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# Bark beetle outbreaks alter biotic components of forested ecosystems

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## 1 Introduction

Native bark beetles (Coleoptera: Curculionidae: Scolytinae) are among the most significant biota affecting the health and resilience of forested ecosystems worldwide (Raffa, Grégoire, Lindgren, Vega, & Hofstetter, 2015). These tree phloem- and xylem-inhabiting guilds are diverse, consisting of around 6000 species worldwide and accounting for 10% of weevil diversity, and are ubiquitous and abundant in both forested as well as urban areas (Knížek & Beaver, 2007; Oberprieler, Marvaldi, & Anderson, 2007). As a natural disturbance agent, along with abiotic disturbances (e.g., wildfires and hurricanes), bark beetles play critical roles in creating habitat heterogeneity. This in turn creates spatially and temporally complex habitat templates affecting other biotic elements and their ecological interactions at multiple scales.

Almost every below- and above-ground subcortical part of the tree may have a bark beetle species associated with it (Wood, 1982). At the smallest spatial scale of impact, bark beetle colonization and tree mortality results in a local and patchy availability of resources that are utilized by a multitude of floral, faunal, and microbiotic species (Zuo et al., 2016). If bark beetle populations are high enough, entire stands and even multiple stands across the landscape can be colonized, resulting in altered forest attributes and processes such as structure, composition, and nutrient cycling that also have trickle-down impacts on biota (e.g., Bentz et al., 2009; Sommerfeld et al., 2020). Such ecological effects may persist for centuries until the forest regenerates (Hicke, Meddens, Allen, & Kolden, 2013; Kurz et al., 2008). In addition, economic and social impacts worth millions of dollars can reverberate from local to regional levels through loss of timber supply, property values, and outdoor recreation opportunities (Grégoire, Raffa, & Lindgren, 2015; Morris et al., 2018).

Life-history strategies of native bark beetles are tightly associated with their host trees, indicating a long co-evolutionary history (Raffa et al., 2015). Adult bark beetles colonize trees and bore into the bark to lay eggs in the phloem. From there, the larvae girdle the main bole through feeding and tunneling activities, and the trees eventually die. Many

species are associated with fungi, both facultative and obligate (Kirkendall, Biedermann, & Jordal, 2015) (Chapter 10). Fungal associates may assist with overcoming tree defenses, but also constitute a nutritional resource for the larvae (Klepzig & Six, 2004). Most bark beetle species are considered secondary colonizers (i.e., they colonize stressed, damaged, dying, and dead trees); however, there are a few species that are primary colonizers, as they can kill presumably healthy trees (Raffa et al., 2008; Weed, Ayres, & Bentz, 2015). Overcoming host defense is achieved primarily through mass attacks by beetles using species-specific aggregation pheromones (Byers, 1989; Raffa, 2001). Bark beetle species that are primary colonizers and that kill healthy trees have distinct endemic and outbreak phases; examples include southern pine beetle (*Dendroctonus frontalis*) in the southeastern USA, and mountain pine beetle (*D. ponderosae*) and North American spruce beetle (*D. rufipennis*) in the western USA. The European spruce bark beetle (*Ips typographus*), while typically considered a secondary pest, can act as a primary pest following a major disturbance in Europe. Some nonnative bark and ambrosia beetle species in association with pathogenic fungi have devastated trees in their nonnative range, such as the European elm bark beetle (*Scolytus multistriatus*) on American elms (*Ulmus* spp.) and redbay ambrosia beetles (*Xyleborus glabratus*) on redbay (*Persea borbonia*) trees in the USA (Karnosky, 1979; Koch & Smith, 2008). Direct and indirect environmental factors and changes in host quality are implicated in outbreaks of native beetles (see this chapter and Chapter 9), whereas introduction to naive hosts that lack necessary defenses are implicated in outbreaks of nonnative beetle species (Gandhi & Herms, 2010) (also Chapter 1).

## 1.1 Bark beetles and climate change

Because bark beetles are a natural disturbance agent, forests are adapted to ensuing tree mortality during outbreaks. However, this disturbance regime is being altered under global climate change (i.e., warming temperatures and variable precipitation levels), which is enhancing the distribution, frequency, and severity of bark beetle outbreaks on the landscape (Cudmore, Björklund, Carroll, & Lindgren, 2010; Jönsson, Appelberg, Harding, & Bärring, 2009; Marini, Ayres, Battisti, & Faccoli, 2012; McMillin, Allen, Long, Harris, & Negrón, 2003; Raffa et al., 2008; Yan, Sun, Don, & Zhang, 2005). Yet, undamaged stands are often attacked simply because outbreaks that develop in nearby areas move across the landscape (Simard, Powell, Raffa, & Turner, 2012). In warmer environments, bark beetles can complete a reproductive life cycle faster, and when population growth is unrestrained, beetle outbreaks can quickly overwhelm a forest within days or months (Hubbard, Rhoades, Elder, & Negron, 2013). In colder climates, beetles may take longer to complete a life cycle, leading to slower population growth (Hansen & Bentz, 2003), and outbreaks that persist for years (Frank, Massman, Ewers, Huckaby, & Negrón, 2014). Bark beetles tend to attack larger, older trees, resulting less dense forests of smaller, younger trees—this common trend was found in lodgepole pine (*Pinus contorta*) forests across five western USA states where mountain pine beetle outbreaks had caused 16%–88% pine mortality (Audley et al., 2020).

Geographic boundaries of bark beetles are changing as both southern pine beetle and mountain pine beetle have expanded their distribution from south to north and west to east in the USA, respectively (Carroll, Taylor, Régniere, Safranyik, & Shore, 2004; Dodds et al., 2018). In the case of mountain pine beetles, they have crossed the Rocky Mountain barrier, are killing naive jack pine (*P. banksiana*) hosts in Alberta, Canada, and are expected to continue this trend eastwards, thus encountering more naive conifer species (Cullingham et al., 2011). Changes in precipitation patterns, particularly drought, under a warming climate will further stress trees and lead to impaired host defense and more successful colonization and reproduction by bark beetles (Dobbertin et al., 2007; Negron, McMillin, Anhold, & Coulson, 2009; see Chapters 2–6, this chapter).

Climate change is also implicated in rapidly intensifying and more severe tropical cyclones (or hurricanes) (Bhatia et al., 2019; Zhang, Murakami, Knutson, Mizuta, & Yoshida, 2020); such alterations in disturbance regimes provide a sudden, high pulse of resources such as stressed, broken, and dying host trees (Gandhi et al., 2007; Vogt, Gandhi, Bragg, Olatinwo, & Klepzig, 2020; see Chapter 7). This high volume and heterogeneous composition of coarse-woody debris are optimal habitats for many bark beetles to colonize easily, and potentially increase in numbers to infest residual green trees, thus extending the damage. While most of the devastating bark beetle species are in the genus *Dendroctonus*, a few native *Ips* species, such as *I. avulsus* in the southeastern USA and *I. typographus* in Europe, have undergone spectacular outbreaks due to changes in water availability and/or wind disturbances (e.g., McNichol et al., 2019; Müller, Bußler, Goßner, Rettelbach, & Duelli, 2008) (this chapter and Chapter 7). As climate change continues, this anthropogenic disturbance will overlay on top of natural disturbances, resulting in compounded and unpredictable impacts to forested ecosystems. Hence, management and long-term solutions for bark beetle outbreaks will invariably include a consideration of current and future climatic changes to best mitigate the impacts.

## 1.2 Chapter objectives

One of the major impacts of bark beetle outbreaks is on native and nonnative forest species. These impacts can occur directly, by the bark beetles acting as prey, predator, parasitoid, or symbiont, and/or indirectly, through major alterations to forested habitats with cascading effects on other species. Such impacts can occur at the population- and community levels, particularly on biological diversity—one of the key ecosystem services outlined in the Millennium Ecosystem Assessment (2005). There are many threats to our current biodiversity (e.g., loss and fragmentation of original habitat and invasive species) (Gandhi & Herms, 2010; Newbold et al., 2015; Porter et al., 2013). A growing body of literature is developing on how biota can respond in linear or nonlinear ways to bark beetle-induced disturbances, with feedback loops to other abiotic and biotic elements in forested ecosystems. Currently, however, there is no holistic literature synthesis available on this important and timely topic. The main objective of this chapter is therefore to provide a framework for the cascading impacts of severe bark beetle outbreaks on both the (1)

abiotic components and (2) biotic components such as plants, animals (invertebrates and vertebrates), fungi, and bacteria worldwide, and the interactions therein. When the literature was particularly robust, we categorized impacts as either positive, negative, variable, or neutral. While we recognize that postoutbreak management activities can alter forest patterns and processes, due to the voluminous nature of that work, it will not be presented here. Finally, we will address knowledge gaps, areas for future research, and recommendations for management under bark beetle outbreaks in a rapidly changing world.

