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Trends in Bark Beetle Impacts in North America During a Period (2000–2020) of Rapid Environmental Change

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Abstract

Of the more than five hundred and fifty species of North American bark beetles (Coleoptera: Curculionidae, Scolytinae), approximately twenty species occasionally cause large amounts of tree mortality in conifer forests. During 2000–2020, trends in bark beetle impacts changed dramatically across North America compared to those observed during the mid- to late 20th century. We review tools and tactics available for bark beetle suppression and prevention and provide an overview of temporal and spatial trends in bark beetle impacts in North American forests during 2000–2020. Higher impacts were observed for several bark beetle species in western North America accompanied by substantial declines in eastern North America driven by large reductions in southern pine beetle (*Dendroctonus frontalis*) activity in the southeastern United States. Regional differences likely result from a higher species richness of both bark beetles and their hosts in western North America, stronger direct and indirect effects of climate change (warming and drying) on bark beetles in western North America, and differences in forest composition, management history, and other abiotic stressors and disturbances.

Study Implications: Compared to the mid- to late 20th century, bark beetles have had increased impacts in western North America and reduced impacts in eastern North America, the latter driven by large reductions in southern pine beetle (*Dendroctonus frontalis*) activity in the southeastern United States. We review tools and tactics available to foresters and other natural resource managers to reduce the negative impacts of bark beetles on forests. Furthermore, we provide several potential explanations for recent trends in bark beetle impacts between eastern and western North America.

Keywords: *Dendroctonus*, *Ips*, *Pinus*, *Picea*, resilience, *Scolytus*, tree mortality

Table 1. Bark beetles noted for causing mortality of conifers in North America.

Common name	Scientific name	Common host(s)	Impact[a]
Eastern North America			
Eastern fivespined ips	*Ips grandicollis*	*Pinus echinata*, *P. elliottii*, *P. taeda*, *P. virginiana*	2
Eastern larch beetle	*Dendroctonus simplex*	*Larix laricina*	2
Eastern six-spined engraver	*Ips calligraphus*	*P. echinata*, *P. elliottii*, *P. ponderosa*, *P. taeda*, *P. virginiana*	2
Pine engraver	*Ips pini*	*P. resinosa*	2
Small southern pine engraver	*Ips avulsus*	*Pinus echinata*, *P. elliottii*, *P. taeda*, *P. virginiana*	2
Southern pine beetle	*Dendroctonus frontalis*	*P. echinata*, *P. rigida*, *P. taeda*, *P. virginiana*	1
Spruce beetle	*Dendroctonus rufipennis*	*Picea rubens*	2
Western North America			
Arizona fivespined ips	*Ips lecontei*	*P. ponderosa*	2
California fivespined ips	*Ips paraconfusus*	*P. contorta*, *P. lambertiana*, *P. ponderosa*	2
Douglas-fir beetle	*Dendroctonus pseudotsugae*	*Pseudotsuga menziesii*	1
Eastern larch beetle	*Dendroctonus simplex*	*Larix laricina*	2
Fir engraver	*Scolytus ventralis*	*Abies concolor*, *A. grandis*, *A. magnifica*	1
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*	2
Mountain pine beetle	*Dendroctonus ponderosae*	*P. albicaulis*, *P. contorta*, *P. flexilis*, *P. lambertiana*, *P. monticola*, *P. ponderosa*	1
Northern spruce engraver	*Ips perturbatus*	*Pi. glauca*, *Pi. x lutzii*	2
Pine engraver	*Ips pini*	*P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*	2
Pinyon ips	*Ips confusus*	*P. edulis*, *P. monophylla*	1
Roundheaded pine beetle	*Dendroctonus adjunctus*	*P. arizonica*, *P. engelmannii*, *P. flexilis*, *P. leiophylla*, *P. ponderosa*, *P. strobiformis*	2
Southern pine beetle	*Dendroctonus frontalis*	*P. engelmannii*, *P. leiophylla*, *P. ponderosa*,	2
Spruce beetle	*Dendroctonus rufipennis*	*Pi. engelmannii*, *Pi. x lutzii Pi. glauca*	1
Western balsam bark beetle	*Dryocoetes confusus*	*A. lasiocarpa*	1
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri*, *P. ponderosa*	1

[a]Scale of impact in forests dominated by common host(s), 2000–2020: 1, caused high levels of host tree mortality on >100,000 ha in a single year; 2, caused high levels of host tree mortality on ≤100,000 ha in a single year.

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are an important disturbance in conifer forests in North America (Table 1). Each species exhibits unique host preferences, life history traits, and impacts, but many exhibit a preference for colonizing larger-diameter trees growing in dense stands with a high proportion of host type (Fettig et al. 2007). Bark beetles introduce a variety of organisms (e.g., fungi, bacteria, nematodes, and mites) (Hofstetter et al. 2015) into the tree. The best studied are the symbiotic blue-stain fungi in the family Ophiostomataceae (Paine et al. 1997), which serve as important food sources for larvae and adults and negatively affect tree health. Bark beetles also encounter numerous predators, parasites, and competitors (Wegensteiner et al. 2015) that play a role in the regulation of bark beetle populations under certain conditions (Weed et al. 2015). At endemic levels, bark beetles create small gaps in the forest canopy by killing individual trees or small groups of trees. This differs from epidemic levels (outbreaks), which can result in large amounts (>50%) of tree mortality affecting many ecosystem goods and services at local to regional scales (e.g., Fettig 2019, Nowak et al. 2008, Schwab et al. 2009).

Adult bark beetles are susceptible to predation, starvation, and weather when searching for hosts. Therefore, they must detect and locate efficiently the correct habitat, host tree species, and the most susceptible trees within these species (Borden 1997). If the tree is accepted by the beetle, the beetle bores through the bark and initiates gallery construction in the phloem upon which some species release aggregation pheromones that attract other bark beetles of the same species (conspecifics). Successful colonization of living hosts requires overcoming tree defenses (Franceschi et al. 2005), which in the case of vigorous hosts can only be accomplished by recruiting large numbers (hundreds to thousands) of beetles to mass-attack the tree and overwhelm its defenses. Some bark beetle species release antiaggregation pheromones during the latter phases of host colonization, presumably to reduce competition among beetles within the host tree (Borden 1997). Following completion of the life cycle and emergence from the host, progeny beetles initiate searches for new hosts. Life cycles may be completed once every 1–3 years (e.g., spruce beetle, *Dendroctonus rufipennis*; SB), or multiple times per year (e.g., southern pine beetle, *D. frontalis*; SPB).

During endemic populations, weakened and damaged trees are often colonized and killed by bark beetles. For example, endemic populations of engraver beetles (*Ips* spp.) infest recent forest debris and dead and dying trees (Connor and Wilkinson 1983, Kegley et al. 1997, Burnside et al. 2011). Other disturbances (e.g., windstorms) may produce large quantities of damaged, dead, and dying trees that serve as hosts. If favorable weather coincides with large quantities of host material, engraver beetle populations may erupt, resulting in mortality of healthy trees over large areas (e.g., >10,000 ha; Burnside et al. 2011). In the absence of such disturbances, damage to individual hosts from other subcortical insects, defoliators, drought, lightning strikes, or root pathogens may reduce host resistance and facilitate colonization by bark beetles.

