns and frequencies [1, 2], which vary across North America. For example, wildfires in longleaf pine-bluestem, *Pinus palustris-Andropogon* spp., forests in the southeastern US are of low severity, with historic mean fire return intervals of < 5 years [3]. Similarly, wildfires in dry conifer forests in the southwestern US were historically of low severity and high frequency, occurring about every 8 years [4]. However, a century of livestock grazing, logging, and fire suppression and exclusion, among other factors, has led to less frequent and more severe wildfires in the southwestern US [5] and elsewhere [6, 7]. Wildfires in many other forest types in North America are less frequent. For example, wildfires in spruce-fir, *Picea-Abies*, forests in the Intermountain West, US are of high severity, with historic mean fire return intervals of ~ 150–350 years [8]. Beech-maple, *Fagus-Acer*, forests in the northeastern US and eastern Canada rarely burn, with historic mean fire return intervals of > 1000 years [9].

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As a result of climate change, the amount of forest burned by wildfires in the western US is increasing [10, 11] due to warming and associated increases in vapor pressure deficit and evapotranspiration [12] and decreases in precipitation [13]. Notably, the amount of area burned at high severity has also increased in the western US [14]. Similar trends are being observed or projected for other regions of North America (e.g., [15–17]). It is likely that climate change will make it more difficult to control future wildfires and to use prescribed fire [18–20]. Wildfires consume ~3 million hectares per year in the US (mean, 2012–2021) [21] and ~2.6 million hectares per year in Canada (mean, 2011–2020) [22].

Efforts to lower wildfire hazards have focused on reducing surface fuels, increasing the height to the base of live crowns, decreasing crown bulk density, and retaining large trees of fire-resistant species, such as pines [23]. Prescribed fire and its mechanical surrogates (thinning from below) are effective in meeting these goals [24–26]. For example, the effectiveness of prescribed fire for reducing the incidence of passive crown fire is well supported by modeling of predicted fire behaviors [27] and by empirical research [28]. Furthermore, results from the National (US) Fire and Fire Surrogate Study indicate that the incidence of active crown fire is best reduced by combinations of prescribed fire and mechanical fuel treatments [25]. In 2019, ~4 million hectares were treated with prescribed fire in the US, an increase of ~28% compared to 2011. Most prescribed fires occurred in the southeastern (59%) and western US (37%) [29]. There is a renewed interest in restoring fire-adapted forest ecosystems. For example, the USDA Forest Service just released a 10-year strategy that recognizes wildfire risks have reached “crisis proportions in the West.” Under this strategy, the USDA Forest Service will increase the application of fuel treatments [30•]. Recent wildfires in Canada have led to similar initiatives [31]. In addition to prescribed fire and thinning, practitioners are increasingly using managed wildfires (natural ignitions that are allowed to burn under certain conditions) to restore fire-adapted forest ecosystems [32–34].

Insects are important components of forest ecosystems representing most of the biological diversity and affecting virtually all ecological processes [35]. While most species are beneficial (e.g., pollinators and detritivores), others (e.g., bark beetles and defoliators) occasionally threaten ecological, economic, social, and/or aesthetic values [36, 37]. 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. Forest insects are directly and indirectly affected by other biotic, abiotic, and anthropogenic (e.g., management activities and land use patterns) disturbances [38••]. These disturbances may, in turn, be affected by forest insects. Below, we review the

current state of knowledge concerning interactions between fire (prescribed fire and wildfire) and insects in North American forests. We focus on the effects of fire on bark beetles, defoliators, and pollinators, and on the effects of bark beetle and defoliator epidemics on fuels and wildfires. Our review concentrates on the most recent literature (2017–present), but we also draw from earlier literature.

## Effects of Prescribed Fire and Wildfire on Bark Beetles

Trees of all species, ages, and sizes may be colonized and killed by bark beetles, but each bark beetle species exhibits unique host preferences, life history traits, and impacts. Pioneering beetles bore through the outer bark and initiate gallery construction in the phloem. In response to this wounding, conifers release oleoresin that exudes at the entrance hole and may encapsulate and kill beetles, thwarting attacks [39] (Fig. 1). Successful host colonization requires overcoming this and other conifer defenses, which generally requires an abundance of beetles (hundreds to tens of thousands) to mass attack the tree.

Fire directly affects bark beetles by causing beetle mortality, which has received less study than the indirect effects of fire as mediated through changes in beetle hosts and forest conditions (see below). Fire is recognized as a direct control tactic for bark beetles [40]. Burning of infested host material (e.g., slash) is commonly practiced and may cause significant beetle mortality. Attempts to burn standing infested trees have produced mixed results. In British Columbia, Canada,



**Fig. 1** Resin ducts synthesize, store, and transport oleoresin, which serves as a physical and chemical defense against bark beetles. In ponderosa pine, *Pinus ponderosa*, low-severity fire induces resin duct production, increasing resistance to bark beetles [60]. The effect has not been well studied in other tree species. Photo credit: C. Fettig, USDA Forest Service

lodgepole pines, *Pinus contorta*, colonized by mountain pine beetle, *Dendroctonus ponderosae*, before prescribed fires were applied had lower brood production (by ~48%) after fire [41]. Several bark beetle species overwinter in duff and litter as adults and are susceptible to mortality from surface fires [42].

