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ARTICLE

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Overlapping outbreaks of multiple bark beetle species are rarely more severe than single-species outbreaks

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Abstract

Biotic disturbances that overlap in space and time may result in important shifts in forest structure and composition, with potential effects on many ecosystem services. Starting in the late 1990s, outbreaks of multiple bark beetle species caused widespread mortality of three co-occurring conifer species in the ca. 40,000-km^2 subalpine zone of the southern Rocky Mountains (SRM), USA. To better understand the implications of such outbreaks, our goal was to determine if overlapping outbreaks of multiple bark beetle species caused greater tree mortality than single-species outbreaks in stands with multiple susceptible host tree species. We mapped stand susceptibility to outbreaks of spruce beetle (SB, *Dendroctonus rufipennis*), mountain pine beetle (MPB, *Dendroctonus ponderosae*), and western balsam bark beetle (WBBB, *Dryocoetes confusus*) by combining aerial survey data and forest composition variables in a random forest modeling framework. Then, we used existing maps of cumulative forest mortality from bark beetles to investigate the extent and severity of overlapping outbreaks from 1999 to 2019. We found that 46% of stands with two or more of the three studied hosts species—Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*), or subalpine fir (*Abies lasiocarpa*)—were susceptible to overlapping outbreaks (25% of all sampled stands). Of those stands, 31% experienced outbreaks of two or more beetle species. Stands affected by outbreaks of both MPB and SB had higher tree mortality than stands affected by one species alone, though stands susceptible to both MPB and SB were uncommon (<4% of all sampled stands). No other combinations of beetle outbreaks increased tree mortality above levels caused by single-species outbreaks. Thus, contrary to expectations, overlapping outbreaks were rarely more severe than single-species outbreaks in the SRM. This suggests that diverse forest communities may buffer against the most severe effects of bark beetle outbreaks, even during warm, dry conditions.

KEYWORDS

bark beetle, Colorado, *Dendroctonus*, disturbance interactions, *Dryocoetes*, mountain pine beetle, outbreak, southern Rocky Mountains, spruce beetle, tree mortality, western balsam bark beetle

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INTRODUCTION

Global change has altered disturbance regimes around the world, a trend that is likely to continue (Sommerfeld et al., 2018; Turner, 2010). Changing disturbance regimes will influence forest ecosystem structure and function, including vegetation patterns (Anderegg et al., 2015), wildlife communities (Ivan et al., 2018), nutrient cycling (Edburg et al., 2012; Turner et al., 2007), and hydrology (Sexstone et al., 2018). However, given their complex spatial and temporal drivers, forecasting the characteristics and consequences of future disturbances remains a challenge (Albrich et al., 2020). Additionally, most forests are subject to multiple types of disturbances, which may interact in time and space to further complicate our ability to forecast ecosystem change (Buma, 2015; Johnstone et al., 2016). Thus, understanding the causes and consequences of disturbance interactions remains a high research priority (Kleinman et al., 2019; Trumbore et al., 2015; Turner, 2010). This is especially true for biotic disturbances (Harvey et al., in review; Kautz et al., 2017), which are often driven by climate, yet whose interactions can vary widely among vegetation communities.

Disturbance interactions occur when an ecosystem that has not fully recovered from an initial disturbance is affected by a secondary disturbance (Burton et al., 2020). Spatial co-occurrence (i.e., overlap) of disturbances is expected to occur more frequently when disturbances share common drivers. For example, warm and dry conditions can simultaneously lead to increases in both fire activity and bark beetle activity by lowering fuel moisture and accelerating beetle population development rates (Bentz et al., 2010; Parks & Abatzoglou, 2020), respectively. Overlapping disturbances may also occur due to a causal link, where the first disturbance increases the likelihood, extent, or severity of the second (Simard et al., 2011). For example, wind disturbance events can initiate subsequent bark beetle outbreaks in subalpine forests (Veblen et al., 1991; Wermelinger, 2004). "Compounded effects" may also arise when multiple disturbances interact to influence ecosystem recovery (Paine et al., 1998). For instance, recovery following fire can be compromised if a prior bark beetle outbreak eliminates mature trees that would have acted as seed sources in the postfire environment (e.g., Andrus et al., 2021). While recent studies have examined interactions between abiotic disturbances (e.g., drought and wildfire) and between abiotic and biotic disturbances (e.g., windthrow and bark beetle outbreaks), few studies have examined interactions between two or more biotic disturbances (Buma, 2015; Kleinman et al., 2019). Given that many biotic disturbances are widespread and facilitated by climate warming (Bentz et al., 2010; Hicke et al., 2020), there is a salient need to understand the extent and implications of interactions resulting from co-occurring biotic disturbances.