During 2000–2020, bark beetle impacts (based on levels of tree mortality) have varied dramatically across North America. For example, mountain pine beetle (*D. ponderosae*; MPB) has killed billions of trees across tens of millions of hectares in western North America, while at the same time the area affected by SPB in the southeastern United States has been at historic lows (Asaro et al. 2017) (Figure 1). We discuss (1) tools and tactics for management of bark beetles, (2) recent impacts of notable tree-killing species across North America, and (3) factors that help explain differences in trends in regional impacts.

Tools and Tactics for Bark Beetle Management

Several tools and tactics are available to reduce the impacts of bark beetles that colonize conifers in North America (Table 2). Suppression involves short-term tactics designed to address current infestations, and includes the use of sanitation harvests, insecticides, semiochemicals (chemicals released by one organism that elicit a response in another organism) or a combination of these and other treatments (Fettig and Hilszczański 2015). Suppression requires prompt and thorough applications of the most appropriate tactics as influenced by the bark beetle population and the spatial scale of the infestation (Carroll et al. 2006). Decisions regarding suppression are often based on resource availability, market conditions, logistical constraints, and environmental concerns (Clarke 2001, Fettig and Hilszczański 2015, Fettig et al. 2022).

Prevention is designed to reduce the probability and severity of future bark beetle infestations. This requires manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, or other treatments (Fettig and Hilszczański 2015) (Table 2). Thinning is widely accepted as an effective means for increasing resistance and resilience to several notable bark beetles in North America, a relationship attributed primarily to reductions in tree competition; increases in tree vigor; increases in tree spacing; and changes in microclimatic conditions that disrupt aggregation pheromone plumes (e.g., Bartos and Amman 1989, Thistle et al. 2004, Whitehead et al. 2004, Fettig et al. 2007, Nowak et al. 2015) (Figure 2). In recent years, the efficacy of thinning for reducing levels of tree mortality has even been demonstrated under extreme drought conditions (e.g., Knapp et al. 2021, McCauley et al. 2022). When feasible, prevention should account for the spatial distribution of forest cover types and host-tree species distributions. In many cases, treatments may be needed to increase forest heterogeneity (e.g., of tree ages, tree sizes, and tree species compositions) as homogeneous landscapes promote creation of large contiguous areas susceptible to similar disturbances (Safranyik et al. 1974, Whitehead et al. 2004, Marini et al. 2022). Efficacy varies widely, but in general, bark beetle management is most effective when applied under low-to-moderate bark beetle populations. Thinning is often regarded as most effective (Fettig et al. 2007).

Bark Beetles in the Northeastern United States

Forests and landscapes of the northeastern United States are diverse and shaped by a relatively long period of European settlement (Thompson et al. 2013).

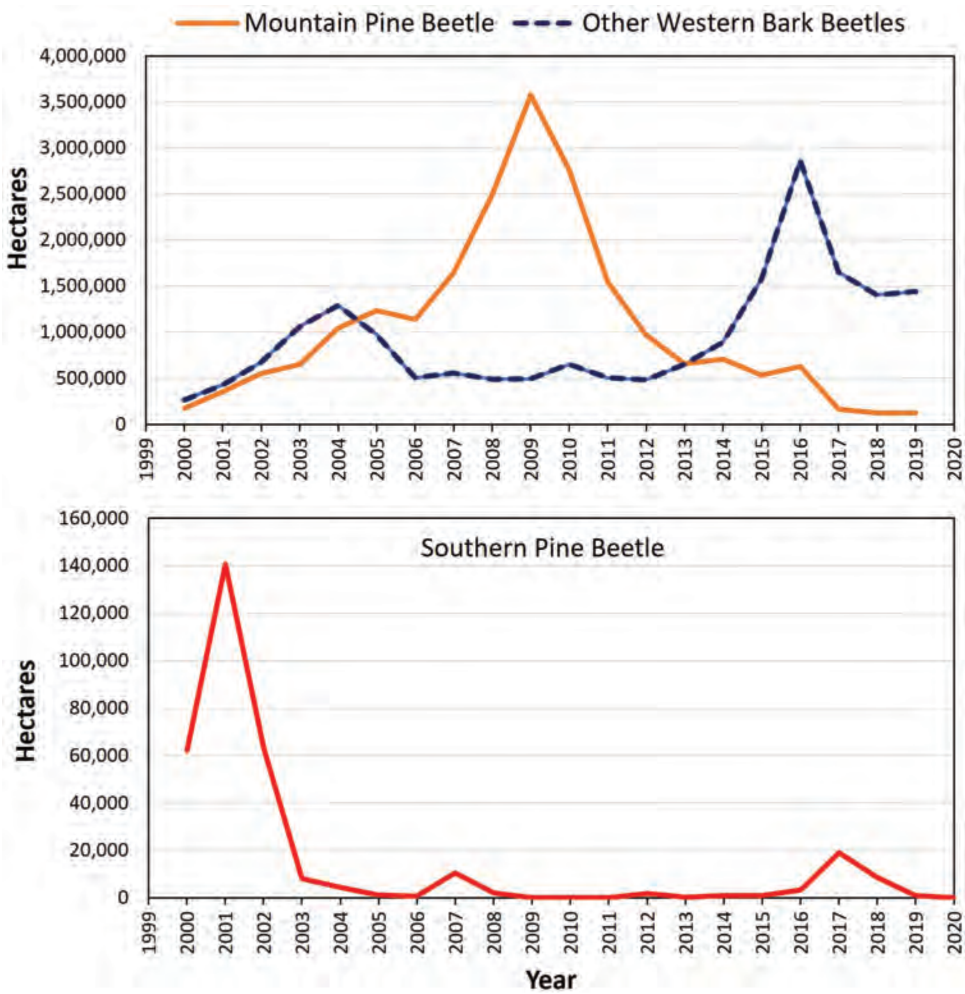

Figure 1. Area affected by mountain pine beetle and other bark beetles in the western United States (top) and southern pine beetle in the southern United States (bottom). Data obtained from the National Insect and Disease Survey database, USDA Forest Service. Data for 2020 for the western United States are not included because of limitations in aerial survey data due to COVID-19.

Conifer forests include spruce–fir forests primarily in northern portions of the region, with pine present in pure and mixed stands throughout. Forests in these areas range from unmanaged stands to areas that are actively managed for timber production. Bark beetles are not an important disturbance in the Northeast like they are in other regions of North America. Outbreaks rarely occur, although several important tree-killing species are native to the region. Historically, the most notable are SB and eastern larch beetle (*D. simplex*).