Following a fire, tree mortality due to fire injuries to the crown, bole, and/or roots may be immediate or delayed, occurring over the course of several years [43•, 44]. Levels of tree mortality caused by bark beetles following prescribed fires and low-severity wildfires depend on several factors (Table 1). A common concern is that bark beetles may colonize and kill fire-injured trees that otherwise would have survived. These trees may then serve as a source of beetles and semiochemicals that attract other beetles into the vicinity, resulting in additional tree mortality over time. Most long-term (> 5 years) studies indicate that following prescribed fires and low-severity wildfires, levels of bark beetle-caused tree mortality increase, but that the effect is limited (< 5% mortality), short-lived, and concentrated in smaller-diameter trees (e.g., [45–48]). Trees that have been moderately injured are the most susceptible [49–51]. The effect of fire seasonality is mixed among the limited studies that exist. Some studies show increases in tree mortality associated with certain bark beetle species following fall prescribed fires [52] when fuels tend to be drier and fires more intense [53]. Others show stronger effects following early season fires when bark beetles tend to be more active [54, 55]. During 2002–2017, Westlind and Kerns [48] studied the effects of spring and fall prescribed burns repeated at 5-year and 15-year intervals in thinned ponderosa pine, *Pinus ponderosa*, in eastern Oregon, US. Fall burning reduced mortality of ponderosa pine from pine butterfly, *Neophasia menapia*, and western pine beetle, *Dendroctonus brevicomis*.

In western Montana, US, Douglas-fir beetle, *D. pseudotsugae*, pine engraver, *Ips pini*, and western pine beetle caused some (< 5%) tree mortality the first 2 years following

prescribed fire [56]. A mountain pine beetle epidemic started ~5 years after treatments were implemented and caused 50% mortality of ponderosa pines in untreated plots with almost no tree mortality in thinned-and-burned plots [46]. A 3-year study by Davis et al. [57] found that brood production of the western pine beetle in ponderosa pine did not differ between fire-injured and uninjured trees following prescribed fire in Idaho, US, and wildfire in Montana. Beetle responses to fire-injured trees pulsed and receded within 2 years. Similarly, Tabacaru et al. [58] found that fire-injured lodgepole pines in western Canada were more susceptible to colonization by mountain pine beetle but provided only short-term resource pulses. In the southeastern US, Sullivan et al. [59] found mortality of longleaf pine was positively correlated with fire intensity following prescribed fires but amounted to < 5% of trees. Most mortality occurred in the second and third years following prescribed fires, and nearly all dead and dying trees had signs of colonization by bark beetles. There is evidence that low-severity fire may increase conifer defenses against bark beetles by inducing resin duct production [60] (Fig. 1).

Taken together, these results suggest that bark beetle responses to fire-injured trees most likely will not interfere with management objectives and could be viewed as short-term losses suffered for long-term gains [45, 61••]. In addition to increasing the long-term health and vigor of residual trees, fire also affects the size, distribution, and abundance of bark beetle hosts and other trees, as well as the physical environment within forests. Associated reductions in tree density reduce host availability, increase tree spacing, reduce crown cover, and dilute pheromone plumes [62], which collectively reduce host finding and colonization [63]. Some of these effects may extend to predators, parasites, and competitors, which in turn may influence bark beetles, although these relationships have not been adequately studied. In the southeastern US, the use of prescribed fire in loblolly pine, *Pinus taeda*, is recognized as an effective means for reducing stand

**Table 1** Factors influencing bark beetle responses to fire-injured trees following prescribed fires and low-severity wildfires and moderate- and high-severity wildfires

Prescribed fires and low-severity wildfires	Moderate- to high-severity wildfires
Tree species	Survival of sufficient numbers of suitable and susceptible host trees (i.e., with live phloem to support bark beetle populations). This is often lacking, especially after high-severity wildfires
Tree size	Fire seasonality
Tree phenology	Patch size and amount of edge. Bark beetle populations often increase in moderately injured trees along the edges of wildfires
Degree of fire-caused injuries	Other predisposing, inciting, and contributing factors
Initial and post-fire levels of tree vigor	Post-fire environment
Fire seasonality. Late-season fires may occur after bark beetles have flown and fire-injured trees may no longer be suitable for colonization the following year. Early season fires occur when bark beetles are more active	Scale, density, and composition of local bark beetle populations
Other predisposing, inciting, and contributing factors	
Post-fire environment	
Scale, density, and composition of local bark beetle populations	

susceptibility to the southern pine beetle, *Dendroctonus frontalis* [64]. McNichol et al. [65] suggested a similar relationship exists for engraver beetles, *Ips* spp.

While most of the delayed tree mortality caused by bark beetles occurs during the first few years following prescribed fires within treated areas, this may differ for adjacent untreated areas due, in part, to unburned areas not benefiting from the positive effects of prescribed fire (e.g., increases in growing space due to reductions in tree density). Infestations in adjacent unburned areas are uncommon but occur and should be monitored for in case additional management is warranted [45, 61••]. In some cases, concerns about large-diameter pines being killed by bark beetles following prescribed fires have been realized [45, 61••], but treatments are available to protect these trees. Raking of litter and duff from the bases reduces fire intensity and severity [66, 67]. Insecticides and semiochemicals are available in some cases to protect trees from bark beetles [67–69]. Additional research is needed to determine under what conditions large-diameter trees are most susceptible to delayed mortality following prescribed fire and when tree protection treatments are warranted.