Outbreaks of native bark beetles are particularly important biotic disturbances in conifer forests of North America, where they have affected over 60 million hectares of forest area in the western United States since the late 1990s (Hicke et al., 2020, 2016). Outbreaks of many species of bark beetle are initiated by the same set of common drivers, such as stand age and favorable climate conditions (Bentz et al., 2010; Chapman et al., 2012; Hart et al., 2017; Hart, Veblen, Eisenhart, et al., 2014; Howe et al., 2022; Koontz et al., 2021). This may lead to overlapping outbreaks that are not necessarily causally linked to each other (Andrus et al., 2020; Harvey et al., in review). The United States Forest Service (USFS) estimates that almost 2 million hectares of forested area across the western United States are at risk for outbreaks of more than one bark beetle species over the next 15 years and beyond (Krist et al., 2015; USDA, 2019b). Like other biotic disturbances, the effects of bark beetle outbreaks depend strongly on forest community characteristics such as tree age structure and diversity (Guo et al., 2019; Klutsch et al., 2009). Though forests composed of multiple tree species can allow for the occurrence of multiple overlapping outbreaks, some research has suggested that tree diversity may buffer against severe tree mortality (Connor et al., 2014; Jactel & Brockerhoff, 2007). While many studies have demonstrated that bark beetle outbreaks can lead to severe mortality in stands composed primarily of their host tree species, the potential for outbreaks to overlap in space and time—and the consequences for tree mortality—are poorly understood (Harvey et al., in review; Kautz et al., 2017).

Subalpine forests of the southern Rocky Mountains (SRM) have already experienced widespread mortality from outbreaks of multiple species of bark beetle, which have affected multiple co-occurring tree species, including Engelmann spruce (*Picea engelmannii* Parry), lodgepole pine (*Pinus contorta* Douglas var. *latifolia*), and subalpine fir (*Abies lasiocarpa* Nuttall). These forests are characterized by an infrequent (200–500 years), high-severity fire regime (Buechling & Baker, 2004; Sibold et al., 2006) that can create extensive even-aged stands that are consequently more susceptible to bark beetle outbreaks when they reach maturity. Through the same mechanism, widespread fire and logging activity in the 1800s may have increased landscape-scale susceptibility to bark beetle outbreaks in recent decades (Veblen & Donnegan, 2005; Windmuller-Campione et al., 2021). In these outbreaks, tree mortality was mainly driven by three beetle species: the spruce beetle (SB; *Dendroctonus rufipennis* Kirby), which affects Engelmann spruce; the mountain pine

beetle (MPB; *Dendroctonus ponderosae* Hopkins), which predominantly affects lodgepole pine; and the western balsam bark beetle (WBBB; *Dryocoetes confusus* Swaine), which affects subalpine fir. Like other tree-killing bark beetles, these species are specialist herbivores that primarily attack a single tree species or genus, feeding and reproducing beneath the bark by mining galleries in the phloem. When bark beetle populations are low (i.e., endemic), beetles generally feed on weakened or recently dead trees (Safranyik & Carroll, 2006). Under these conditions, healthy trees can physically expel attacking beetles through resin exudation and/or repel and kill them through the production of defensive compounds (Raffa et al., 2005). However, during an outbreak beetles can overcome tree defenses through pheromone-mediated mass attacks, at which point extensive beetle colonization and the introduction of associated fungal pathogens can kill healthy trees (Wallin & Raffa, 2004).