SB and eastern larch beetle colonize spruce and eastern larch (*Larix laricina*), respectively. Sporadic, localized infestations of SB are not uncommon in northern portions of the region, and large outbreaks (>1,000 ha) were documented in the late 1800s and early 1900s (Weiss and Millers 1988). However, recent SB activity has been much lower. Eastern larch beetle was not viewed as an important pest until the 1970s and 1980s, when increased levels of larch mortality occurred in the Northeast and eastern Canada (Langor and Raske 1989). Although an outbreak of eastern larch beetle began in the early 2000s in the midwestern United States and continues today (McKee et al. 2022), larch mortality in northeastern forests has not occurred at similar levels and scales.

The recent climate-driven range expansion by SPB has resulted in a new pest–tree interaction in New England and New York. Since the early 2000s, damaging SPB populations have persisted in New Jersey, in what has been described as an initial northern range expansion (Trân et al. 2007). SPB was first found infesting pitch pine (*P. rigida*) at multiple locations on Long Island, New York, in 2014, and then further delineated across New England in subsequent years

Table 2. Tools and tactics for management of bark beetles in North America.

Methods	Tools	Tactics
Survey and detection	Trapping surveys, ground-based surveys, aerial surveys, remotely sensed data	Used to locate and determine the severity and extent of bark beetle infestations, which is used to determine whether management interventions are warranted. For review, see Billings (2011), Fettig and Hilszczański (2015), and Fettig et al. (2022).
Risk and hazard rating models	Models based on measures of host abundance and tree competition (stand density). Occasionally incorporate estimates of bark beetle populations, weather, and climate modelling.	Used to identify stand and forest conditions conducive to the initiation and spread of bark beetle infestations. For review, see Fettig and Hilszczański (2015), and Fettig et al. (2022).
Suppression		
Insecticides	Bole sprays, bole injections	Used to protect individual high-value trees from colonization by bark beetles. For review, see Fettig et al. (2013).
Semiochemicals	Attractants, repellents	Attractants (aggregation pheromones and host volatiles) are used in traps for survey and detection, population monitoring, predicting levels of tree mortality, and mass trapping (to reduce bark beetle populations). Attractants may also be used to induce infestations for a variety of research and management purposes. Inhibitors (antiaggregation pheromones and nonhost volatiles) are used to protect individual trees and small areas (e.g., <10 ha). Efficacy varies widely, especially for inhibitors. For review, see Sullivan and Clarke (2021) for southern pine beetle, Ross (2021) for Douglas-fir beetle, and Seybold et al. (2018) for other bark beetles in western North America.
Sanitation	Identification of trees infested by bark beetles, and subsequent felling and removal or treatment to destroy adults and/or brood beneath the bark.	Used to reduce bark beetle populations at local scales. Used to reduce the quantity of aggregation pheromones released into stands (e.g., southern pine beetle spot suppression), but this is difficult due to complications regarding the identification of newly infested trees and the level of responsiveness required in their removal and/or felling. For review, see Carroll et al. (2006), Fettig et al. (2007), Billings (2011), and Fettig and Hilszczański (2015).
Biological control	None	None

Table 2. Continued

Methods	Tools	Tactics
Prevention		
Thinning	Mechanical thinning, prescribed fire, managed wildfire (under certain conditions)	Mechanical thinning is an effective means of reducing the susceptibility of forests to bark beetles. Thinning from below may optimize the effects of microclimate, inter-tree spacing, and tree vigor although residual trees are of diameters considered more susceptible to colonization by some bark beetles (e.g., mountain pine beetle). Tree removals should account for the spatial distribution of forest cover types and host-tree species distributions. In some cases, treatments may need to be implemented to increase forest heterogeneity (e.g., of tree ages, tree sizes, and tree species compositions). For review, see Fettig et al. (2007) Prescribed fire may be used, with or without mechanical thinning. Care should be taken to avoid damaging desired residual trees as fire-injured trees may be more susceptible to colonization by bark beetles. For review, see Nowak et al. (2015) and McNichol et al. (2019) for bark beetles in the southeastern US, and Fettig et al. (2021b) for bark beetles in western North America.
Restoration	Hazard tree removal, salvage, surface fuel reduction, planting	Requires a flexible approach with management decisions influenced by landowner objectives, severity of tree losses, and the overall condition and location of the affected area. In most forests, little or no restoration occurs.

(Dodds et al. 2018). Since detection, SPB has caused noticeable tree mortality each year in New York, with dispersed tree mortality common in central and eastern portions of Long Island. In 2021, SPB was detected for the first time in New Hampshire and Maine (Kanoti et al. 2021, Lombard et al. 2021). Inland and coastal pitch pine barrens are rare in the Northeast (with ~50% loss of historical cover) and their persistence is at risk (Bried et al. 2014, Marschall et al. 2016). Many stands that maintain overstory pitch pine have largely gone unmanaged and are currently susceptible to SPB infestations (spots). Furthermore, pitch pine is difficult to regenerate without fire and other disturbances, which have been suppressed in many of these forests (Van Wieren and Simons 2019). The combined effects of low regeneration success and increased overstory mortality by SPB make persistence of pitch pine in some forests unlikely (Heuss et al. 2019) without management interventions (e.g., prescribed fire) that promote pitch pine. SPB spot suppression has become an important tool in New York to limit tree mortality in infested stands on Long Island (Dodds et al. 2018) (Table 2). During these treatments, all infested pines and a green (live) pine buffer are cut to disrupt spot growth (Swain and Remion 1981, Billings 2011). Thinning focused on improving resistance and resilience of pitch pine forests to SPB is also important (Nowak et al. 2015).

Although tree mortality from bark beetles is rare across the Northeast, a large community of secondary bark and woodboring species occur. Red turpentine beetle (*D. valens*) and black turpentine beetle (*D. terebrans*) colonize living pines, and eastern five-spined

Figure 2. Thinning has long been advocated as an effective means of reducing the probability and severity of bark beetle infestations. The Southern Pine Beetle Prevention Program represents a comprehensive approach for managing southern pine beetle on federal, state, and private forests in the southern United States. Program guidelines set targets for residual stand densities following pre-commercial and commercial thinnings. Restoration and re-establishment of longleaf pine also help suppress impacts of southern pine beetle in this region (Nowak et al. 2008).

ips (*I. grandicollis*) and other engraver beetles inhabit damaged, dead, and dying pines (Dodds et al. 2016). Many other bark and ambrosia beetles occur, including exotic species, but cause little or no impact (Dodds 2014, Dodds et al. 2019). For example, the exotic pine shoot beetle (*Tomicus piniperda*) was first detected in Ohio in 1992 and in several adjacent states shortly thereafter (Haack and Poland 2001). Pine shoot beetle was initially viewed as a threat to forests in the Northeast, but little pine mortality has been attributed to this species (Morgan et al. 2004).