## 2  Changes to the abiotic forest environment

During an outbreak's green phase (in which trees are infested but needles remain green), the direct effect on the abiotic environment is primarily on the water cycle due to the occlusion of the xylem by beetle-associated fungi (Croisé, Lieutier, Cochard, & Dreyer, 2001). The loss of hydraulic conductivity can occur quickly after attack: e.g., within weeks in lodgepole pine (Hubbard et al., 2013) or months in Engelmann spruce (*Picea engelmannii*) (Frank, Massman, Ewers, Huckaby, & Negrón, 2014). As the water cycle is disrupted, both the atmospheric and soil moisture environments are affected. From the atmospheric perspective, reduced transpiration (Frank, Massman, Ewers, Huckaby, & Negrón, 2014) directly contributes to reduced humidity; though considering that air advects freely in the atmosphere (Yi et al., 2008), it would be difficult to quantify whether reduced transpiration causes a detectable reduction in humidity in the air above an infested stand. Importantly, the loss of transpiration reduces the consumption of groundwater by trees within the beetle-impacted environment. This was detectable as a doubling of soil moisture within a lodgepole pine forest between 2 and 4 years after an outbreak (Brouillard, Mikkelson, Bokman, Berryman, & Sharp, 2017; Norton, Ewers, Borkhuu, Brown, & Pendall, 2015) and within the deeper rooting zone of an Engelmann spruce dominated forest (Frank, Massman, Ewers, Huckaby, & Negrón, 2014). The consequence of increased soil moisture on the water cycle becomes more difficult to summarize as the spatial extent grows beyond the stand and the temporal extent grows beyond the initial attack. Whether stream flow through and out of the watershed increases (Bethlahmy, 1974; Potts, 1984) or is unchanged (Biederman et al., 2014; Biederman et al., 2015) is difficult to predict, often due to compensatory factors within nearby ecosystems or flow through subsurface fracturing (St. Clair et al., 2015; Thayer et al., 2018). Similarly, whether soil moisture remains elevated over time is uncertain, especially as other processes such as evaporation (Reed, Ewers, & Pendall, 2014), growth release (Mast & Veblen, 1994), and succession (Winter et al., 2015), begin to offset the loss of transpiration. During the green phase of attack, other physiological changes occur within the plant, including reduced photosynthesis (Frank, Massman, Ewers, Huckaby, & Negrón, 2014), and carbon and nitrogen reallocation (Page, Jenkins, & Runyon, 2014); however, these events would not typically manifest as impacts on the abiotic environment until later.

As the outbreak advances, the direct effects on the abiotic environment are caused by the loss of needles as the red phase (infested trees are dying or dead and needles are reddish and beginning to drop) progresses to the gray phase (infested trees are dead and

without needles). First, a more open canopy will allow more sunlight to reach the understory, leading to secondary effects. For example, in Czechia, forest disturbance from the European spruce bark beetle tripled the average net shortwave radiation, which in turn increased snowmelt rates (Hotovy & Jenicek, 2020). In other studies, increased light into the canopy relaxed light-limitations on photosynthesis (Brown et al., 2012), and increased the radiant forcing of evaporation and sublimation (Frank, Massman, Ewers, & Williams, 2019; Huang et al., 2020). The effect on surface temperature is determined by the cumulative effect of sunlight, wind, and water in the abiotic ecosystem. For example, a Colorado, USA spruce-fir (*Picea-Abies*) forest impacted by the North American spruce beetle experienced colder minimum temperatures reaching $-1.3°C$ colder for 100% overstory mortality (Carlson, Sibold, & Negrón, 2021), and in a Wyoming, USA lodgepole pine forest impacted by mountain pine beetle, soils were also cooler (Griffin, Turner, & Simard, 2011). Second, a loss of canopy will reduce the surface drag on the atmosphere, which lowers the vertical profile of wind such that wind and turbulence will be higher throughout much of the canopy (Burns, Frank, Massman, & Patton, 2021), which can increase sublimation and evaporation (Monteith, 1965) and drive transpiration from needles of surviving trees (Baig & Tranquillini, 1980). Third, the loss of canopy will decrease interception of precipitation. In Colorado, a mountain pine beetle outbreak caused snow interception to be less than half when compared to an undisturbed lodgepole pine stand (Pugh & Small, 2013). In snow-dominated forest types, these three factors have direct effects on snow hydrology, from interception, sublimation, redistribution, and melt (Biederman et al., 2014; Pugh & Small, 2012). However, they can have opposing effects: in two nearby forests in Wyoming, a mountain pine beetle attack ultimately increased sublimation in a lodgepole pine forest due to the increased sunlight and wind (Biederman, Brooks, et al., 2014), while a North American spruce beetle outbreak caused less sublimation because snow that would have easily sublimated from the canopy instead fell to the surface and was retained by the snowpack (Frank et al., 2019). Finally, needles that drop to the surface will add litter to the forest floor. For lodgepole pine, these needles can increase nitrogen levels in the litter layer when compared to undisturbed forests (Griffin et al., 2011). Engelmann spruce needles can stay green and maintain their biological integrity for years after attack (Frank, Massman, Ewers, Huckaby, & Negrón, 2014; Mast & Veblen, 1994), such that needles with little difference from those of healthy trees fall to the ground during grey phase (Leonard et al., 2020).

These direct impacts to the abiotic environment often characterize the first few years after beetle attack. Subsequently, the cumulative effects of water, light, and nutrients will stimulate plant succession, which in turn can steer the postoutbreak environment toward different conditions. While increased sunlight in the canopy will likely persist for a long time, as surviving trees and understory plants grow (Stone & Wolfe, 1996), the microclimate around them will change. Water availability in the early years postoutbreak can promote plant growth in the surviving trees and understory plants, and the additional transpiration can essentially make up for the amount of water lost from the attacked trees. Hence, within a short time, the water cycle returns to a balance similar to the prebeetle forest, as observed in

a lodgepole pine forest in Wyoming (Biederman, Harpold, et al., 2014; Reed et al., 2014). In contrast, in an old-growth spruce forest in Novgorod Oblast, Russia impacted by the European spruce bark beetle, total ecosystem transpiration remained low at least four years after the disturbance (Karelin et al., 2020). The litter from fallen needles can decompose relatively quickly, leading to pulses of carbon respiration from the snowpack that return to normal within a few years (Berryman, Frank, Massman, & Ryan, 2018), such that nitrogen is retained in the ecosystem without exiting through streamflow and groundwater (Rhoades et al., 2013). The postoutbreak effect on snow sublimation may be the most stable over time. Regardless of whether a forest experiences a net increase or decrease in sublimation based on fundamental changes in forest structure, such as the loss of centuries old dominant spruce trees and their ability to intercept snow (Frank et al., 2019), it is likely that the new conditions that drive sublimation will persist for decades or centuries.

# 3  Changes to forest structure by bark beetle outbreaks

Forest structural changes during and following bark beetle outbreaks are influenced by climate, preattack forest conditions and management, and bark beetle biology. Outbreaks of bark beetles often start in landscapes where climate has stressed trees through drought, disease, or has allowed the survival of beetles and their larvae because of warmer winter temperatures (Raffa et al., 2008). Outbreaks can also start in dense, even-aged, mature stands, or in stands that have experienced a recent disturbance like fire or windthrow (McMillin et al., 2003; Reed et al., 2014).

Beetle outbreaks are often categorized into green, red, and grey phases. The green phase marks the beginning of the outbreak. During the green phase, outwardly the tree may appear somewhat normal, though the presence of pitch tubes on the stem indicates the tree is actively defending itself against the attack (Schmid & Frye, 1977). Inwardly, the tree is often experiencing severe water stress due to hydraulic failure in the occluded xylem or severe nutrient stress due to beetle consumption of the phloem (Paine, Raffa, & Harrington, 1997). On a stand scale, the green phase describes a forest mosaic dominated by trees in this state, and when beetle activity is prolonged across the landscape, the green phase can last for multiple years (Simard, Romme, Griffin, & Turner, 2010). With time, many trees transition into a red phase when needles discolor, die, and begin to drop. Eventually, the outbreak will end when most of the suitable host trees have been killed or when a climatic driven event, such as a hard freeze occurs (Miller, 1933). Trees enter the gray phase when they fully shed their needles and become snags. Over time, snags drop their bark and branches and fall over. A forest can remain in the gray phase for years or decades (Hyde, Peckham, Holmes, & Ewers, 2016). In a lodgepole pine forest in Colorado that experienced 78% mortality due to mountain pine beetle, only 17% of the snags fell within the first decade after attack, and 50% of snags are expected to fall within 15–20 years postattack (Rhoades et al., 2020).