There are several factors that influence interactions among bark beetles and moderate- to high-severity wildfires (Table 1). While these overlap, to some degree, with those identified for prescribed fires and low-severity wildfires, an important distinction is that high-severity wildfires may reduce susceptibility to bark beetles by killing an abundance of host trees over extensive (e.g., > 10,000 ha) areas. Recent modeling of mountain pine beetle epidemics in lodgepole pine forests found that high-severity wildfires suppress future epidemics [70], as lodgepole pines that regenerate are not of susceptible size for mountain pine beetle colonization for many decades [71]. Alternatively, wildfire has been observed to increase the risk of some epidemics (e.g., [42, 72–74]). Powell et al. [51] concluded that fire-injured lodgepole pines provide a reservoir for mountain pine beetle when populations are too low to overcome the defenses of healthy trees. However, the likelihood of mountain pine beetle populations increasing to epidemic levels is offset by the scarcity of moderately injured trees [51], especially in mesic, high-elevation forests where high-severity wildfires are the norm [75]. Overall, the effect of wildfires on bark beetle epidemics depends on complex interactions among wildfire severity, wildfire extent, and the spatial structure of biological legacies, among other factors (Table 1).

## Effects of Prescribed Fire and Wildfire on Defoliators

Defoliators consume, mine, and/or skeletonize foliage. Feeding may result in tree mortality depending on the timing, frequency, and extent with species such as eastern spruce

budworm, *Choristoneura fumiferana*, and spongy moth, *Lymantria dispar*, occasionally causing large amounts of tree mortality [37]. Relative to bark beetles, the direct and indirect effects of fire on defoliators are poorly studied. Direct effects focus on the mortality of defoliators following exposure to fire. It is important to note that some defoliators are attracted to light and may be killed when attracted to flames. For example, during a prescribed fire conducted after dark in central Oregon, 2–17% of the local pandora moth, *Coloradia pandora*, population was killed by the fire [76].

Prescribed fire and wildfire may indirectly affect defoliators by altering the chemical and physical properties of soils and trees (e.g., [77]). Rieske et al. [78] assessed the effects of prescribed fire on the phytochemical properties of hardwood foliage. No effects were observed except for decreases in non-structural carbohydrates in scarlet oak, *Quercus coccinea*, and red maple, *Acer rubrum*, and calcium in red maple. Not surprisingly, no differences in the development of spongy moths were observed due to the fire [78]. The authors concluded that more intense fires would have resulted in greater changes in foliar chemistry and palatability, perhaps influencing spongy moth development.

A reduction in the frequency of wildfires has increased the impacts of some defoliators through their effects on forest composition and succession. Bergeron et al. [79] developed a simple empirical model that allowed for the estimation of tree mortality due to eastern spruce budworm in eastern Canada. Tree mortality increased with time since wildfire, which was attributed to an increase in the abundance of balsam fir, *Abies balsamea*, a fire-intolerant species and a preferred host of eastern spruce budworm. According to this model, changes in fire frequency could explain a large portion of the spatiotemporal variation among eastern spruce budworm epidemics in recent decades. In western North America, forests most at risk from western spruce budworm, *Choristoneura occidentalis*, are multistoried with true firs (e.g., white fir, *Abies concolor*) and Douglas-fir, *Pseudotsuga menziesii*, in the understory. Fire suppression has reduced fire frequencies in these forests, facilitating the establishment of white fir and Douglas-fir [80, 81]. Relatedly, the first recorded epidemic of Douglas-fir tussock moth, *Orgyia pseudotsugata*, in southern California, US was attributed to fire suppression causing significant increases in the density and continuity of white fir, a host of Douglas-fir tussock moth [82].

## Effects of Prescribed Fire and Wildfire on Insect Pollinators

Forests provide important floral and nesting resources for a wide range of pollinating insects, including bees, butterflies, hover flies, and beetles. There is great interest in better

understanding how forest management activities and other disturbances affect pollinators given the growing evidence that these insects are in decline [83–85]. Although pollinators are widely thought to be favored by the more open forest conditions and greater floral resource availability following fire [86–88], some taxa (e.g., butterflies and above-ground nesting bees) can be negatively affected by fires [89••], and overall effects are complicated by six variables that have interacting effects on biotic assemblages. As outlined by He et al. [90], these include fire severity (low vs. high), fire interval (short vs. long), fire size (small vs. large), vertical spread (ground vs. crown), horizontal spread (patchy vs. continuous), and seasonality (summer/autumn vs. winter/spring). Current knowledge of how each of these variables affects pollinators in forests is reviewed below and in Table 2 before we discuss the importance of pyrodiversity at the landscape scale.

Fires have direct and indirect effects on pollinator communities that increase with increasing fire severity. Direct effects concern mortality resulting from exposure to fire and vary widely among taxa. Whereas most bee species are ground-nesting and typically build nests deep enough to survive the most intense and severe wildfires [91–93], other pollinator species are more vulnerable to fire. These include a large diversity of bees, hoverflies, and flower-visiting beetles that nest in dead wood or in the stems of plants, as well as butterflies that spend their immature stages confined to host plants. These species are thought to be more susceptible to mortality from fire [94, 95] but more resilient in regions characterized by low-severity fires [88, 96, 97•].