Bark Beetles in the Southeastern United States

SPB has long been considered the most important bark beetle in the eastern United States due to the prevalence of its primary hosts and the economic importance of pine plantations in the southeastern United States. SPB is capable of pheromone-mediated mass attacks of healthy hosts and exponential population growth after invasion of weakened hosts. In this manner, aggregations of spots can expand rapidly into large-scale outbreaks (Birt 2011, Hain et al. 2011). During 1960–1990s, expansive outbreaks in forests dominated by loblolly pine (*P. taeda*), shortleaf pine (*P. echinata*), and Virginia pine (*P. virginiana*) occurred every 5–7 years in the Southeast (Asaro et al. 2017). Often, these outbreaks enveloped multiple states and affected tens to hundreds of thousands of hectares. Surprisingly, since 2003, a multistate, multiyear outbreak of SPB has not occurred in the Southeast (Figure 1). The last large-scale outbreak occurred in the Southern Appalachians, Cumberland Plateau, and upper Piedmont during 1999–2002, primarily in natural stands and unmanaged pine plantations (Nowak et al. 2016).

There are four species of engraver beetles in the Southeast including the small southern pine engraver (*I. avulsus*), eastern six-spined engraver (*I. calligraphus*), eastern five-spined ips, and pine engraver (*I. pini*). The first three occur primarily on southern pines whereas pine engraver occurs primarily on eastern white pine (*P. strobus*) in the Southern Appalachians (Connor and Wilkinson 1983). These species tend to colonize damaged, dead, and dying pines. Together with SPB and black turpentine beetle, they form the southern pine bark beetle guild, and there is evidence of intra- and interspecific chemical communication among them (Hedden et al. 1976, Allison et al. 2012). The impacts of engraver beetles may be underestimated in the Southeast (and in other regions of North America) due in part to a lack of spot growth dynamics and a diffuse spatial distribution of colonized trees across the forest landscape. However, notable engraver beetle outbreaks have occurred in recent years and often have been associated with windthrow and drought (Vogt et al. 2020, McNichol et al. 2022). For example, in 2016–2017, large infestations (including >250 infestations 2–25 ha in size) occurred in several southern states (McNichol et al. 2019). In northern Florida, Hurricane Michael (October 2018) incited engraver beetle infestations that affected >1,000 ha in 2019 (Gomez et al. 2020), but these infestations subsided quickly thereafter.

Disturbances such as windstorms (e.g., hurricanes, tornadoes, and derechos), lightning strikes, floods, and fires (primarily prescribed fires) are common in the Southeast. Windstorms tend to exert positive effects on most bark beetle species in the region, including pine engravers and black turpentine beetle (Vogt et al. 2020). SPB populations often increase in lightning-struck (Hodges and Pickard 1971, Coulson et al. 1983) and salt-stressed pines (Williams and Lipscomb 2002). Extreme weather events, particularly hurricanes or tropical cyclones, are intensifying in the region (Ting et al. 2019) and will exert greater effects on interactions between pine forests and bark beetles.

Bark Beetles in the Western Continental United States

Bark beetles are a major disturbance in western forests and often affect an area larger than wildfire (Hicke et al. 2016). Several recent outbreaks of species such as MPB, SB, western pine beetle (*D. brevicomis*; WPB), and pinyon ips (*I. confusus*) are among the most severe in recorded history (Fettig et al. 2021a). Several of these have been correlated with shifts in temperature and precipitation (Bentz et al. 2010, Kolb et al. 2016). Forest densification, promoted in many forests by fire suppression and exclusion, livestock grazing, and/or reductions in harvesting, has contributed to some outbreaks due to increased competition among trees for water, nutrients, and growing space, thereby increasing their susceptibility to bark beetles (Fettig et al. 2007). Although about fifteen species cause significant levels of tree mortality in the region (Table 1), we focus on MPB, SB, Douglas-fir beetle (*D. pseudotsugae*; DFB), and WPB.

Unlike most other bark beetles, MPB has a large host range consisting of at least fifteen species, notably lodgepole pine, ponderosa pine, sugar pine (*P. lambertiana*), limber pine (*P. flexilis*), western white pine (*P. monticola*), and whitebark pine (*P. albicaulis*). Since 2000, ~10.3 million ha have been affected by MPB, which represents almost half of the total area affected by all bark beetles combined in the region (Figure 1). Outbreaks tend to be most severe in lodgepole pine forests. Based on data from a network of monitoring plots in lodgepole pine forests in five western states, significant reductions in tree diameter at breast height (dbh) (5%), tree height (16%), number of trees (41%), and basal area (53%) occurred due to the most recent (2004–2012) outbreak (Audley et al. 2020). The range of MPB is restricted by climatic conditions unfavorable to brood survival but is expanding due to climate change and other factors. Interactions among MPB, white pine blister rust, and climate change prompted the US Fish and Wildlife Service to announce in 2011 that whitebark pine warranted protection under the Endangered Species Act. In December 2020, the US Fish and Wildlife Service published a proposed rule (85 FR 77408) to list whitebark pine as a threatened species.

SB is the most significant mortality agent of mature spruce in the region. Engelmann spruce (*Picea engelmannii*) is the primary host, although other species may be colonized (Jenkins et al. 2014). High summer temperatures increase the proportion of SB that complete their life cycle in 1 year (univoltine) compared to 2 years (Hansen and Bentz 2003, Bentz and Jönsson 2015), which has contributed to SB population growth in some areas. Contrary to the positive effects of warming on SB populations, Hart et al. (2014) demonstrated that recent SB outbreaks in Colorado were incited by drought.

DFB is an important biotic disturbance in Douglas-fir (*Pseudotsuga menziesii*) forests in the Rocky Mountains. Occasionally, western larch (*Larix occidentalis*) is colonized. The coastal Douglas-fir region, ranging in the United States from northern California to Washington, has sporadic DFB outbreaks of short duration that usually develop following windthrow or wildfires (Fettig et al. 2021a). However, Agne et al. (2018) suggest that DFB outbreaks will become more prevalent in western Oregon and Washington due to increases in wildfire and host tree stress associated with climate change.

WPB is a significant cause of ponderosa pine mortality. The only other primary host is Coulter pine (*P.

coulteri), a species indigenous to the Transverse and Peninsular Ranges of southern California. In response to extreme drought, WPB activity increased in 2014 and peaked in 2016 when 892,041 ha were affected, mostly in California. This prompted Governor Jerry Brown (California) to declare a state of emergency. This event foreshadows future impacts of WPB as the intensity and duration of droughts, important inciting factors (Kolb et al. 2016), are projected to increase with climate change.

Bark Beetles in Western Canada

Western Canada has experienced multiple large-scale outbreaks in recent years. Most notable is a MPB outbreak that peaked in 2007, affecting >9 million ha in British Columbia (BC) in that year alone. More recently, there have been notable increases in levels of tree mortality attributed to SB, DFB, and western balsam bark beetle (*Dryocoetes confusus*, WBBB) (Figure 3). BC is still dealing with the environmental and socioeconomic impacts of the recent MPB outbreak while addressing concerns related to current SB, DFB, and WBBB outbreaks.