In the aftermath, the severity and extent of an outbreak often relate back to preattack forest characteristics (Fig. 1). In a study of concurrent outbreaks of Douglas-fir beetle (*Dendroctonus pseudotsugae*), mountain pine beetle, and North American spruce beetle
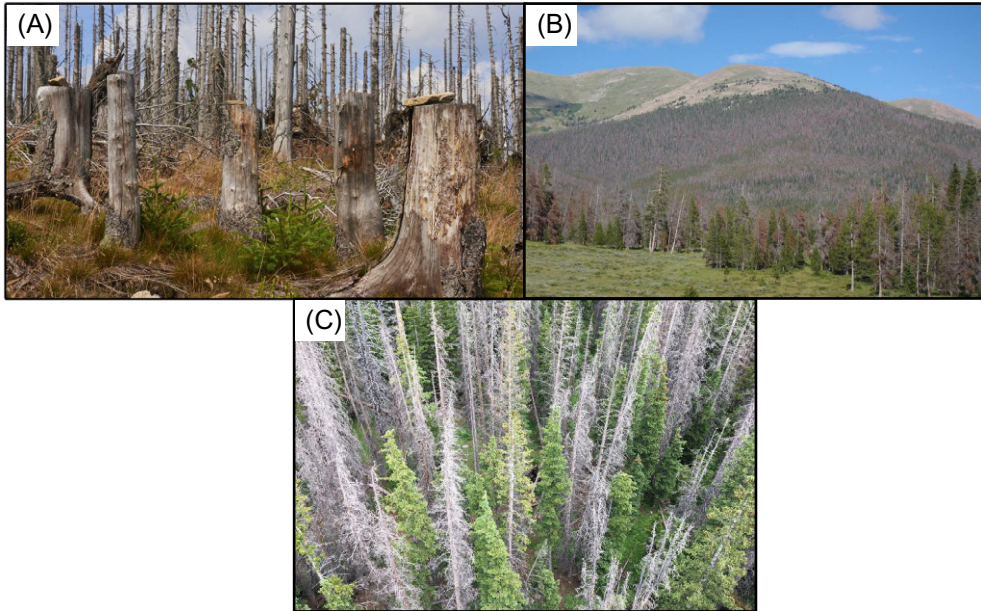
**FIG. 1** Extensive forest mortality due to bark beetle infestations in the: (A) Dreisessel Mountains at the border of Germany and Czech Republic, (B) Rocky Mountains in Colorado, USA, and (C) Rocky Mountains in Wyoming, USA. *(A) Photo Credit: Petr Bonek, Shutterstock. (B and C) Photo Credit: Paula Fornwalt, USDA Forest Service.*

in the greater Yellowstone area of Wyoming, mortality rates of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine, and Engelmann spruce were related to preattack landscape-scale basal area, forest cover, elevation, and nearby beetle pressure; lodgepole pine mortality was also related to stand-scale basal area (Simard et al., 2012). Similarly, in a nearby forest, a Douglas-fir beetle outbreak that caused 40%–70% basal area mortality was correlated with the prebeetle basal area and percent composition of Douglas-fir (McMillin & Allen, 2003).

## 4  Responses of flora following bark beetle outbreaks

By altering abiotic conditions as described above, bark beetle outbreaks can indirectly trigger a wide range of changes to plant communities and populations. Here, we synthesize the available literature to describe how three broad taxonomic classes of plants have been found to respond to outbreaks. We first summarize tree responses, and specifically the responses of regenerating trees, as an understanding of tree regeneration dynamics is critical to predicting future forest recovery trajectories. Where feasible, we distinguish between older, larger regenerating trees that established prior to outbreaks (i.e., advance regeneration) and younger, smaller trees that established postoutbreak. We also summarize responses for herbs and shrubs, which often comprise the vast majority of plant diversity in forests, as well as for mosses, which can likewise be a major component of the forest flora.

## 4.1 Regenerating trees

### 4.1.1 Positive responses

Bark beetle outbreaks commonly lead to community-level increases in tree regeneration in the first few years or decades following disturbance (e.g., Pappas, Tinker, & Rocca, 2020; Pelz & Smith, 2012; Zeppenfeld et al., 2015). For example, two separate mountain pine beetle outbreaks in Colorado lodgepole pine forests spurred notable increases in the overall density of tree regeneration (Pappas et al., 2020; Pelz & Smith, 2012; Perovich & Sibold, 2016). Similarly, in Wyoming, forests that experienced an infestation of Douglas-fir beetles had nearly four times more tree regeneration than those that did not (McMillin & Allen, 2003).

At the population level, regenerating trees of many species often establish and/or grow well in the wake of bark beetle outbreaks (e.g., Pappas et al., 2020; Perovich & Sibold, 2016; Zeppenfeld et al., 2015). Perhaps the most well-documented example is lodgepole pine, a shade-intolerant conifer (Collins, Rhoades, Hubbard, & Battaglia, 2011; Pappas et al., 2020; Pelz & Smith, 2012; Perovich & Sibold, 2016). In Rocky Mountain National Park in Colorado, lodgepole pine regeneration density nearly doubled in the five years following the peak of a mountain pine beetle outbreak (Pappas et al., 2020). Elsewhere in Colorado, regenerating lodgepole pine height growth also increased following a mountain pine beetle outbreak (Collins et al., 2011). Regeneration of other shade-intolerant species that have established and/or grown well after outbreaks include birch (*Betula* spp.) (Fischer, Fischer, Kopecký, Macek, & Wild, 2015), quaking aspen (*Populus tremuloides*) (Pappas et al., 2020; Pelz & Smith, 2012), and rowan (*Sorbus aucuparia*) (Jonášová & Prach, 2004). More shade-tolerant species such as subalpine fir (*A. lasiocarpa*) (Collins et al., 2011; Pappas et al., 2020; Perovich & Sibold, 2016), Norway spruce (Fischer et al., 2015; Macek et al., 2017; Zeppenfeld et al., 2015), and Engelmann spruce (Pappas et al., 2020; Pelz & Smith, 2012; Perovich & Sibold, 2016) can also do well after outbreaks, especially when overstory tree mortality is not complete.

Outbreak severity and time since outbreak are two factors that are commonly positively correlated with the postoutbreak responses of regenerating trees (e.g., Pappas et al., 2020; Pelz, Rhoades, Hubbard, & Smith, 2018; Perovich & Sibold, 2016; Winter, Baier, & Ammer, 2015; Zeppenfeld et al., 2015). Working in lodgepole pine forests attacked by mountain pine beetles in Colorado, Pelz et al. (2018) found that the density of both pine advance regeneration and pine postoutbreak regeneration was greater in plots with higher mortality rates. They also found that height growth of lodgepole pine regeneration was greater for higher levels of mortality. Using a large data set collected in Norway spruce forests in Germany and the Czech Republic, Zeppenfeld et al. (2015) found that total regeneration densities increased fivefold through time, from $\sim 400 \, \text{stems ha}^{-1}$ preoutbreak to $\sim 800 \, \text{stems ha}^{-1}$ 1–5 years postoutbreak to $\sim 2000 \, \text{stems ha}^{-1}$ 11–15 years postoutbreak. Winter, Baier, and Ammer (2015) found similar temporal trends in Norway spruce forests.