Indirect effects of fire on pollinator communities involve changes to forest structure, nesting habitats (e.g., coarse woody debris), and floral resources. There appears to be a positive correlation between fire severity and post-fire pollinator abundance. Whereas several studies have shown that prescribed fires have little effect on pollinators in forests unless combined with mechanical thinning [98, 99], moderate- or high-severity wildfires can result in large increases in pollinators, likely due to reductions in forest cover and increases in flowers [87, 95, 100]. The weak effects of prescribed fires on pollinators compared to wildfires is likely because prescribed fires are usually of lower severity and often conducted during the dormant season [89••], especially in the southeastern US. A recent review found that prescribed fires in US forests had neutral ( $n=7$ ) to positive ( $n=6$ ) effects on pollinator abundance, richness, and diversity [101••].

Many studies have reported higher bee and hoverfly abundances soon after prescribed fires and wildfires, followed by a rapid return to pre-fire levels as flowering plants are replaced by grasses and regenerating trees [87, 88, 102]. While one might expect frequent fires to help maintain elevated pollinator abundances over time, they may have

**Table 2** Potential direct and indirect effects of six interacting factors influencing pollinator responses to fire

Fire attribute	Direct effects	Indirect effects
Severity	Pollinator mortality increases with fire severity	Immediate elimination of floral resources (greater with high-severity fire) followed by potentially greater floral resource availability, particularly when fire results in more open canopy conditions
Interval	High fire frequency may reduce fire severity and consequently pollinator mortality. However, high fire frequency may reduce populations of the most sensitive species	High fire frequency maintains open conditions that favor high floral resource availability
Size	Large burns will result in higher mortality of fire-sensitive species	Some taxa will be negatively affected by large burns if unable to find adequate floral resources within their foraging range or if unable to fully recolonize burned areas before the next fire
Vertical spread	Crown fires will result in higher mortality of species nesting or overwintering in standing dead trees or canopy habitats	The more open conditions resulting from crown fires will likely result in greater increases in floral resource availability
Horizontal spread	Patchy fires will result in less pollinator mortality than continuous fires	Patchy fires increase the likelihood of floral resources being available to sustain pollinators following a fire
Seasonality	For some taxa, dormant-season burns may result in less direct mortality than growing-season burns, especially for species that are confined to their host plants during the immature stages	Growing-season burns may temporarily eliminate flowers, requiring pollinators to visit neighboring unburned patches

negative effects on pollinator diversity if applied over large areas or at intervals shorter than the historical fire regime [89••]. For example, a landscape study from open loblolly pine forests in Florida, US, where prescribed fire return intervals ranged from ~ 1.6 to 3.2 years, found a somewhat negative effect of high fire frequency on the diversity of bees and a strong negative effect on butterflies [97•]. At the species level, high fire frequency had a positive effect on some bee taxa and a negative effect on other bee taxa [97•], showing that there is no one-size-fits-all best management practice regarding the effects of prescribed fire on pollinators. Rather, a given fire frequency acts as an ecological filter, selecting for a particular combination of species from the local pool of pollinator taxa.

The effects of the spatial extent of fire on pollinators are largely unstudied and recognized as a major knowledge gap. Mason and Lashley [103] reported that naturally extinguished lightning-generated wildfires tend to be smaller on average than prescribed fires in the US, suggesting that ecosystems were historically adapted to smaller fires than are common today. The sensitivity of a species to fire size will depend on its ability to survive the fire as well as its dispersal ability. Fire severity, fire seasonality, and horizontal spread (i.e., patchy vs. continuous) are also important. As mentioned above, most bee species nest below-ground, and most of these are expected to survive the most intense and severe wildfires. Bees nesting in wood are also likely to survive fires, especially prescribed fires, as observed for other wood-dwelling insect taxa [96, 104]. Although persistence within the habitat obviates recolonization, dispersal ability is still important given the absence of floral resources for some period following a fire. Foraging ranges of many solitary bees are limited to a few hundred meters of the nest [105, 106], which suggests that species capable of surviving a fire may be negatively affected if their nests are far from the fire perimeter. This is especially likely for homogenous fires, as opposed to patchy fires (see below), and for specialist pollinator species that depend on certain flower species [92]. Dormant season fires may ensure better floral resource availability by the time bees begin foraging in the spring [107], and this may be an important consideration when planning large, prescribed burns. Crown fires are likely to have a negative effect on bees nesting in standing dead trees while also creating standing dead trees for future use as well as more open conditions that favor pollinator communities overall [95, 100].

As mentioned above, the horizontal spread of a fire (i.e., how uniformly the area is burned) has important consequences for pollinators. Not only are more sensitive pollinator species likely to survive more heterogeneous burns, but the remaining patches of flowers also provide critical resources during the post-fire recovery period. Love and Cane [92] sampled the sagebrush steppe bee community

within 21 days of a large wildfire in Idaho. To assess survivorship, bees were sampled  $\geq 7$  km into the burned area, a distance believed to be too far for bees to reach from neighboring unburned areas [106]. Although the richness and abundance of bees were reduced in the burned area relative to unburned areas nearby, most bee species appeared to survive the fire and were sustaining themselves on patches of wild sunflowers, *Helianthus annuus*, along drainage ditches. Although not addressed by Love and Cane [92], it is probable that the fire would have resulted in greater bee mortality without the surviving patches of sunflowers. The presence of wet areas or other topographic features that result in less homogeneous fires may mitigate some of the negative effects of large fires on pollinator communities.