MPB not only caused unprecedented levels of pine mortality in BC but expanded its geographic and host range within northern BC and Alberta (Cullingham et al. 2011, De la Giroday et al. 2021). As such, there is some concern that MPB could expand eastward across the boreal forest of Canada and into eastern North America (e.g., Safranyik et al. 2010, but see Bentz et al. 2010 and Cook and Carroll 2017). The outbreak started in northwestern BC during the mid-1990s and some infestations are ongoing. To date, >18 million ha have been affected. The outbreak is attributed to several factors, including extensive areas of even-aged lodgepole pine resulting from wildfire suppression and other forest management practices, warming (Taylor et al. 2006, Bentz et al. 2010), the ability of MPB to spread over large distances (Jackson et al. 2008), and limited management interventions due to a rugged and often inaccessible landscape. Although salvage of dead standing pines continues, the MPB outbreak affected the short- and mid-term timber supply with far-reaching socioeconomic impacts. Schwab et al. (2009) projected the outbreak will drastically alter the structure of BC's forest sector. In the short term, the timber supply has shifted almost entirely to harvest of spruce, Douglas-fir, and subalpine fir (*Abies lasiocarpa*).

In 2014, SB populations increased in north central BC and continue to expand throughout BC where there are susceptible host trees. During 2014–2020, the total area affected by SB was >1.8 million ha, most of which occurred in the northern interior of BC. Unlike MPB (Jackson et al. 2008), SB dispersal primarily occurs within a few hundred meters of the brood tree, although SB is capable of flights >11 kilometers in mill tests (Nagel et al. 1957, Werner and Holsten 1997). Limited dispersal, in combination with a mix of univoltine and 2-year life cycles (MPB is primarily univoltine), appears to explain, in part, the lower rate of spread of SB compared with MPB in BC.

Although affecting less area than MPB or SB (Figure 3), DFB populations are high throughout the range of Douglas-fir. Wildfires have contributed to the rise in DFB populations in some areas as fire-damaged trees are highly susceptible to colonization by DFB (Cunningham et al. 2005). Unprecedented wildfires in southern BC in the last 5 years and altered fire regimes (Brookes et al. 2021), combined with elevated temperatures and drought, are likely to result in continued increases in Douglas-fir mortality attributed to DFB in the region.

WBBB causes widespread but low severity mortality of subalpine fir (Bleiker et al. 2003), locally referred to as "balsam fir". Over the past 5 years, WBBB has affected a larger area than any other bark beetle in BC (Figure 3). Much of this is considered trace severity,

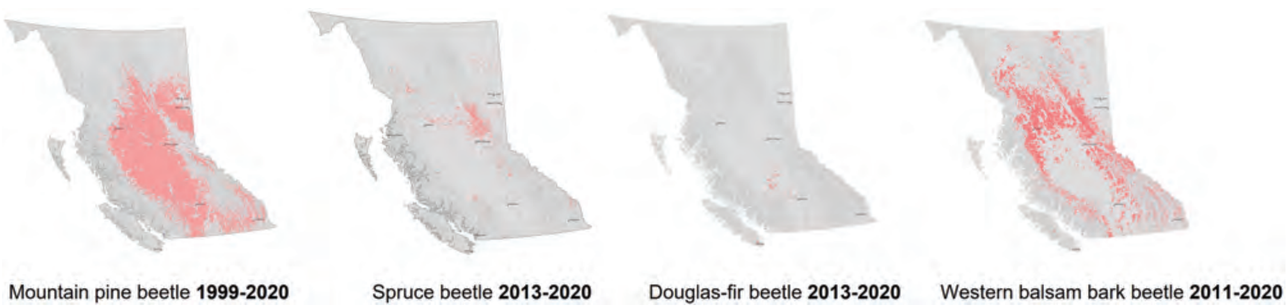

Figure 3. Cumulative area affected by mountain pine beetle, spruce beetle, Douglas-fir beetle, and western balsam bark beetle in British Columbia.

although cumulative losses are significant. The amount of subalpine fir mortality is likely to increase with warming (Maclauchlan 2016). Since 2014, >2 million ha per year have been affected. The current scale of subalpine fir mortality from WBBB and potential indirect effects on caribou (*Rangifer tarandus*) warrants more attention (Nagy-Reis et al. 2021).

Bark Beetles in Alaska

SB and northern spruce engraver (*I. perturbatus*) are the primary tree-killing bark beetles of concern in Alaska. SB exerts the largest impacts and although SB outbreaks can occur in all forested regions in the state they are concentrated in the boreal forests of Southcentral Alaska (Holsten 1990). SB activity is less prevalent in Interior Alaska (Werner et al. 2006), where northern spruce engraver exerts larger impacts than SB (Burnside et al. 2011), and is thought to be regulated by cold winter temperatures (Miller and Werner 1987).

Southeast Alaska is the primary focus of the state's timber industry, but volumes harvested in all regions have been declining (Marcille et al. 2017). Timber harvest is constrained in many parts of the state by a decreasing and limited number of mills, limited road systems, lack of markets, high transportation costs, and existing timber defects. These factors are especially apparent in Southcentral Alaska, where an ongoing SB outbreak has affected ~650,000 ha since 2016 (FS-R10-FHP 2022) (Figure 4) and is the first large-scale SB outbreak since the 1990s, when >1.2 million ha were affected (Werner et al. 2006). The geographic extent of this outbreak and the rate at which it has expanded across the region, when combined with timber harvesting-related issues, has presented challenges for natural resource managers. The outbreak is occurring in the most populous part of Alaska, with substantial areas of wildland–urban interface, adding further complexity. As a result, management responses have focused on human safety and protection of infrastructure. Recent observations place the northern extent of the outbreak within the Alaska Range, which separates Southcentral Alaska from Interior Alaska. Forest health professionals are evaluating the possibility of outbreak-level SB populations expanding into Interior Alaska and whether SB activity will become more prevalent in Interior Alaska because of climate change.

Bark beetle management tactics in Alaska have been adjusted, and likely will need to be further adjusted in the future, to meet the changes brought about by our rapidly changing climate. Whereas a 2-year timeline may have been sufficient in the past for sanitation of SB-infested trees (i.e., before the next generation of beetles emerged), this may not be sufficient with increasing proportions of univoltine beetles. A mix of univoltine and 2-year life cycles has been observed in the current outbreak, though the proportion of each has not been determined, and with continued warming, the likelihood for higher proportions of univoltine beetles increases (Bentz et al. 2010). The recommended timing of suppression activities has been adapted for a higher proportion of univoltine beetles. In addition, the timing of SB emergence in the spring and duration of beetle flight are being closely monitored. Seasonal recommendations regarding harvesting and processing of live spruce will be adjusted based on changes in SB flight activity.