There is considerable interest in examining whether abundant tree regeneration may enable the future maintenance of preoutbreak forest composition following bark beetle outbreaks, or whether it may trigger a future shift in composition (Fig. 2). Perhaps
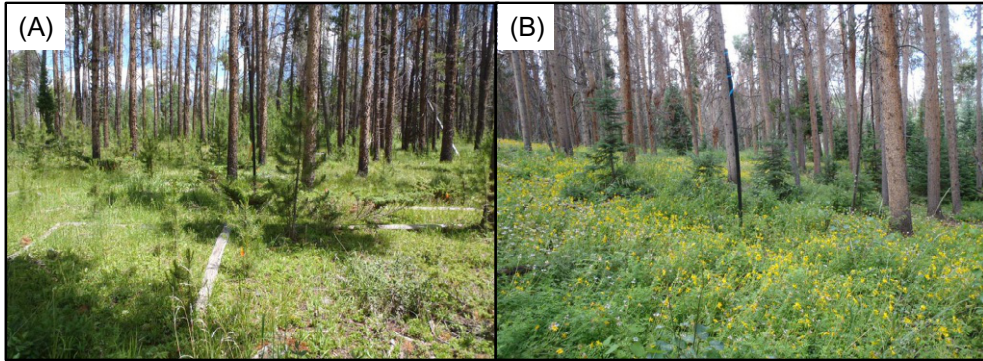
**FIG. 2** Forest compositional trajectories following a mountain pine beetle outbreak in lodgepole pine—dominated forests, Colorado, USA: (A) composition likely to be maintained, with lodgepole pine seedlings, saplings, and poles growing underneath a mostly dead lodgepole overstory; and (B) composition likely to be shifted, with Engelmann spruce and subalpine fir seedlings, saplings, and poles poised to replace a mostly dead lodgepole overstory. *Photo Credit: Paula J. Fornwalt, USDA Forest Service.*

unsurprisingly, the available literature suggests that the prevailing outcome will be variable across, and even within, forest types. For Norway spruce forests of Germany and the Czech Republic, for example, ample spruce regeneration suggests that this species is likely to remain dominant for the foreseeable future (Jonášová & Prach, 2004; Winter, Baier, & Ammer, 2015; Zeppenfeld et al., 2015). For lodgepole pine forests of Colorado and Wyoming, both outcomes may unfold (Collins et al., 2011; Diskin, Rocca, Nelson, Aoki, & Romme, 2011;Kayes & Tinker, 2012 ; Perovich & Sibold, 2016). Whether or not lodgepole pine remains dominant in a given stand in the future may depend on the stand's moisture availability and age, which affects its suitability for lodgepole pine regeneration versus the regeneration of associated Engelmann spruce and subalpine fir (Kayes & Tinker, 2012; Perovich & Sibold, 2016).

### 4.1.2 Negative responses

While negative effects of bark beetle outbreaks on tree regeneration have been documented (e.g., Allen, Wesser, Markon, & Winterberger, 2006; Klutsch et al., 2009; Macek et al., 2017), these generally appear to be less common than positive effects. Klutsch et al. (2009) found that the density of Engelmann spruce and subalpine fir regeneration was lower in plots infested by mountain pine beetles 4–7 years prior than in plots that were not infested. Allen et al. (2006) found that in Alaska, USA, where a North American spruce beetle outbreak in a heterogeneous forest landscape resulted in an overstory mortality gradient, both white spruce (*P. glauca*) and black spruce (*P. mariana*) regeneration declined sharply as mortality increased from trace to high. They suggested that stands with high mortality may therefore take much longer to recover to their late-successional, preoutbreak state than those with a lesser amount of mortality. Jonášová and Prach (2004) observed tree regeneration during the first five years following a European spruce bark beetle outbreak in a Norway spruce forest and reported an abundance of spruce

regeneration in the first year; however, many of the spruce were young and some died over the observation period. Nonetheless, the authors indicated that the numbers of spruce were more than sufficient for forest recovery.

### 4.1.3 Neutral responses

Several studies describe neutral tree regeneration responses to bark beetle outbreaks (e.g., Astrup, Coates, & Hall, 2008; Klutsch et al., 2009; Zeppenfeld et al., 2015), although generally speaking, these studies also seem to be less common than those that describe positive responses. At the community scale, Astrup et al. (2008) documented sparse regeneration after a mountain pine beetle outbreak in British Columbia, Canada, which they attributed to a lack of disturbance to the moss-dominated forest floor. Klutsch et al. (2009) found that the density of tree regeneration (including both advance and postoutbreak regeneration) was comparable in lodgepole pine stands infested and not infested with mountain pine beetles in Colorado. At the population scale, lodgepole pine (Klutsch et al., 2009), quaking aspen (Klutsch et al., 2009), and rowan (Zeppenfeld et al., 2015) have been found to respond neutrally to beetle outbreaks, although positive responses tend to be more common for these shade-intolerant species.

## 4.2 Herbs and shrubs

### 4.2.1 Positive responses

As the review by Runyon et al. (2020) highlights, herb (i.e., graminoid, forb, and fern) and shrub communities generally respond positively to bark beetle outbreaks. Total biomass and cover, in particular, can increase markedly (e.g., McMillin & Allen, 2003; Stone & Wolfe, 1996; Winter, Ammer, et al., 2015). Total biomass in lodgepole pine stands in Utah, USA, for example, was an order of magnitude greater where mountain pine beetles caused high levels of tree mortality than where they caused little to no mortality (Stone & Wolfe, 1996). Likewise, in Douglas-fir stands in Wyoming, total cover in those that had been attacked by the Douglas-fir beetle was about three times greater than in those that were not attacked (McMillin & Allen, 2003). While both herbs and shrubs contributed to the patterns captured by these two studies, herbs played a more outsized role. Like total biomass and cover, total diversity can also be promoted by bark beetle outbreaks (e.g., Beudert et al., 2015; Jonášová & Matějková, 2007; Pappas et al., 2020). Total richness, a diversity metric that reflects the number of unique species in a given area, increased following outbreaks of the European spruce bark beetle in the Czech Republic and Germany (Beudert et al., 2015; Jonášová & Matějková, 2007; Jonášová & Prach, 2008), the North American spruce beetle in the USA (Carter, 2021), and the mountain pine beetle in the USA and Canada (Pappas et al., 2020; Steinke, McIntosh, Schroeder, & Macdonald, 2020). Other metrics of total diversity, such as the Shannon Index and the Simpson Index, have also increased following outbreaks (Pappas et al., 2020).

Many herb and shrub populations also generally have positive responses to bark beetle outbreaks (e.g., Fischer et al., 2015; Holsten, Werner, & Develice, 1995; Lehnert, Bässler, Brandl, Burton, & Müller, 2013). Lehnert et al. (2013) used an indicator species analysis

to show that 15 years after a European spruce bark beetle outbreak in Germany, many more species were indicative of transitional and open forests (where beetle-caused tree mortality was generally moderate to high) than of closed forests (where mortality was generally absent to low), suggesting that the outbreak benefitted more species than it harmed. Similarly, Carter (2021) found that most of the common species in a Wyoming, Engelmann spruce—subalpine fir forest increased in cover following a beetle outbreak. Carter (2021) also found that species' responses were positively related to preoutbreak frequency, which reflects species' abilities to grow and/or spread to new areas, as well as height at maturity, which reflects species' abilities to capture light.

The positive effects of bark beetle outbreaks on herbs and shrubs are often amplified by increasing outbreak severity (e.g., Stone & Wolfe, 1996; Pec et al., 2017; Carter, 2021; Fig. 3).
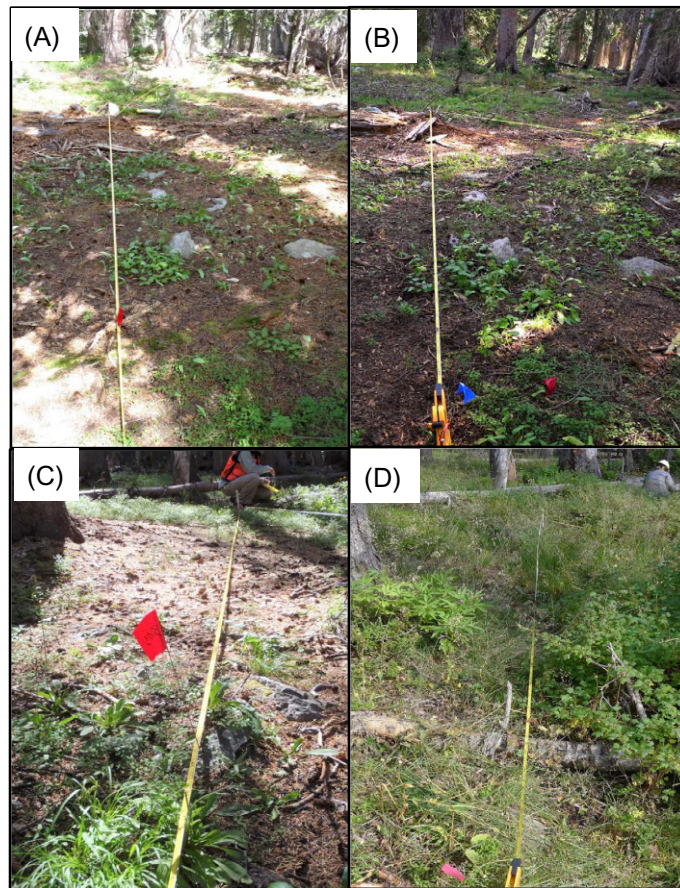


**FIG. 3** Understory plant responses to outbreak severity in a Wyoming, USA, Engelmann spruce—subalpine fir forest that was attacked by North American spruce beetles: (A) a plot with low understory cover 1–2 years after the onset of a low-severity outbreak; (B) still had low cover 8 years later; and (C) a plot with low understory cover 1–2 years after the onset of a high-severity outbreak (D) experienced a marked increase in cover 8 years later. *Photo Credit: (A and C) Paula J. Fornwalt and (B and D) John M. Frank, USDA Forest Service.*

For example, as lodgepole pine mortality from mountain pine beetles increased, so did various metrics of herb and shrub biomass (Pec et al., 2017; Stone & Wolfe, 1996), cover (Pappas et al., 2020), and diversity (Pappas et al., 2020; Pec et al., 2017). Similarly, as Engelmann spruce mortality from North American spruce beetles increased, the total number of species in flower also increased, to the benefit of wild bees that provide important pollination services (Davis, Rhoades, Mann, & Griswold, 2020; Section 5.1.1).