Although rarely studied, fire seasonality has the potential to influence pollinator assemblages. Some pollinator and plant life stages are more vulnerable to fire at certain times of the year. Fire seasonality may also influence floral resource availability. Hiers et al. [107] compared the effects of summer prescribed burns and winter/early spring prescribed burns on the reproductive phenology and fruit initiation (i.e., a surrogate for pollination rates) of legumes in a longleaf pine forest in Georgia, US. They reported significantly altered flowering phenology depending on fire seasonality (and relative to unburned areas) but found no differences in fruit initiation. Bees capable of pollinating legumes were present during all flowering periods, indicating pollinators may be resilient to alterations in plant phenology after a fire. Hiers et al. [107] further suggested that prescribed burning at different times of the year can be a way to stagger floral resource availability across the landscape. Fire seasonality can also affect the availability of nesting resources. For example, growing-season prescribed burns in tallgrass prairies in Illinois, US resulted in more bare ground and a greater abundance of belowground nesting bees than dormant season burns [108]. Overall, we have little understanding of how fire seasonality affects pollinators in forests. More research is needed before we can apply prescribed fires at times that maximize benefits to pollinators in forests.

Taken together, these results indicate that prescribed fires and wildfires can benefit pollinators by creating more open forest conditions, which, in turn, enhance floral resource availability. Fire clearly has negative effects as well, especially at high frequencies and for some vulnerable taxa. As predicted by the pyrodiversity hypothesis [109, 110], landscapes with a diversity of fire histories may support a greater abundance and diversity of pollinators than those that burn more homogeneously [111]. Ulyshen et al. [97•] found pyrodiversity to be a positive predictor of bee and butterfly abundance in Florida. Efforts to introduce more variability in fire history are expected to benefit pollinators overall, including altering fire frequency, fire size, and fire seasonality as well as leaving unburned refugia. The importance

of heterogeneity in fire-adapted landscapes is perhaps best exemplified by well-studied species of conservation concern, such as the Karner blue butterfly, *Lycia melissa samuelis*, which is both dependent on fire for suitable habitat [112] and highly vulnerable to it [113].

## Effects of Bark Beetle Epidemics on Fuels and Wildfires

Bark beetle epidemics and wildfires have increased in frequency, extent, and severity in recent decades in response to warming and drought [10, 114] as well as the spatial legacies of human activities. Recent epidemics of bark beetles in the genus *Dendroctonus* alone have affected tens of millions of hectares in western North America [37, 114, 115] and caused large changes to forest structure and fuels [116–119]. The increased spatial extent of recent bark beetle epidemics [120], coupled with increases in the frequency and size of wildfires [2•, 121], has triggered concerns regarding their interactions. It is important to note that the severity and impact of bark beetle epidemics vary widely, which complicates generalizations of their effects on fuels and wildfires. For example, in ponderosa pine forests in California, *Ips* epidemics typically cause low levels of tree mortality (< 10%) at small spatial scales (< 100 ha) concentrated in smaller-diameter trees (< 20 cm dbh, diameter at 1.37 m in height) [122]. By contrast, western pine beetle epidemics in these same forests may cause large amounts of tree mortality (> 80%) at large spatial scales (> 10,000 ha) concentrated in larger-diameter trees (> 41 cm dbh) [117].

Despite well-described physical changes to fuels following epidemics, as well as a common public perception that bark beetle epidemics worsen wildfires [123], the literature is mixed on precisely if, when, and how beetle epidemics affect wildfires. Some studies report little to no effects (e.g., [124–128]), whereas others find epidemics exacerbate wildfires (e.g., [129–131, 132•, 133]). These contradictions can largely be explained by the different metrics used to assess wildfires (e.g., behavior versus occurrence and severity), time since the epidemic (stages), the spatial scale of studies, and the confounding effects of fire weather and beetle impacts (i.e., recognizing that most bark beetles are host specific (see above) and that most forest types exhibit variability in tree composition). Below, we summarize how beetle epidemics affect fuels and wildfire behavior and then review the effects of these changes on wildfire occurrence and severity.

The effects of bark beetles on fuel abundance, structure, and connectivity, and hence their potential to affect fire activity, change over time. Following epidemic initiation, there are at least three distinct fuel stages [75, 116, 134, 135]: “red,” “gray,” and “post-epidemic” (Fig. 2). The duration of each stage varies with habitat and tree species,