The initiation of an outbreak is complex but generally requires landscapes composed of large, abundant, susceptible hosts (Buonanduci et al., 2020; Hart, Veblen, & Kulakowski, 2014; Harvey et al., 2021; Klutsch et al., 2009). Given a susceptible landscape, warm temperatures and drought can facilitate population eruptions by increasing bark beetle development rates, decreasing overwintering mortality of bark beetles, and inhibiting tree defenses (Chapman et al., 2012; Hart et al., 2017; Kolb et al., 2016). When these climate drivers are shared by multiple bark beetle species, outbreaks of different species may be synchronized across broad landscapes, potentially leading to hotspots of bark beetle activity (Harvey et al., in review). In order for overlapping outbreaks of bark beetles that feed upon different host species to occur, stands must be composed of mature individuals of multiple different tree species. In general, greater tree diversity is hypothesized to decrease the effects of individual herbivore species on their hosts (Jactel & Brockerhoff, 2007). For bark beetles, this is expected to result in a lower probability of outbreak occurrence and lower host mortality (Lalande et al., 2020; Schmid & Hs Frye, 1976; Shore & Safranyik, 1992). However, when bark beetle populations are very large or host trees are particularly stressed, stand diversity may fail to constrain outbreak dynamics (Hart, Veblen, & Kulakowski, 2014; Raffa et al., 2008). Under such conditions, greater tree diversity may lead to greater richness of tree-feeding insects (Guo et al., 2019) and potentially hotspots of bark beetle outbreak. Critically, if the combined mortality of multiple host species is greater than the mortality caused by a single-species outbreak, forest recovery may be compromised.

In this study, we used broadscale geospatial data to explore the extent and severity of co-occurring multispecies outbreaks of SB, MPB, and/or WBBB across susceptible subalpine forests in the SRM from 1999 to 2019. Because multispecies outbreaks are not possible in monospecific stands, we used stand structure and composition to confine our analyses to stands with host composition susceptible to multiple bark beetle species. Specifically, we asked: (1) Across the SRM, how widespread are forest stand conditions that are susceptible to outbreaks of multiple bark beetle species? (2) When stand conditions are susceptible to multispecies outbreaks, how common is the spatial overlap of outbreaks of multiple bark beetle species? (3) In areas susceptible to multispecies outbreaks, is cumulative tree mortality greater in stands affected by overlapping outbreaks of different bark beetle species when compared with stands affected by outbreak of only one bark beetle species? We expected that most forests were susceptible to at least one bark beetle species prior to the recent outbreaks due to their existing size and age structures (USDA, 2019b; Windmuller-Campione et al., 2021). Because most forests are composed of more than one host species, we expected that stands susceptible to multiple bark beetle species would be similarly widespread, as would the occurrence of overlapping outbreaks (Guo et al., 2019). Alternatively, if dilution of host abundance in mixed-species stands limits susceptibility to individual bark beetle species (Connor et al., 2014; Jactel & Brockerhoff, 2007), then stands susceptible to multiple bark beetle species may be relatively rare, and the occurrence of overlapping outbreaks may be uncommon. Finally, when outbreaks of multiple species do occur in the same stand, we expected that their effects would be additive, leading to greater cumulative tree mortality in comparison to single-species outbreaks.

METHODS

Study area

The study area is the subalpine zone (2700–3600 m) of the SRM, which extends from northern New Mexico to southern Wyoming, USA (Figure 1), covering ca. 40,000 km^2. This region typically experiences warm summers (mean July maximum temperature 24.1°C) and cold winters (mean January minimum temperature −12.3°C). Precipitation is distributed bimodally throughout the year, with peaks in March–May and July–August (mean annual precipitation 625 mm) (PRISM Climate Group, 2020; Romme et al., 2009). About 55% of the SRM is forested (Homer et al., 2020), and subalpine forests occupy the highest forested elevations (Peet, 1981; Romme et al., 2009).