Positive herb and shrub responses to beetle outbreaks can also be amplified as time since outbreak increases (e.g., Griffin et al., 2011; Kovacic, Dyer, & Cringan, 1985; Winter, Ammer, et al., 2015). This phenomenon was captured by Kovacic et al. (1985), who established a chronosequence of sites in Colorado ponderosa pine (*P. ponderosa*) stands that had been attacked by mountain pine beetles up to 10 years prior. In their study, total understory biomass peaked in 5-year postattack stands, with values in these stands two orders of magnitude greater than in unattacked stands; herbs comprised the vast majority of the biomass, and similarly peaked 5-years postattack. Herbs and shrubs will likely eventually attenuate toward preattack conditions as forests redevelop and reduce available resources, although this shift may not be initiated for several years or even decades after the bark beetle outbreak (Griffin et al., 2011; Kovacic et al., 1985; Winter, Ammer, et al., 2015).

### 4.2.2 Negative responses

To our knowledge, only a few studies have documented negative responses of herb and shrub communities and populations to bark beetle outbreaks (e.g., Holsten et al., 1995; Lehnert et al., 2013; Winter, Ammer, et al., 2015). Work by Holsten et al. (1995) in an Alaskan Lutz spruce (*P. sitchensis*) forest during and following a North American spruce beetle outbreak perhaps provides the clearest illustration of a negative community response; the study shows that total richness (which was dominated by herb and shrub species but also included tree and moss species) decreased through time. They hypothesized that the decrease in total richness was driven by the increased abundance of two highly competitive species, bluejoint grass (*Calamagrostis canadensis*) and fireweed (*Chamerion angustifolium*).

### 4.2.3 Neutral responses

While herb and shrub communities and populations tend to be promoted by bark beetle outbreaks, neutral effects are not uncommon (e.g., Allen et al., 2006; Jonášová & Prach, 2008; Klutsch et al., 2009). Total cover, as well as grass, forb, and shrub cover, did not differ between unattacked Colorado lodgepole pine stands and stands that had been attacked 4–7 years prior to sampling (Klutsch et al., 2009). Similarly, for Norway spruce stands in the Czech Republic, total cover did not differ between preoutbreak and 5-year postoutbreak time periods, although total richness did increase with time (Jonášová & Prach, 2008). Total richness did not vary for white spruce plots distributed across four beetle infestation levels in Alaska (Allen et al., 2006); moreover, the cover of 15 common herb and shrub species also did not vary across the four infestation levels. Klutsch et al.

(2009) posited that the herb and shrub communities they studied may respond positively to the outbreak in subsequent years, although Jonášová and Prach (2008) and Allen et al. (2006) suggested that the lack of ground disturbance would probably preclude future postoutbreak changes in their study systems.

## 4.3 Mosses

Given the general proclivity of moss for shady, damp environments, it is unsurprising that they are often negatively impacted by bark beetle outbreaks at both community and population scales (Edwards, Krawchuk, & Burton, 2015; Jonášová & Prach, 2008). The cover of red-stemmed feathermoss (*Pleurozium schreberi*) was cut in half as a mountain pine beetle outbreak in a lodgepole pine forest advanced from the red to the early grey stage in British Columbia, for example (Edwards et al., 2015). That said, mosses can also be unaffected (Allen et al., 2006; Beudert et al., 2015), and even positively affected by bark beetle outbreaks (Beudert et al., 2015; Lehnert et al., 2013).

# 5  Responses of fauna following bark beetle outbreaks

There are direct and indirect mechanisms by which bark beetle outbreaks can impact faunal communities and populations. Direct mechanisms are limited to beetles as a food resource; for example, mountain pine beetle is an important source of food for several avian species in North American forests (Chan-McLeod, 2006). The remaining mechanisms by which bark beetles impact wildlife are indirect and mediated through vegetation changes (Sections 3 and 4), which result in significant alterations to wildlife habitats. Defoliation of the tree canopy, loss of living tree bark, cessation/loss of cone production, proliferation of standing dead trees, falling of dead trees, and enhanced understory plant production can cause positive or negative, and linear or nonlinear impacts on faunal communities (Chan-McLeod, 2006). These impacts occur on a temporal scale, as time since outbreak and resulting forest regeneration is an important factor. In this section, we review spatial and temporal effects of habitat changes due to bark beetle outbreaks on arthropods, birds, mammals, reptiles, and microbial populations and communities.

## 5.1 Arthropods

### 5.1.1 Positive responses

Several studies of arthropod community responses to bark beetle outbreaks have reported positive effects on biodiversity in central European study systems. Müller et al. (2008) found that insect biodiversity increased in association with increasing habitat heterogeneity due to tree mortality and gaps created by the European spruce bark beetle in the Bavarian Forest National Park. Of 60 indicator insect species, 29 preferred bark beetle-generated gaps; 24, 3, 3, and 1 species, respectively, preferred meadows, meadow edges, bark beetle-generated gap edges, and intact forest. In an assessment of species richness of 19 taxonomic groups following a large-scale European spruce bark beetle infestation in

spruce forests in southeastern Germany, Beudert et al. (2015) found increases in richness for five arthropod groups (saproxylic beetles, spiders, cicadas, hoverflies, and bees/wasps). The International Union for Conservation of Nature (IUCN) red-listed species specifically, carabid beetles, saproxylic beetles, spiders, and bees/wasps showed an increase in species richness (Beudert et al., 2015). Additionally, sawflies that are red-listed occurred only in bark beetle-affected areas. A significant focus has been placed on saproxylic insects that utilize deadwood during any part of their life cycle; many of these species are red-listed, and are especially known to respond positively to increased habitats after bark beetle outbreaks in European forests (e.g., Hilszczański, Jaworski, Plewa, & Horák, 2016; Thorn, Bässler, Svoboda, & Müller, 2017). Based on the results of these studies, European spruce bark beetle is considered as a keystone species in central Europe (Müller et al., 2008) because it alters forested environments in a manner that increases arthropod biodiversity, especially of IUCN red-listed species.

North American studies corroborate many of the positive responses documented in central Europe. In an Engelman spruce forest in the southern Rockies, Davis et al. (2020) reported that bee captures were not affected by North American spruce beetle outbreaks; however, bee species richness and diversity were higher in postoutbreak stands, particularly early in the growing season. Forest stands postoutbreak had higher floral density and flowering species richness during peak bloom than nonaffected stands (Section 4.2.1), and hence, bee responses seemed to be linked to foraging habitat. Similarly, insect abundance and species diversity increased linearly with lodgepole pine tree mortality due to the mountain pine beetle epidemic in Utah (Stone, 1995). Increases in species diversity and abundance have also been reported after a Douglas-fir beetle outbreak in Idaho, USA, that were correlated with percent tree mortality (Foote, Foote, Runyon, Ross, & Fettig, 2020). Many wild bees tend to be positively associated with open canopy conditions, greater availability of nesting resources such as coarse woody debris (Fortuin & Gandhi, 2021), and greater availability of food resources such as understory flowering plants (Sections 3 and 4) (Hanula, Ulyshen, & Horn, 2016), and these few studies corroborate these patterns.

### 5.1.2 Negative responses

Woodboring beetles (Buprestidae and Cerambycidae) comprise an important taxonomic group of insects that have a complex relationship with bark beetles. Woodboring beetles are secondary forest pests as they colonize trees weakened, stressed, or killed by fire, blowdown, timber harvest, or bark beetle infestations. Hence, any disturbance or stress event that results in damage to trees and stands greatly benefits woodboring beetle populations and communities. A few studies have, however, also established the potential for interspecific competition between larval woodborers, who inhabit the cambium layer and then tunnel into the sapwood and heartwood, and bark beetle larvae, who inhabit the phloem and cambium layers (Dodds, Graber, & Stephen, 2001). Ray et al. (2019) found a negative relationship between bark and woodboring beetle activity, but patterns of woodboring beetle colonization on trees weakened by bark beetle outbreak and fire did not differ,

indicating that the interactions between these two taxa may remain the same under various disturbances. Similarly, Costello, Jacobi, and Negrón (2013) reported that 2–3 times higher numbers of woodboring beetles emerged from trees killed by wildfire than by mountain pine beetles, and these trees had different beetle species composition. Such differences could be due to variable host conditions created by the two disturbances (beetle versus fire killed).