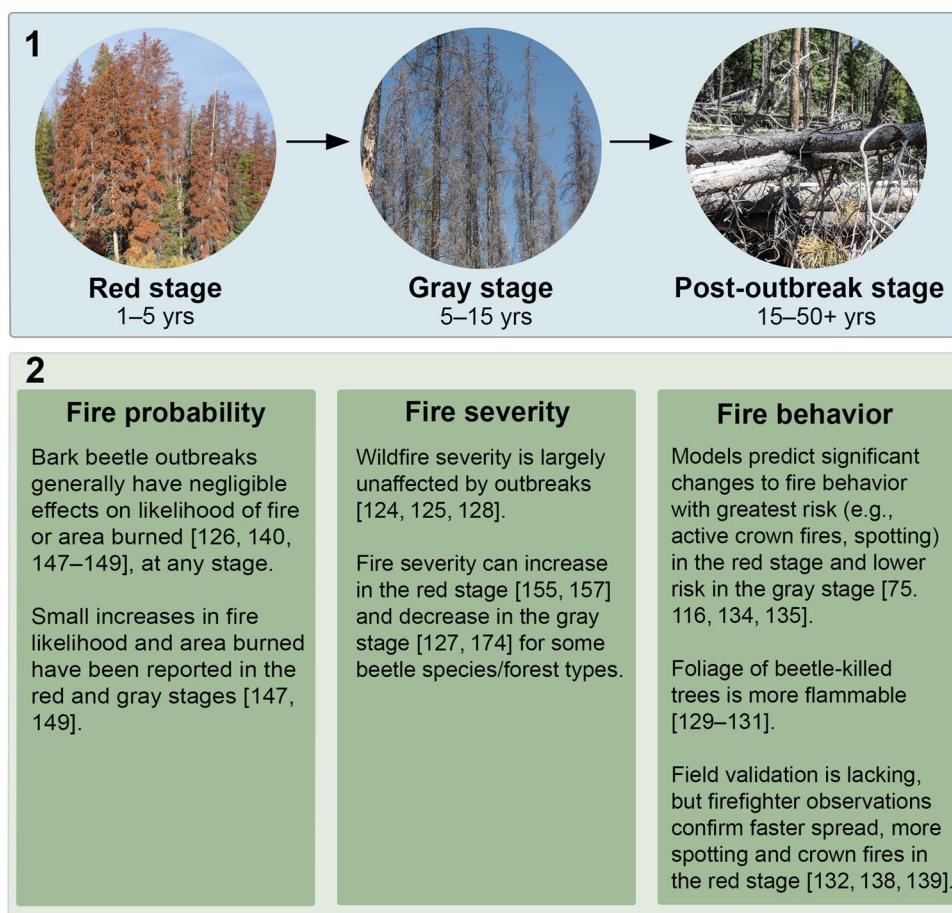
among other factors. Moreover, trees are attacked and killed by bark beetles over several years, creating heterogeneous forests in multiple stages. The red stage occurs ~ 1–5 years after epidemic initiation and is characterized by the retention of twigs and needles in the crown with significantly reduced foliar moisture. In lodgepole pine killed by mountain pine beetle, twigs and needles lose 80–90% of their moisture within 1 year of the attack. This dry foliage ignites more quickly, at lower temperatures, and releases more heat when burned [129, 131]. Significant decreases in moisture content and increases in flammability also occur in Engelmann spruce, *Picea engelmannii*, killed by spruce beetle, *Dendroctonus rufipennis*, although increases in crown flammability are shorter lived as spruce needles fall to the forest floor more quickly [130]. Similar reductions in foliar moisture have been reported in whitebark pine, *Pinus albicaulis*, killed by mountain pine beetle [136] and in Douglas-fir killed by Douglas-fir beetle [137], suggesting that rapid drying of foliage and concomitant increases in flammability are common.

Although the loss of moisture explains most (~ 80%) of the increase in needle and twig flammability [129], changes in the proportions of fat, fiber, lignin and cellulose, starches, and sugars also occur [129–131]. Both emission and within-plant concentrations of highly flammable terpenes increase in several conifer species following an attack by bark beetles [129, 130, 137]. In lodgepole pine and Engelmann spruce, increases in terpenes shorten the time to ignition, lower temperature at ignition, and increase the burning rate of foliage [129, 130]. While these effects suggest an increased probability of unusual fire behavior in red-stage forests, there has been limited field validation. Experimental fires [138] and firefighter observations ([132•, 139], but see [140•]) support the idea that fires in the red stage spread faster and exhibit more spotting.

The gray stage occurs ~ 5–15 years after epidemic initiation when snags have lost their needles but remain standing (Fig. 2). During this stage, fine fuels accumulate on the forest floor and the loss of crown fuels increases the exposure of surface fuels to solar radiation and wind [134]. Fuel bed depth and litter fuel load often increase, but few changes are expected in ground (duff) fuels [134, 141, 142]. More fine branches may be attached to trees at the beginning of the gray stage but will fall over time, decreasing crown bulk density [135]. Wildfires during the gray stage (and beyond) have been found to have higher intensities for a given wind speed than expected [143]. Both increases and decreases in crown fire potential have been reported during the gray stage [142, 143], an effect likely contingent on fire weather conditions.

Large accumulations of coarse woody debris (e.g., 1000-h timelag fuels) occur during the shift from the gray stage to the post-epidemic stage. This shift occurs as snags fall and

**Fig. 2** Bark beetle epidemics dramatically alter forest fuels, causing concerns about bark beetle and wildfire interactions in North American forests. (1) The effects epidemics have on fuels change over time, with at least three stages recognized (shown here for *Pinus contorta* killed by *Dendroctonus ponderosae*). (2) Available evidence indicates that bark beetle epidemics generally have minimal effects on fire probability and fire severity but exacerbate fire behavior. Importantly, the influence of climate and extreme weather on fire probability, fire severity, and fire behavior can override that of bark beetle epidemics. Furthermore, the impacts of bark beetle epidemics on forests vary widely, with some having minimal effects on forest structure and others resulting in extensive tree mortality (> 80%) at large spatial scales (> 10,000 ha)



are deposited into the surface fuel pool. The rate of snag fall following a bark beetle epidemic is dependent on tree species, tree size, environmental conditions, and other factors [75, 119, 144] and varies widely (years to decades), although snag retention is not well studied overall. Increased coarse fuel loading from fallen snags may lead to increased surface fire intensity [145•], although evidence for such increases is mixed [146]. Crown bulk density is lowest during the early part of the post-epidemic stage, although ladder fuels increase as trees regenerate and grow. A corresponding reduction in average crown base height is also observed [142, 145•]. The post-epidemic stage begins ~ 15 years after epidemic initiation but can occur earlier in some locations and forest types and lasts for decades to centuries (Fig. 2).