Potential Factors Influencing Trends in Bark Beetle Impacts between Eastern and Western North America

Whereas mechanisms contributing to bark beetle outbreaks are complex (e.g., Wallin and Raffa 2004, Raffa et al. 2005, 2008, Martinson et al. 2013, Weed et al. 2015, Howe et al. 2022), there must be favorable weather conducive to beetle survival and beetle population growth and an abundance of susceptible host trees (Bentz et al. 2010). We consider several factors that may explain some of the variability in recent bark beetle impacts across North America (Table 3). Furthermore, we estimate the relative contribution of each factor. We chose these factors based on our collective experiences working on bark beetle–related issues for many years, and their frequency of reference in the scientific literature. Our hope is that this information provides a better understanding of these relationships and an appreciation for the complexity involved in their assessment and attribution. Knowledge gaps of consequence to better anticipating and responding to future infestations and outbreaks are identified (Table 3).

Bark Beetles

The number of bark beetle species with the potential to kill large numbers of host trees is greater in western North America (West) than in eastern North America (East). Among these, a greater number of species in the West causes high levels of host tree mortality (Table 1). Interestingly, SPB and SB occur in both regions, yet the severity of their impacts

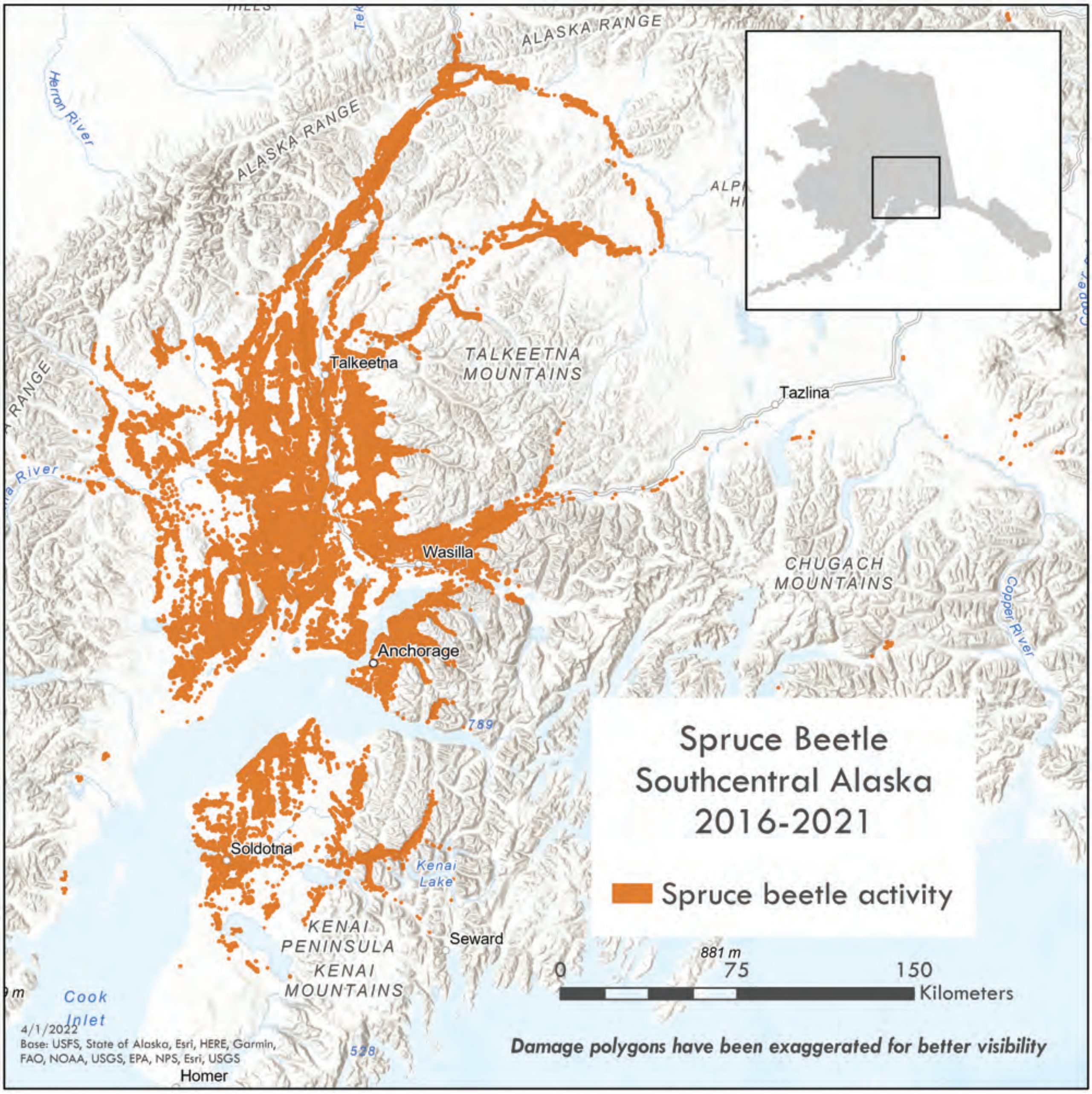

Figure 4. The cumulative area affected by an ongoing spruce beetle outbreak in Southcentral Alaska.

varies dramatically between regions. Unlike in the East, SPB is rarely a pest in the West. Conversely, SB is rarely a pest in the East but causes large impacts in the West. The difference in behavior between eastern and western populations of SPB may be explained in some part by genetic differences between SPB populations (Anderson et al. 1979, Havill et al. 2019), but other factors such has host differences likely exert greater effects. Of note, SPB populations in East Texas and portions of nearby states may be functionally extinct. Pheromone-baited traps deployed during annual spring surveys for SPB have failed to capture even a single SPB for many years (Clarke et al. 2016, Asaro et al. 2017). Historically, SPB exerted some of its largest impacts in East Texas with >15,000 SPB spots recorded in 1985 alone (Texas Forest Service 2001). It is unknown why SB is not as problematic in the East as it is in the West. There is overlap in host species (white spruce, *Pi. glauca*) between regions, but SB also colonizes additional host species in the West (Table 1). Differences in climate, SB behavior, land use, or other factors may explain some of the variation in SB impacts between regions (Bleiker et al. 2021).

Table 3. Potential factors influencing trends in bark beetle impacts between eastern and western North America, 2000–2020.