## 5.2  Birds

### 5.2.1  Positive responses

Numerous studies have considered the impacts of bark beetle outbreaks on avian communities. The majority have found increases in various metrics of avian biodiversity due to an increase in habitat complexity and resource availability (Fig. 4), although often they have noted important caveats to these trends in the western North America. Saab et al. (2014) identified positive responses of cavity-nesting species, species nesting in the shrub-level, bark-drilling species, and bark-gleaning species primarily reliant on live trees (weak association) after mountain pine beetle outbreaks. Janousek, Hicke, Meddens, and Dreitz (2019) found that avian species richness did not differ between outbreak and nonoutbreak sites, and weak evidence existed for a community-level response to increasing outbreak severity and time since the beetle outbreak. There was a turnover in community composition, with >50% of bird species having different occurrence rates after beetle outbreaks. Species richness, therefore, alone does not fully express changes in the forest bird community engendered by beetle outbreaks; many species, particularly cavity nesters, utilize beetle-killed forests and persist at higher occurrence rates for up to 10 years postoutbreak. Latif, Ivan, Seglund, Pavlacky, and Truex (2020) also reported that bark



**FIG. 4** Spruce tree killed by bark beetles being used for nesting habitat by Eurasian treecreeper. *Photo Credit: mbobrik, Shutterstock.*

beetle outbreaks benefit wildlife biodiversity, as understory-associated birds, aerial insectivores, and snag-associated avian species all correlated positively with beetle outbreak resulting from understory vegetative release. Finally, Saab, Latif, Dresser, and Dudley (2019) noted increases in the density of hatched woodpecker nests for beetle-foraging species, and strong relationships between variables associated with nonoutbreak forests and nest survival. Hence, beetle-foraging woodpeckers responded numerically rather than functionally (e.g., nest survival) to bark beetle outbreaks.

Similar trends regarding the short-term positive associations between bark insectivorous bird species and bark beetle outbreaks are expected for southeastern USA forests. Tchakerian and Coulson (2011) described the relationship between woodpeckers and the southern pine beetle as "boom and bust": as an outbreak proceeds, woodpecker densities initially increase in accordance with beetle abundance, followed by a rapid decline as beetles run out of susceptible trees and their populations decline. They reported on a study by Kroll, Conner, and Fleet (1980) on the interactions between four woodpecker species (downy [*Picoides pubescens*], hairy [*P. villosus*], pileated [*Dryocopus pileatus*], and red-cockaded [*P. borealis*]) on southern pine beetle populations in east Texas; all four species were observed to prey heavily on beetles and to have strong impacts on the density of beetle pupae and adults. Woodpeckers were found in higher numbers in bark beetle-infested than in uninfested stands. This could be due to either birds foraging more in the beetle outbreak areas and/or their numbers increasing due to greater availability of prey items (Fayt, Machmer, & Steeger, 2005).

Generally positive associations between avian biodiversity and bark beetle outbreaks in western North America also hold true for European coniferous forests. In old-growth coniferous forests in Poland, there were 25% more bird species in gaps created by European spruce beetles than in the closed-canopy forest (Przepióra, Loch, & Ciach, 2020). Avian species richness correlated positively with the number of snags due to outbreak damage. The number of individual birds recorded in the gaps was 40% higher than in the closed-canopy forest and correlated positively with the number of fallen logs. An assessment of species richness of 19 taxonomic groups following a European spruce beetle outbreak in German spruce forests determined that those of IUCN red-listed bird species increased due to bark beetle outbreak (Beudert et al., 2015). Taken together, the majority of studies of the effects of bark beetles on birds support the notion that canopy gaps resulting from outbreaks generally increase avian species richness, diversity, and abundance by providing suitable habitats for cavity-nesting, ground-nesting and insectivorous birds.

Bark beetle outbreaks can further have positive impacts on complex ecological networks that persist for many years. For example, Cockle and Martin (2015) conducted a 13 year-long study on "nest webs," which are commensal networks linking secondary cavity-nesting birds with excavators that create cavities (primarily woodpeckers). Excavator species were determined to increase in abundance corresponding to a rapid increase in adult and larval mountain pine beetles, which serve as a food resource. Cavity availability increased at the onset of the outbreak in 1998, reaching a peak in 2005. During and after the outbreak in 2011, secondary cavity-nesters increased their use of cavities made by five species of beetle-eating excavators, decreasing their use of cavities produced by Northern

flickers (*Colaptes auratus*) (an excavator species that did not experience a population increase due to the beetle outbreak). The overall network was determined to increase in evenness and diversity of interactions and to decline in nestedness and niche overlap; these patterns persisted for several years after the outbreak. Bark beetle outbreaks can, therefore, increase interaction diversity within forest ecosystems at various temporal scales, impacting more complex components of biodiversity beyond that of single species or feeding guilds.

### 5.2.2 Negative responses

Negative responses of specific avian species have been reported in several forest types. Latif et al. (2020), which established generally positive effects of mountain pine beetle outbreaks on avian communities in lodgepole pine forests, found that the spruce-fir forests had primarily negative relationships with outbreak damage severity. Open-cup canopy nesters and canopy insectivorous birds comprised most of the guilds negatively associated with outbreak severity in spruce-fir forests. Similarly, Klenner and Arsenault (2009) predicted the impacts of the *Dendroctonus* beetle outbreak over time (1–50 years) in British Columbia. Among the taxa negatively impacted by the outbreak were the ponderosa pine habitat specialists: Clark's nutcracker (*Nucifraga columbiana*), pygmy nuthatch (*Sittidae pygmaea*), and white-headed woodpecker (*Picoides albolarvatus*). While hairy woodpecker (*Leuconotopicus villosus*) and pileated woodpecker populations initially increased, these species began to decline five years after the outbreak as the influx of food and habitat resources declined. It seems that there are differences in ecological significance of bark beetle outbreaks for bird communities as based on forest types (and associated changes in prey) and that forest type may be an important consideration when making management decisions post-bark beetle outbreak.

Southern pine beetle outbreaks can negatively impact the habitats of red-cockaded woodpecker, a species of conservation concern, endemic to the southeastern USA that is reliant on a constant supply of living, old pines with decaying heartwood for cavity excavation (Conner, Rudolph, Kulhavy, & Snow, 1991; Tchakerian & Coulson, 2011). Because these are the same trees that are most susceptible to southern pine beetles, outbreaks are also a major cause of red-cockaded woodpecker cavity tree mortality in loblolly and shortleaf (*P. echinata*) pines. Southern pine beetles can eliminate active single cavity trees, cavity tree clusters, and foraging habitat of this endemic woodpecker, posing serious threats to conservation and recovery efforts (Conner, Saenz, Rudolph, & Coulson, 1998).

There may be different outcomes for avian biodiversity as time since the beetle outbreak progresses. While mountain pine beetle outbreaks can initially result in improved conditions for cavity-users and other birds that feed on insects in dying trees, these enhanced conditions deteriorate for many species as the supply of forest insects and old trees declined with time (Martin, Norris, & Drever, 2006). The cumulative effects of outbreaks in the context of other habitat and environmental changes (e.g., anthropogenic) on the landscape has the potential to negatively affect the stability of avian populations, despite initial positive responses.

### 5.2.3 Neutral responses

Bark beetle outbreaks can produce effectively neutral responses in faunal communities through a variety of means such as at intermediate disturbance (e.g., at low and high levels of disturbance, species will respond negatively, but at medium levels, they respond positively); by engendering different effects as time progresses (e.g., "boom and bust"); or by simply not impacting species in any meaningful quantitative way. Abundance and diversity of avian species were highest in stands with moderate lodgepole pine tree mortality due to mountain pine beetle in Utah (Stone, 1995). Aerial, ground, and foliage-gleaning insectivorous and omnivorous bird species did not exhibit consistent patterns in relation to mountain pine beetle-killed forests; and pine seed-foragers were apparently nonresponsive to bark beetle outbreaks (Saab et al., 2014). Only bark insectivore bird species responded positively to tree mortality due to mountain pine beetle outbreaks, while other foraging guilds did not show a significant response in British Columbia (Drever, Goheen, & Martin, 2009).