While the effects of bark beetle epidemics on ground, surface, and crown fuels have been well documented, there is a diversity of opinion regarding the consequences of these effects on wildfires. Researchers often examine if epidemics affect fire occurrence, including ignition probability and area burned. Despite the intuitive appeal, little evidence exists suggesting epidemics affect wildfire ignition or the area burned at any stage [126, 140•, 147, 148]. However, mountain pine beetle epidemics have been demonstrated to affect wildfire spatial patterns [149] and to increase the area

burned in some ecoregions in the Pacific Northwest during the red stage [147]. Overall, the effects of mountain pine beetle epidemics on wildfires have been the most studied among all bark beetle species [61••]. It is important to note that even if the area burned is unaffected by epidemics, fire behavior (e.g., the rate of fire spread) could still be affected. A recent landscape simulation study suggests that fire probability increases in fuel-limited forests (35-year mean fire return interval) but decreases in fuel-abundant and fire-limited forests (200-year mean fire return interval) following bark beetle epidemics in Idaho [150•].

The effects of bark beetle epidemics on wildfires have also been assessed through the examination of fire severity and fire behavior [61••, 139, 145•]. Here, severity refers to retrospective assessments of the effects of wildfire on forest vegetation and soils [151]. Fire behavior describes active fire characteristics, including flame length, fire intensity, rate of fire spread, probability of fuels igniting, and the potential for crown fire initiation and spread [75]. Thus, while fire severity tells us about ecological change (e.g., biomass loss), fire behavior informs decisions for fire management and firefighter safety [132•, 152]. Bark beetle epidemics generally have minimal effects on fire severity, although this seems highly contingent on fire weather [124, 125, 128, 146, 153].



However, some studies have found an increase in fire severity [154, 155•] and canopy loss [156]. Using a simulation approach, Sieg et al. [157] found that fire severity increased during the red stage through the post-epidemic stage in ponderosa pine, although the effect was contingent on fire weather (i.e., wind).

Consensus regarding the effects of bark beetle epidemics on wildfires has been confounded by several factors. The first, noted above, is that researchers have used different metrics to assess effects, which explains some discrepancies among studies. For example, it appears that many ecosystems are resilient to wildfires after bark beetle epidemics (severity) but that epidemics can alter the behavior of fires (Fig. 2). Second, to date, semiempirical models have been the primary method used to assess the effects of epidemics on fire behavior, but available models cannot account for highly heterogeneous fuels and the large changes to crown and surface fuels in beetle-altered forests [75, 158, 159]. Unfortunately, field validation of these models has been limited but is essential for safe and effective fire management. Third, extreme fire weather and topography can override the effects of beetle epidemics on fuels and their effects on wildfires [124, 125, 128, 140•, 157], masking important but more subtle effects. This is noteworthy as most of the area burned by wildfires in North America occurs during extreme fire weather [140•, 160]. A better understanding of these cross-scale interactions [161] is nonetheless essential to fire and forest managers.

## Effects of Defoliator Epidemics on Fuels and Wildfires

Unlike bark beetles, defoliators often do not kill their hosts, and as such, their effect on fuels is often more subtle and drawn out over time. While the effects of defoliators on forest structure and fuels have been discussed in North America for almost a century [162–164], surprisingly few empirical studies have been published. Those available report neutral, positive, and negative effects. Below, we discuss what is known of the effects of eastern spruce budworm, western spruce budworm, and jack pine budworm, *Choristoneura banksiana*, epidemics on fuels and wildfires. Each of these species exhibits cyclic and spatially synchronous epidemics that can affect millions of hectares of susceptible host trees.

As is the case for bark beetles, the effects of defoliators on wildfires depend on how fuel loading, fuel connectivity, and fuel complexity change with time since the epidemic. In a series of experimental burns, Stocks [165] identified an increase in fire behavior due to increased surface fuel loading that affected crowning and wildfire spread 5–8 years following an eastern spruce budworm epidemic in Ontario, Canada. Spring fires prior to green-up showed the greatest

change in fire behavior in response to defoliation, although summer fires also exhibited an effect as the time since mortality increased [165, 166]. Elsewhere in Ontario, vertical fuel abundance and connectivity following eastern spruce budworm defoliation peaked ~16 years post-epidemic [167]. Similarly, crown breakage, surface fuels, and ladder fuels were found to increase 9 years after defoliation began [168]. These lagged effects are formalized as distinct fuel types (i.e., M-3, M-4) within the Canadian Forest Fire Behavior Prediction System [169]. However, these fuel types are static and do not explicitly account for fuel development from epidemic initiation through tree mortality and altered fire risk.

The area burned has been shown to increase following eastern spruce budworm epidemics during a lagged “window of opportunity” of ~8–10 years [170]. Likewise, the probability of ignition increases with a similar lag [171•]. A slight decrease in the risk of ignition has been reported immediately following defoliation, possibly due to an increase in the abundance of understory vegetation and site level moisture due to canopy opening [171•]. These effects were identified after controlling for fire weather. Temporal lags in area burned and ignition probability correspond with previously identified lags for surface fuel abundance and vertical connectivity following eastern spruce budworm epidemics in Ontario [165, 167, 168]. We currently lack information on the effects of western spruce budworm and jack pine budworm epidemics on areas burned.