Factor	East[1]	West	Examples and notes[2]
<u>Bark beetles</u>			
Number of important tree-killing species	--	++	Three-fold higher in the West
Number of tree-killing species that cause high levels of host-tree mortality	--	++	Seven-fold higher in the West
Increases in geographic and host ranges	+	++	Southern pine beetle (SPB) in the Northeast and mountain pine beetle (MPB) in the West. The resultant impacts from MPB outbreaks in high-elevation forests in the West were greater than for SPB in the Northeast. However, the persistence of pitch pine is challenged in some areas of the Northeast.
Decreases in geographic ranges (functional extinction)	-	NA	SPB in parts of the South (e.g., East Texas)
<u>Climate change</u>			
Cooling	Unknown	NA	The effects of cooling on SPB in portions of the mid-South have not been adequately studied.
Warming	+	++	Several notable effects on bark beetles in the West. Warming facilitated the expansion of SPB in Northeast but had little or no overall effect on SPB populations in the Southeast. The effects of warming on most aggressive tree-killing species have not been adequately studied.
Drought	0	++	Several notable effects on bark beetles in the West, especially in the Southwest. Drought has had little or no effects on SPB or other bark beetles in the East, except for increases in engraver beetles in the Southeast. The effects of drought on SPB warrant additional study given climate projections (hotter, drier) for the Southeast.
Decreases in lightning	-	NA	Lightning-struck pines serve as epicenters for the initiation of SPB spots in the Southeast.
<u>Forests</u>			
Forest composition	-	+	Conifer diversity, the number of conifer species colonized by bark beetles, and average patch size of susceptible hosts is higher in the West. Natural forests in the Southeast and Northeast often contain mixtures of pines (SPB hosts) and hardwoods (nonhosts).
Forest fragmentation	-	+/-	Fragmentation is higher in the East and rapidly increasing in some areas due to development, especially in the Southeast. Although the relationship has not been adequately studied, evidence suggests there are negative effects on SPB in the Southeast but little or no effects on other bark beetle species in the East. There are mixed effects on MPB and perhaps other bark beetle species in the West.
Forest density (relative density)	+	+	Notable effects for several bark beetle species at stand levels. Relative density (based on carrying capacity of different forest cover types, stand density index [SD]/maximum SDI) of forests in East and West were similar at the beginning of 21st century. Since then, there have been large increases in the relative density of forests in the East and smaller increases in relative density in the West, the latter due largely to recent increases in forest disturbances such as bark beetle outbreaks and wildfires.

Table 3. Continued

Factor	East[1]	West	Examples and notes[2]
Other disturbances	+/-	+/-	Other disturbances influence bark beetle impacts, but the effects vary widely. For example, mixed-severity wildfires may increase impacts whereas high-severity wildfires can kill large numbers of bark beetle hosts over extensive areas dampening future outbreaks in affected areas for decades (Fettig et al. 2021b). Similarly, severe bark beetle outbreaks dampen future outbreaks. Some disturbances only affect nonhosts increasing the amount of growing space available to hosts which then are better able to thwart bark beetle attacks. Windthrow often results in increases in bark beetle impacts. For example, prior to recent climatic changes all spruce beetle outbreaks in the West are thought to have originated from other disturbances, primarily windthrow (Gandhi et al. 2007, Jenkins et al. 2014).
Management			
Fertilization	0	0	Fertilization has mixed effects (e.g., increases tree growth but some trees may be more susceptible to bark beetle attack due to reductions in terpene-based defenses) but is applied at limited scales relevant to the amount of forestland in each region.
Genetic tree improvement	0	0	Effect is unknown but applied at limited scales relevant to the amount of forestland in each region, except for plantations in the Southeast.
Herbicide	0	0	Herbicide reduces stand susceptibility (e.g., increases tree growth), but is applied at limited scales relevant to the amount of forestland in each region.
Prescribed fire	-	0	Prescribed fire has mixed effects. Bark beetle may colonize and kill trees stressed by prescribed fire resulting in additional tree mortality in the near-term. In the longer term, reductions in tree density and competition caused by prescribed fire exert the same effects as thinning (below). Prescribed fire is applied at limited scales relevant to the amount of forestland in each region but is more common in the Southeast.
Thinning	-	0	Thinning reduces stand susceptibility (e.g., reduces tree competition, increases tree vigor, increases tree spacing, and causes changes in microclimate) but is applied at limited scales relevant to the amount of forestland in each region. Our rating for the East is influenced by well-coordinated SPB prevention activities in pine plantations in the Southeast (Nowak et al. 2008, Asaro et al. 2017) (Fig. 2). The scale of thinning in the West was likely insufficient to influence regional trends.
Ability to address infestations (e.g., through sanitation and thinning)	-	0	The strength of response is greater in the East (based on Southeast) than in the West. In the West, rugged terrain, a lack of mill capacity, and great haul distances to mills are notable challenges.

[1]++, large positive effect on impacts; +, positive effect; -, negative effect; --, large negative effect; +/-, mixed effects; 0, no or little effect; unknown, insufficient data to make reasonable inference; NA, not applicable.

[2]See text for more discussion.

Climate Change

Climate and weather have important direct and indirect effects on bark beetles and their impacts on forests. Shifts in temperature and precipitation can affect (1) the fecundity, fitness, phenology, and voltinism of bark beetles and their predators, parasites, competitors, and symbionts; (2) the overwintering survival of bark beetles; (3) the geographic and host ranges of bark beetles; (4) the geographic distribution of host trees; (5) host finding and selection; and (6) host susceptibility (Bentz et al. 2010). The effects of climate change have been more severe in the West than in the East. For example, increases in mean annual and seasonal surface air temperatures in the United States (based on differences between the present day [1986–2016] and the average for the first half of the last century) have been highest in the Great Northern Plains, Alaska, and the Southwest (Figure 6.1 in Vose et al. 2017).

There is evidence that warming has increased the voltinism of some bark beetle species in the West in recent years, but to our knowledge, this has not been demonstrated for any species in the East. As discussed, warm summer temperatures can avert the facultative prepupal diapause of SB (Hansen et al. 2001), resulting in higher proportions of SB that are univoltine (Hansen and Bentz 2003, Bentz et al. 2010). Work by Robbins et al. (2022) indicates contemporary (2001–2018) warming resulted in increases in WPB voltinism in California that explain ~30% of the increase in ponderosa pine mortality in the Sierra Nevada. In addition, there is evidence that warming has facilitated the spread of MPB in boreal forests of western Canada (Cullingham et al. 2011, De la Giroday et al. 2021), MPB in high-elevation forests in the West (Logan et al. 2010), and SPB in the Northeast (Dodds et al. 2018). Lombardo et al. (2018) concluded that winter temperatures in the expanded range of SPB in the Northeast cause a convergence of population life stage structure that leads to synchrony in spring flight emergence that, unlike in the Southeast, increases the likelihood of outbreaks.

Lombardo et al. (2022) studied the effects of heat on SPB survival in the South and reported that temperatures warm enough to kill SPB were rare or absent, and that there has been no change in the duration or severity of heat waves over the last 80 years. They concluded alternative explanations for the reduction in SPB activity in the South during the last two decades must be considered. Recent modelling of SPB suitability based on climate variables indicates suitability increased from 1981 to 2019 in portions of Alabama, Mississippi, and Georgia, but was low in Arkansas, East Texas, Kentucky, Louisiana, North Carolina, Tennessee, and Virginia (Munro et al. 2021). Projections indicate SPB populations will decline in the South under higher warming scenarios (Munro et al. 2021).