## 5.3 Mammals

### 5.3.1 Positive responses

Several studies have reported positive impacts of bark beetle outbreaks on mammals in Europe and North America. Large mammals appear to be responsive to habitat alterations and changes in plant communities during and after bark beetle outbreaks (Fig. 5). Small and medium-sized mammal species were more abundant and diverse in lodgepole pine stands with moderate and severe tree mortality due to mountain pine beetle than those with no or low (26%–50% dead) tree mortality in Utah (Stone, 1995). Fecal pellet groups of large ungulates were found to increase linearly with tree mortality indicating that there was a higher use of damaged than undamaged stands. The progression of forest dieback stemming from a massive European spruce bark beetle infestation in the mid-1990s in the Bavarian Forest National Park has been advantageous to mammalian herbivore populations, due to understory vegetative release and a corresponding increase in food resource availability (Heurich, Baierl, Günther, & Sinner, 2011).

Due to greater gap formations and presence of snags, many animals, particularly bats, that utilize such habitats show positive responses. For instance, foraging activity increased with forest openings due to European spruce bark beetle outbreaks in Germany in the barbastelle bat (*Barbastella barbastellus*); this species also tended to selectively roost in trees killed by bark beetles (Kortmann et al., 2018). Bats utilized *Dendroctonus*-killed lodgepole pine stands, but their presence and activity were not affected by the level of tree mortality in British Columbia, Canada (Lawson et al., 2019). While little brown bats (*Myotis lucifugus*) did not seem to respond to severity of North American spruce beetle infestation, their activity increased with decreased tree density in Alberta (Randall, Barclay, Reid, & Jung, 2011).

Bark beetles may provide additional prey items to smaller mammals (as they did for birds). Pretzlaw, Trudeau, Humphries, LaMontagne, and Boutin (2006) reported a unique direct benefit of spruce bark beetles to red squirrel (*Tamiasciurus hudsonicus*) populations in Canada. Following an outbreak in the mid-1990s, squirrels were observed in

**FIG. 5** A decade after North American spruce beetles caused extensive tree mortality in a Wyoming, USA, Engelmann spruce—subalpine fir forest, a lush herb layer provides habitat for wildlife. *Photo Credit: John M. Frank, USDA Forest Service.*

the early 2000s feeding on North American spruce bark beetles. Further, there was an increase in the prevalence of autumn beetle foraging by squirrels, corresponding to a decrease in squirrels' preferred food resource of spruce seeds. By 2003, 73% of monitored squirrels fed on beetles; this translated to 20% of squirrels' daily energy requirements. Hence, red squirrels seemed to feed on larval North American spruce bark beetles as a short-term solution to a climate-mediated beetle outbreak. As decreases in local spruce seed production persisted for at least 10 years following the initial attack, bark beetle outbreaks may ultimately negatively impact food resource availability and habitat suitability for red squirrels.

### 5.3.2 Negative responses

Bark beetle outbreaks following other disturbances, including attacks by other insect taxa, can negatively affect native wildlife communities. For example, numbers of Mt. Graham red squirrels (*T. hudsonicus grahamensis*), an endangered species endemic to the

southwestern USA, declined abruptly following various insect attacks (moths, bark beetles, and introduced aphids) which resulted in catastrophic damage to southwestern conifer forests (Koprowski, Alanen, & Lynch, 2005). This series of insect attacks altered forest habitat for the Mt. Graham red squirrel by reducing basal area and stem density of live stems and decreasing availability of major food resources (i.e., fungi and tree seeds). Compounding disturbances present a significant conservation challenge because disturbance events can interact to result in severity of damage to forests beyond that of a single natural disturbance event. Compound disturbance events involving epidemic bark beetle outbreaks may lead to severe and longer-term consequences for associated faunal communities.

### 5.3.3 Variable responses

In general, extremely variable effects of bark beetle outbreaks at the species-level have been reported for mammals. Herbivorous ungulates exhibited an overall positive response to mountain pine beetle activity in the Rocky Mountains, but with species-specific variation (Ivan, Seglund, Truex, & Newkirk, 2018). Elk (*Cervus canadensis*) were positively associated with severity of damage, but not years elapsed since outbreak, whereas mule deer (*Odocoileus hemionus*) exhibited the opposite relationship. Moose (*Alces alces*) responded in a quadratic fashion; use of forest stands adjacent to preferred habitat peaked 3–7 years after an outbreak commenced, but only when damage was severe. Rodents similarly exhibited a variety of responses, with yellow-bellied marmot (*Marmota flaviventris*) displaying a quadratic relationship with years elapsed since outbreak due to their use of impacted stands adjacent to rock outcroppings, again only when damage was severe. Red squirrel (*T. hudsonicus*) presence declined in severely impacted stands, likely as a response to diminished cone crops, whereas golden-mantled ground squirrels (*C. lateralis*) and chipmunks (*Neotamias* spp.) exhibited a shallow negative relationship with years elapsed since outbreak (Ivan et al., 2018).

Carnivores also exhibited species-specific responses to bark beetle outbreak. Coyotes (*Canis latrans*) exhibited a shallow negative relationship with years elapsed since outbreak, whereas red foxes (*Vulpes vulpes*) positively responded to years elapsed (although their overall presence declined as severity of damage increased). A variety of other mammalian taxa, including black bears (*Ursus americanus*), American marten (*Martes americana*), snowshoe hares (*Lepus americanus*), and porcupines (*Erethizon dorsatum*), did not appear to be influenced by beetle activity (Ivan et al., 2018).

In terms of bats, Beudert et al. (2015) found no effect of bark beetle mortality in German spruce forests on bat species richness, indicating that this taxonomic group is not strongly impacted by bark beetle outbreaks. Mehr, Brandl, Kneib, and Müller (2012) assessed the impact of the European spruce bark beetle combined with postoutbreak salvage logging on guilds of insectivorous bats in central Europe, and determined that open-habitat foraging species increased in stands impacted by bark beetle attacks, while closed-habitat foragers declined. These results illustrate that observations of general bat activity may mask specific responses of different feeding guilds and at the species-level.

## 5.4 Reptiles

### 5.4.1 Positive responses

In the only study on reptiles (though indirectly, through quantification of habitat variables and reptile distributions), Sutton, Wang, and Schweitzer (2010) found that some reptile distributions in the southeastern USA respond positively to the creation of canopy gaps and fallen coarse woody debris attributed to the southern pine beetle. Among those that preferred the more open and heterogeneous habitat associated with southern pine beetle outbreaks in forests were eastern fence lizards (*Sceloporus undulatus*), copperheads (*Agkistrodon contortrix*), and grey ratsnakes (*Pantherophis spiloides*).

### 5.4.2 Negative responses

In the same study on reptiles in southern pine beetle-disturbed forests, little brown skinks (*Scincella lateralis*) and eastern worm snakes (*Carphophis a. amoenus*) were associated with sites with greater litter depth and canopy cover e.g., those that likely remained largely undisturbed by bark beetle outbreaks (Sutton et al., 2010). We are aware of no other studies that directly or indirectly consider the effects of bark beetle outbreaks on reptile populations, communities, or distributions, and thus are unable to draw general conclusions about the responses of reptiles to bark beetles.

## 6 Responses of soil microbiota following bark beetle outbreaks

Relatively few studies have considered the impacts of epidemic bark beetle outbreaks on associated forest litter and soil microbiota even though these taxa are intimately related to many ecosystem services and especially tree community composition, biomass, and biodiversity. Further, trees form significant and extensive root symbiosis with mycorrhizal fungi, on which they rely for nutrient and water uptake. Given the critical role soil bacteria and fungi play in carbon and nitrogen cycling, it is anticipated that epidemic outbreaks of bark beetles, resulting in massive forest dieback, will alter litter and soil microbial communities and thus critical ecosystem services such as nutrient cycling.