Subalpine forests in the SRM are dominated by Engelmann spruce, lodgepole pine, and subalpine fir, with components of trembling aspen (*Populus tremuloides*) and five-needle pines (i.e., bristlecone pine [*Pinus aristata*],

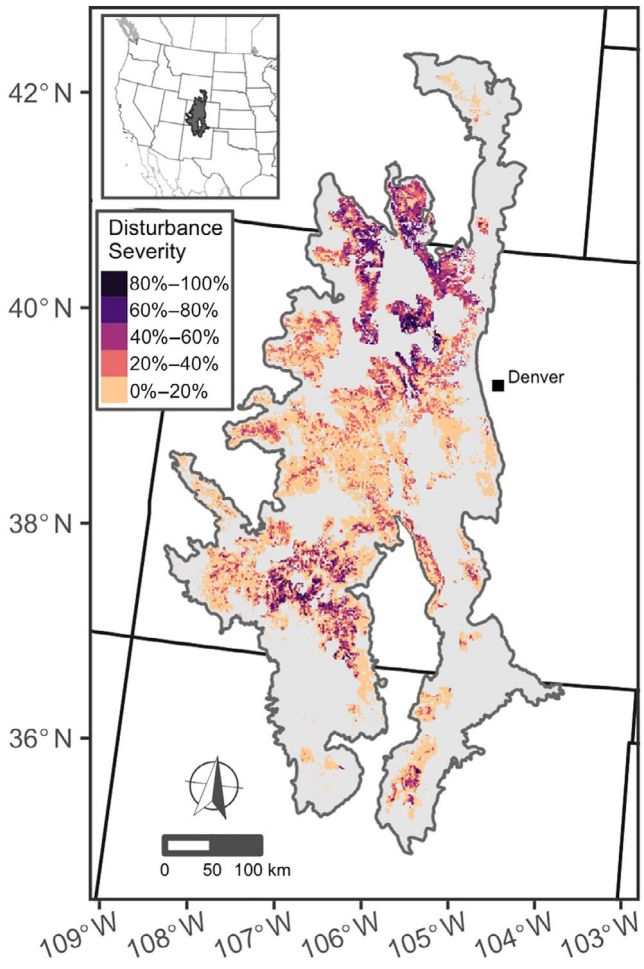


FIGURE 1 The extent of subalpine forest within US Forest Service lands within the southern Rocky Mountains, USA (gray). Colored areas show the cumulative disturbance severity (percent of pre-outbreak tree basal area killed by bark beetles) during the 1999–2019 study period. Disturbance severity data are from Rodman et al. (2021).

limber pine [*Pinus flexilis*], and southwestern white pine [*Pinus strobiformis*]) (Wilson et al., 2013). Douglas fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) may also be present at lower elevations in the subalpine zone (Romme et al., 2009). Widespread bark beetle outbreaks occurred across the SRM from 1999 to 2019, with SB affecting 15%, MPB affecting 19%, and WBBB affecting 14% of subalpine forests (USDA, 2020) (Figure 1). Other bark beetles (e.g., fir engraver [*Scolytus ventralis*]), defoliators (e.g., western spruce budworm [*Choristoneura freemani*]), and pathogens (e.g., white pine blister rust [*Cronartium ribicola*]) are also present in the region but have caused more limited tree mortality (USDA, 2020). These forests support wildlife, timber resources, and recreation, and are the headwaters of the Arkansas, Colorado, Rio Grande, and South Platte rivers, making them ecologically, economically, and socially important.

Data sources

To map the distributions and densities of the three host tree species (Engelmann spruce, lodgepole pine, and subalpine fir) across the SRM, we used Individual Tree Species Parameter Maps created by the National Insect and Disease Risk Mapping project (NIDRM; USDA, 2019b). These maps use Forest Inventory and Analysis data, 30-m resolution Landsat imagery, and biophysical predictors including climate normals to model the extent and abundance of tree species across the United States (Krist et al., 2015). To represent pre-outbreak host availability, we obtained 240 × 240 m gridded datasets of species basal area (BA) and stand density index (SDI), as well as total stand BA in ca. 2002 from the NIDRM program (Appendix S1: Table S1). Additionally, we used these data to calculate the relative abundance (percent BA contribution) of each host species in the stand. Host BA, SDI, and relative abundance have been shown to be important predictors of outbreak occurrence and severity at the stand scale (Fettig et al., 2007; Harvey et al., 2021; Klutsch et al., 2009; Shore & Safranyik, 1992).