The effects of eastern spruce budworm epidemics on fuels and their consequences for wildfires depend on fire weather and climate. While lagged defoliation was found to affect ignitions [171•], no increases in surface fuels or fire hazards were identified following an eastern spruce budworm epidemic in eastern Canada, presumably due to the rapid rate of fuel decomposition in the moist environment [172]. Within Ontario, defoliation-fire effects were found to occur more often within the previously identified window of opportunity and to vary spatially as a function of host availability and climate [173].

Western spruce budworm epidemics also affect fuel structure and fire behavior [81] but have not been found to affect fire severity [174]. Furthermore, fire occurrence appears to be reduced following western spruce budworm epidemics, presumably due to the thinning effect of defoliation [175]. It is interesting to note that this effect has not been identified following eastern spruce budworm epidemics [165, 170, 171•] and may highlight the ephemeral nature of fuel load changes following an epidemic, as well as important differences between defoliator systems. Multiple dendrochronological studies aimed at providing a better understanding of relationships between western spruce budworm epidemics and wildfires have found no consistent effects on fire occurrence [176, 177], although some sites examined by Harvey et al. [177] seem to show increased fire activity 20–40 years

following epidemics. Very little is known about the effects of jack pine budworm epidemics on fuels and wildfires. This is curious given the well-known evolutionary adaptation of jack pine, *Pinus banksiana*, to wildfire through serotiny [178].

Landscape simulation studies consistently do not support a hypothesized positive effect of defoliation on fire activity for either eastern spruce budworm or western spruce budworm. In examining how forest management, eastern spruce budworm epidemics, and fire interact over a temporal scale of several centuries, James et al. [179] found no increase in area burned due to eastern spruce budworm defoliation. In examining fire–insect interactions in northern Minnesota, US at a similar temporal scale, Sturtevant et al. [180] found a decrease in both areas burned and fire severity in the decades following eastern spruce budworm epidemics. Using a physics-based simulation model at a finer spatial and temporal scale, western spruce budworm epidemics were found to reduce fire intensity and crowning due to a reduction in crown fuels [181]. Other studies have found that there is no difference in fire severity under moderate fire weather, although severity can be reduced under extreme fire weather [182].

## Conclusions

1. The direct effects of fire on bark beetles and forest defoliators focus on insect mortality following exposure to fire. This varies with fire intensity and fire severity, among other factors. The direct effects of a fire have received less study than the indirect effects of fire as mediated through changes in insect hosts and forest conditions.
2. The indirect effects of fire on bark beetles vary with the degree of fire-related host tree injuries (as influenced by several factors, Table 1), the post-fire environment, and the scale, density, and composition of local bark beetle populations (Table 1). Moderately injured trees are most susceptible to colonization [49–51]. Most long-term (> 5 years) studies indicate that prescribed fires and low-severity wildfires result in limited, short-term increases in bark beetle-caused tree mortality [45–48]. However, in the longer term, these negative effects are offset by increases in forest resilience [45, 61••].
3. There are examples of wildfires leading to bark beetle epidemics following mixed-severity wildfires or along the perimeters of high-severity wildfires (e.g., [42, 72–74]). However, most high-severity wildfires reduce the susceptibility of forests to bark beetles by killing an abundance of host trees over extensive areas.
4. The indirect effects of fire on forest defoliators are mediated by changes in plant growth and foliar chemistry following a fire, but this relationship has not been adequately studied. A reduction in the frequency of wildfires in some parts of North America has increased the impacts of some forest defoliators (e.g., [79–82]), an effect attributed to increases in the abundance of fire-intolerant conifers (e.g., firs).
5. The effects of fire on pollinators vary with fire severity, fire interval, fire size, vertical spread of fire, horizontal spread of fire, and fire seasonality (Table 2). Prescribed fires and wildfires can benefit pollinators by creating more open forest conditions, which enhance floral resource availability. However, some bees, hoverflies, and flower-visiting beetles nest in dead wood or in the stems of plants and may be negatively affected by the direct effects of fire. Forest landscapes with a diversity of fire histories (i.e., fire frequencies, fire sizes, and fire seasons) may support a greater abundance and diversity of pollinators [97•, 112, 113].
6. Bark beetle epidemics exert large effects on fuels (Fig. 2). Despite this, some studies of the effects of bark beetle epidemics on wildfires report little or no effects (e.g., [124–128]), while others report that epidemics exacerbate wildfires (e.g., [129–131, 132•, 133]). These differences may be largely explained by the metrics and models used to assess wildfires, time since the epidemic (Fig. 2), the severity and spatial scale of the epidemic, and fire weather. Extreme fire weather and topography can override the effects that beetle epidemics have on fuels and their effects on wildfires [124, 125, 128, 140•, 157]. Furthermore, available fire models cannot account for the highly heterogeneous fuels encountered in beetle-altered forests [75, 158, 159].
7. There are surprisingly few studies on the effects of defoliator epidemics on fuels and wildfires. The best studied are epidemics of eastern spruce budworm which have been demonstrated to increase fire behavior and area burned due to increased surface fuel loads that affect crowning and wildfire spread ~5–10 years after an epidemic. Overall, the effects of defoliator epidemics on wildfires vary depending on how fuel loading, fuel connectivity, and fuel complexity change with time since the epidemic.
8. Climate change is increasing the scale, frequency, and severity of wildfires [10–17] and epidemics of some bark beetles and defoliators [183, 184]. As such, additional study of fire and insect interactions in North American forests is warranted.

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## Declarations

**Conflict of Interest** The authors declare that they have no conflict of interest.

**Human and Animal Rights and Informed Consent** This article does not contain any studies with human or animal subjects performed any of the authors.

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