Reductions in precipitation have occurred in some areas in North America, notably the Southwest and Interior West (Easterling et al. 2017). However, warming alone (with little or no reduction in precipitation) can also exacerbate drought stress through increased evaporative demand. Furthermore, in the West, less snow (Wehner et al. 2017) and earlier spring melting of snow have exacerbated summer drought conditions in some locations (Mote et al. 2018). A recent (2012–2015) drought in California characterized by large precipitation deficits and abnormally high temperatures (Aghakouchak et al. 2014) resulted in progressive canopy water stress of 888 million trees and severe canopy water stress of 58 million trees (Asner et al. 2016). Substantial mortality of dominant and co-dominant trees occurred. Most mortality was attributed to WPB, MPB, and fir engraver (*Scolytus ventralis*) colonizing drought-stressed hosts that offered little resistance due to compromised defenses (Kolb et al. 2016). In the East, droughts are often of shorter duration and less severity than in the West but have increased in parts of the Southeast (Seager et al. 2009). Despite this, there is no compelling evidence that recent droughts affected SPB activity in the Southeast (Kolb et al. 2016). However, droughts are thought to have incited some engraver beetle outbreaks (Vogt et al. 2020, McNichol et al. 2022), and some areas affected by engraver beetle outbreaks later became SPB spots.

Lightning strikes play a unique and important role in the epidemiology of SPB (Coulson et al. 1983, 1999) as lightning-struck pines serve as SPB refugia and as epicenters for the initiation of spots when occurring in suitable habitats. Lovelady et al. (1991) studied the effects of lighting on SPB activity in East Texas in the late 1970s and early 1980s and reported that the number of SPB spots increased as a function of cumulative lightning strikes. As SPB populations increased from endemic to epidemic levels, a greater proportion of lightning-struck hosts were exploited by SPB. However, under epidemic populations, a substantial portion of SPB spots resulted from other factors (Lovelady et al. 1991). The frequency of lightning strikes has declined in the Southeast in recent years (Qie et al. 2020), which may explain some of the decline in SPB activity, although the relationship has not been adequately studied.

Forests and Forest Management

The composition, structure, and function of forests vary across North America due to differences in environmental conditions (e.g., climate and soil fertility), disturbances, forest management, and land use. Forests in North America are predominantly natural stands of native tree species, although planted forests represent ~18% of forests in the Southeast. Conifer diversity is higher in the West than the East (The Gymnosperm Database 2021). Unlike eastern forests, many western forests contain a high degree of contiguous hosts and often extreme elevational and other topographic gradients where drought and temperature changes are most impactful.

Landscape heterogeneity and forest fragmentation, the latter of which is higher in the East than in the West (Heilman et al. 2002), has received attention as a potential factor influencing bark beetle impacts. However, the relationship is complex and likely varies by bark beetle species, population phase (endemic vs. epidemic), and other factors. Costa et al. (2013) studied the effects of fragmentation on eastern five-spined ips and one of its predators using mark-recapture studies in red pine (*P. resinosa*) plantations in Wisconsin. The predator was largely confined to forested areas whereas eastern five-spined ips was commonly found in nonforested areas. They concluded that despite the predator having a greater dispersal ability, it was restricted by fragmentation, which provided an opportunity for escape of its prey (eastern five-spined ips). Research on MPB in BC found fragmented forests experienced greater tree mortality than less fragmented forests when MPB populations were low and less tree mortality when MPB populations were high (Bone et al. 2013). A similar relationship has been demonstrated for European spruce beetle (*I. typographus*) and is likely mediated through (1) microclimate, particularly along forest edges, that create favorable conditions for successful colonization of hosts at low bark beetle populations (e.g., Kautz et al. 2013) and (2) contagion (based on host patch sizes) at high bark beetle populations.

Forests in the Southeast have become increasingly fragmented due to development, a trend likely to increase (Terando et al. 2014). As such, fragmentation has been suggested as a factor influencing recent declines in SPB impacts (e.g., Asaro et al. 2017). Cairns et al. (2008) used LANDIS to simulate the effects of landscape composition (proportion of the landscape in host area) and host aggregation on the size and severity of SPB outbreaks in the Southern Appalachians. They found that landscape composition is less important than host aggregation (patch size). However, others have shown that SPB spots become disrupted when they run into patches where hardwoods represent a high proportion of stand composition (Birt 2011), which is likely due to reduced host frequencies and by the mixing of host and nonhost volatiles within stands interfering with host finding (Huber et al. 2021). Ylioja et al. (2005) found that smaller loblolly pine stands were more likely to be infested by SPB in Alabama but experienced less overall tree mortality (based in % area affected) than larger stands when outbreaks occurred. The relationship between fragmentation and SPB impacts is currently under investigation in the Southeast.

Generally, effective bark beetle suppression (e.g., sanitation) and prevention requires strong wood product markets. In the West, rugged terrain, a lack of mill capacity, and great haul distances to mills are notable challenges. As previously mentioned, thinning is widely accepted as an effective means for increasing resistance and resilience to bark beetles (Fettig et al. 2007) (Figure 2). Although the effect of thinning on forest susceptibility is not solely mediated through reductions in tree competition (Tables 2 and 3), surprisingly there was little difference in the relative density (stand density index [SDI]/maximum SDI) of forests in the East and West during 1999–2012 (Woodall and Weiskittel 2021). Overall, the relative density of forests increased during 2012–2020, with the largest increases in the United States occurring in loblolly-shortleaf pine and oak (*Quercus*)-pine, which are cover types where SPB historically has exerted large impacts. These data provide evidence that differences in the (relative) density of forests in the East and West likely do not explain regional differences in recent trends in bark beetle impacts. Of note, the increases in forest density in the South are not driven by densities in plantations, as we calculated a 0.2% reduction (= unchanged) in density (based on numbers of trees >2.5 cm dbh) within plantations during the last two decades. Historically, SPB exerted its largest impacts in plantations. Asaro et al. (2017) considered several hypotheses to explain recent declines in SPB impacts in the Southeast and concluded that wider applications of silvicultural tools in pine plantation forestry (Siry 2002, Wear et al. 2007), a highly fragmented distribution of high-risk host stands, and a rapid response to treat spots (enabled by a relatively robust forestry infrastructure) were the most likely causes.

Conclusions

During 2000–2020, bark beetles had a greater impact in the West than in the East, which we primarily attribute to a larger number of notable tree-killing species in West, and differences in climatic changes (warming and drought) and forest composition (Table 3). In a review of bark beetle outbreaks in western North America and Europe, Hlásny et al. (2021) concluded that recent outbreaks were driven by climate change.

Due to warming (Vose et al. 2017), foresters and other natural resource managers will be increasingly challenged to manage bark beetles in North America, maintain resilient and productive forests, and facilitate recovery of landscapes affected by bark beetles and other stressors and disturbances (Fettig et al. 2022). There are a wide array of tools and tactics available to help meet these needs (Table 2). Successful implementation demands knowledge of several complex fields of study, the effects of climatic and other changes on forests, and of institutional, social, and environmental factors that influence our abilities to implement treatments at appropriate scales (Cottrell et al. 2020). In some areas, altered conditions or expansions of bark beetle ranges (e.g., SPB in the Northeast) have and will require adaptation of existing tactics or development of new tools and tactics.

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