To describe outbreak patterns, we used spatial data from the USFS Aerial Detection Survey program (ADS) (USDA, 2020). ADS data are gathered annually via aerial sketch mapping, where experts record the disturbance agent, host species, and estimated outbreak severity across broad landscapes. These data are useful because of their annual temporal resolution, broad extent, and relatively high identification accuracy (Coleman et al., 2018). While some imprecisions exist (e.g., "lumping" of small mortality patches; Johnson & Ross, 2008), aerial sketch mapping represents the most common approach to mapping and attributing tree mortality to specific biotic agents within the United States (Coleman et al., 2018).

To examine patterns of cumulative tree mortality from different bark beetle outbreaks and their overlap, we used a Landsat-derived map of BA loss due to bark beetles produced by Rodman et al. (2021). Briefly, these data were produced using a Google Earth Engine implementation of LandTrendr (Kennedy et al., 2018), which quantifies declines in vegetation indices for Landsat image time series. Landsat imagery is most sensitive to the mortality of large, main canopy trees, and these individuals represent the majority of stand BA and beetle-caused tree mortality. Landsat time series were then compared with field data from bark-beetle-affected forests to predict percent BA loss from 1997 to 2019 across subalpine forests of the SRM at a resolution of 30 × 30 m. The resulting maps were strongly predictive (cross-validated $R^2 = 0.68$) of field-derived estimates of outbreak severity (Rodman et al., 2021).

Data processing

Percent BA loss was aggregated to 240 × 240 m for this study using the mean value of all 30-m cells (Rodman et al., 2021). A resolution of 240 × 240 m was selected to match the NIDRM species composition data, and because ADS describes coarse-scale patterns of bark beetle activity (Coleman et al., 2018; Johnson & Ross, 2008). For compatibility with our other datasets, we also converted annual ADS data to raster files with a resolution of 240 × 240 m, using Albers Conic Equal Area projection. Specifically, we considered a 240-m cell to have bark beetle presence if an ADS polygon intersected with its centroid. Because our research questions do not focus on the timing or order of disturbances, we created three binary raster datasets describing the presence or absence of each bark beetle species across all years (1999–2019). We excluded 1997–1998 because there was relatively little area affected by outbreaks in these years and mapping of those outbreaks was inconsistent across the region. To increase the reliability of detection, grids of bark beetle presence were then multiplied by grids of host presence derived from NIDRM, which we defined as >1 m^2 ha^{-1} host BA, to remove grid cells where hosts are unlikely to be present (Chapman et al., 2012). Because our study focused solely on bark beetle disturbances, we excluded areas that experienced wildfire or logging within ca. 10 years of the study period from our analyses (USDA, 2019a; USDA and USGS, 2017). Since data on forest management of private lands are unavailable or incomplete, we also restricted our study to public forest lands managed by the US Forest Service (Figure 1). Though these restrictions excluded ca. 30% of subalpine forests in the SRM, they were necessary to ensure that any tree mortality was due to bark beetles and eliminate potentially confounding effects of other disturbances (Rodman et al., 2021). All spatial data were processed using R v. 4.0.2 (R Core Team, 2020), with the raster (Hijmans, 2020), sp (Pebesma & Bivand, 2005), and sf (Pebesma, 2018) packages.

Because beetles disperse outward from eruption epicenters during outbreaks (Aukema et al., 2008), occurrence and severity in a stand depend strongly on the presence and severity in an adjacent stand (Aukema et al., 2006; Simard et al., 2012). Since beetles typically fly <500 m during dispersal events (Schmid, 1970; Turchin & Thoeny, 1993), we used a systematic design to sample every third grid cell (thus separating all sample points by ca. 480 m) to minimize the impact of fine-scale spatial autocorrelation in our analyses. For each sampled pixel, we extracted the BA loss due to bark beetles, presence or absence of each bark beetle species, and stand structure and composition (species-specific BA, SDI, and relative abundance; Windmuller-Campione et al., 2021).