Overall, changes in soil fungal biomass and/or diversity have been reported after bark beetle outbreaks. A European spruce bark beetle outbreak in Norway spruce forest rapidly changed vegetation and litter/soil nutrient availability including a dramatic decrease in photosynthesis and the rate of ecosystem decomposition processes following the large, one-time litter input (Štursová et al., 2014). Both litter and soil fungal communities changed profoundly, as indicated by a 2.5-fold decrease in litter fungal biomass and a 12-fold decrease in soil fungal biomass. As expected, the community of fungal tree root symbionts disappeared, while the saprotrophic fungal community increased. In another study, ectomycorrhizal fungal species also decreased as the intensity of European spruce bark beetle outbreaks increased, whereas saprophytic fungi showed a positive response (Veselá, Vašutová, Edwards-Jonášová, & Cudlín, 2019). Outbreaks of mountain pine beetle resulted in

lower species richness of soil ectomycorrhizal and saprotrophic fungi with altered composition and variable effects of soil nutrients, phenolics, and geographical distance (Pec et al., 2017). Soil fungal biomass was highest at the stands with bark beetle outbreaks and had little differences in species composition than controls, in contrast to those with other disturbances (wildfire and logging) (Rodriguez-Ramos et al., 2020). These disturbances appeared to reduce the dominance of ectomycorrhizal fungi and increase those of saprotrophic and arbuscular mycorrhizal fungi (marginal changes for beetle-killed stands) (Rodriguez-Ramos et al., 2020). Outbreaks of European spruce bark beetle and *I. duplicatus* have resulted in premature shedding of needles, and a dramatic decrease in internal fungi of the needle litter (Przybył, Karolewski, Oleksyn, Łabędzki, & Reich, 2008). In a unique experiment, lodgepole pine seedlings grown in soils with ectomycorrhizal fungi from mountain pine beetle-killed stands had higher mortality, and lower concentrations of certain secondary defensive compounds such as monoterpenes than those from undisturbed stands (Karst et al., 2015). This suggests negative feedback loops of bark beetle outbreaks to tree defenses as mediated via belowground fungi.

Variable effects of bark beetle outbreaks have been reported for soil bacteria. Bacterial biomass, while not the primary focus of this study, appear to be either unaffected or to increase after bark beetle disturbance, resulting in a substantial increase in the bacterial/fungal biomass ratio (Štursová et al., 2014). Alpha diversity of soil bacteria increased with tree mortality due to mountain pine beetle, but after 40% mortality, it stabilized and decreased with increased tree mortality (Mikkelson, Brouillard, Bokman, & Sharp, 2017). Custer, van Diepen, and Stump (2020) observed differences in relative abundance of fungal and bacterial phyla in bark beetle-infested rhizosphere soils as compared to control soils, suggesting a restructuring of the soil microbial community. Functional diversity of bacteria was lower in stands with *Dendroctonus* spp. infestations in Mexico, indicating that soils with healthy trees support a much higher level of bacterial species diversity (Vázquez-Ochoa, Reverchon, Sánchez-Velásquez, Ruíz-Montiel, & Pineda-López, 2020). Changes to the ratio of inactive to active bacterial OTUs have been observed in soils under healthy and beetle-killed trees in a lodgepole pine-dominated region (Mikkelson, Bokman, & Sharp, 2016). This was particularly apparent among the rare taxa, which fluctuated metabolically as time since the outbreak increased, whereby rare taxa transitioned into a state of dormancy as trees went from green to red stage of the beetle infestation, and then returned to a state of metabolic activity as trees transitioned from the red to grey stage (Mikkelson et al., 2016). This suggests that active, rare taxa decrease in accordance with tree death, while active abundant taxa remain more stable, supporting the theory that rare taxa play a disproportionately large role in microbial community dynamics following bark beetle outbreaks (Mikkelson et al., 2016). Changes in soil bacterial communities may be short-term, however, as evidenced by a five-year chronosequence study after mountain pine beetle outbreak which revealed little change in bacterial community structure and assembly; this was also reflected in weak changes to soil nitrogen and carbon pools (Ferrenberg et al., 2014).

Soil organisms affiliated with belowground microbial communities also experience community changes in response to bark beetle outbreaks. Abundance and diversity of proturans (soil microarthropods that are prime indicators of soil environmental

changes due to mycorrhizae) decreased due to multiple forest disturbances, i.e., windthrow in combination with bark beetle outbreaks (Sterzyńska et al., 2020). In bark beetle-impacted compared to control stands, only proturan density was significantly decreased, with abundance and diversity being maintained. Multiple disturbances play a more important role than single disturbance events (e.g., bark beetle outbreak alone) in shaping the response of soil proturan assemblages by causing significant species decline (Sterzyńska et al., 2020). Measuring the effects of bark beetle and other disturbance events on microarthropods affiliated with tree roots and mycorrhizae may constitute a useful indication of disturbance effects on the status of the belowground microbiome.

## 7 Conclusions

Overall, landscape-level bark beetle outbreaks can cause major changes to forest structure and composition, and to many abiotic and other biotic elements. These effects of bark beetle-induced tree mortality can be variable as dependent on previous stand structure and composition, at the species level as based on their life-history requirements, tree mortality levels, time since disturbance, and presence of compounded disturbances. While we did not address salvaging, wildfire, prescribed fire, or other natural or anthropogenic disturbances after bark beetle outbreaks, we expect that those may further alter successional trajectories of these forests (e.g., Fornwalt et al., 2018; Jonášová & Prach, 2004; Rhoades, Pelz, Fornwalt, Wolk, & Cheng, 2018). As climate continues to change, bark beetle species will become even more significant factors affecting tree health, and hence serious considerations need to be made with respect to ecological (and economic) impacts. We expect the effects to be nonlinear, complex, and variable over time and argue to better understand the cascading impacts for restoration and conservation purposes.

As based on this review, we identify the following trends, areas of knowledge gaps, and opportunities to greatly expand our understanding of ecological impacts of bark beetle outbreaks as follows:

1. We found that many of these studies were short-term (1–3 years) with a few that were >5 years after bark beetle disturbance. Several taxa showed short-term positive responses, but negative responses over the long term. Hence, long-term monitoring of these species is needed if bark beetle outbreaks continue to be chronic and persistent on these landscapes.
2. Many studies focused on a few species, providing a coarse-level resolution. Further, very few faunal studies included multitaxa in their approach, thus missing out the simultaneous and potentially interactive (or additive) biotic responses.
3. There are few studies that have in-depth studied both abiotic and biotic components simultaneously in the same bark beetle outbreak areas and attempted to create linkages between the two ecosystem components. This would have provided excellent opportunities to create a cohesive framework to address ecological impacts at various scales to guide restoration, conservation, and management efforts.

4. We are aware of only one study that focused on the effects of bark beetle outbreaks on reptiles in the southeastern USA and no studies that have considered the impacts of bark beetles on amphibians. This is supported by another review that assessed wildlife responses to mountain pine beetle outbreaks in western North America (Saab et al., 2014). Of the studies they reviewed, 16 focused on bird species and 6 on mammals, while none on herpetofauna. Given the dire global threats posed to amphibians by the chytrid fungus and other anthropogenic impacts, understanding additional threats by catastrophic, climate change-exacerbated bark beetle outbreaks are of critical importance.

5. Majority of the studies assessed the effects of bark beetle outbreaks on floral and faunal communities in North America (particularly western forests) and Europe. Fewer studies have been conducted in other regions such as Asia and Mesoamerica where there are native bark beetles.

6. Studies focused primarily on bark beetle outbreaks in Douglas-fir, Engelmann spruce, lodgepole pine, and Norway spruce forests. Douglas-fir, lodgepole pine, and Norway spruce forests generally displayed positive responses of forest regeneration to bark beetle outbreaks, resulting in high habitat heterogeneity and positive numeric effects on floral and faunal abundance and diversity. Engelmann spruce forests showed some negative responses of forest regeneration to bark beetle outbreaks, but whether this was associated with positive or negative effects on flora and fauna is unknown. Other tree taxa that were represented to a lesser degree reviewed here included aspen, birch, black spruce, loblolly pine, Lutz spruce, ponderosa pine, rowan, shortleaf pine, subalpine fir, and white spruce. Forests composed of these overstory trees were the focus of single or very few studies and specific neutral or negative responses of associated flora, fauna, and microbial communities were noted for many of these forest types. Most studies determined numerical responses of species communities, but largely overlooked the functional effects of bark beetle outbreaks on ecosystems. Forest type, age class, whether managed or unmanaged, and history may all impact the trickle-down effects of epidemic bark beetle outbreaks, and additional work is needed to understand multitaxa functional responses across diverse forest types.

7. Little is known about the ecological impacts of introduced bark beetle species in their nonnative habitats (Chapter 1), but they can be high. Examples of such introductions include European elm beetle on American elms and *D. valens* (a North American species) on native pines in China. Most studies on nonnative bark beetles tend to be focused on tree dieback and mortality, and management options, rather than ecological impacts.

8. Finally, studies were restricted to five native species: Douglas-fir beetle, European spruce bark beetle, mountain pine beetle, North American spruce beetle, and southern pine beetle. This may reflect the fact that only a few bark beetle species are capable of large eruptive populations, and some (such as mountain pine beetle and southern pine beetle) have shown range expansion within continents due to climate change (Chapters 2–6, this chapter). However, there is evidence that a few species such as

*I. avulsus* in the southeastern USA can outbreak under climate change (McNichol et al., 2019). A broader focus on bark beetle species may, therefore, assist with forest sustainability and conservation as the planet continues to get warmer with variable responses of precipitation and other weather patterns.

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