Analyses

Defining susceptible stands

To compare the effects of multispecies outbreaks with those of single-species outbreaks, we first had to identify and map forest stands with conditions suitable to outbreaks of all combinations of bark beetle species. Stand hazard ratings, based on stand composition and structure metrics, are widely used to characterize the susceptibility of a stand to beetle outbreaks. Hazard rating systems have been developed for SB (Hart, Veblen, & Kulakowski, 2014; Schmid & Hs Frye, 1976) and MPB (Shore & Safranyik, 1992), but to our knowledge do not exist for WBBB. Because the spatial data necessary to quantify hazard based on these systems (e.g., BA of only trees greater than a certain diameter) are not available across the extent of the SRM, we used a modeling approach to map susceptibility, which also allowed for the inclusion of WBBB. We built random forest (RF) classification models (Breiman, 2001) for each of our three focal bark beetle species to define stand susceptibility. The response variable was bark beetle presence/absence from 1999 to 2019, derived from ADS. For predictor variables, we used BA, SDI, and relative abundance of each respective host (derived from NIDRM), all of which are commonly used in stand hazard ratings (Fettig et al., 2007; Shore & Safranyik, 1992).

We chose an RF modeling approach to account for nonlinear relationships between susceptibility and the host abundance variables available at the broad spatial extent of this study. Furthermore, predictive power from RF models can remain strong when predictors are correlated, as in our data (Cutler et al., 2007). We built the models in R using the ranger package (Wright & Ziegler, 2017) within a tidymodels framework (Kuhn & Wickham, 2020). RF hyperparameters were then tuned through spatial cross-validation using the spatialsample (Silge & Mahoney, 2022) and tune (Kuhn, 2021) packages. To account for a class imbalance in the response variable, we used a Synthetic Minority Over-sampling Technique (Chawla et al., 2002). We assessed the ability of our RF models to predict beetle presence on withheld testing data using 10-fold spatial cross-validation for three common metrics for the performance of binary classifications: area under the receiver operating characteristic curve (AUC), sensitivity (rate of accurately predicted beetle presence), and specificity (rate of accurately predicted beetle absence).

After the models were trained and optimized, we used them to make probability predictions (Malley et al., 2012) of beetle presence for all grid cells with host presence (>1 m^2 ha^{-1} host BA) that did not experience a beetle

outbreak during the study period. Finally, we defined those grid cells (stands) as susceptible to an outbreak of a given beetle species when the RF-predicted outbreak probability was greater than 40%. We chose 40% to give a more liberal estimation of susceptibility; sensitivity analyses showed that the relative amount of forest area classified as susceptible to each beetle was not strongly influenced by this threshold (Appendix S1: Figure S4). To each susceptibility dataset, we added all stands with a recorded outbreak in ADS data, except any stands where host BA was $\leq 1\ m^2\ ha^{-1}$. The three resulting maps were binary, where 1 indicated either ADS-observed beetle presence during the study period or an RF-predicted probability of beetle presence greater than 40% (i.e., susceptible), and 0 indicated no beetle presence and an RF prediction less than 40% (i.e., not susceptible).

Quantifying the extent and effects of overlapping bark beetle outbreaks in susceptible stands

After we modeled stand susceptibility to each beetle species individually, we then defined overlap susceptibility by identifying stands that were either (1) affected by more than one bark beetle species according to ADS, or (2) susceptible to more than one based on our models (i.e., the RF-predicted probability of outbreak was greater than 40% for two or more bark beetle species), or (3) a combination thereof. To quantify the extent of overlapping outbreaks of multiple bark beetle species, we then calculated the percent of all overlap-susceptible forests with the presence of multiple beetles identified by ADS data. Within stands that were susceptible to outbreaks of multiple beetle species, we used nonparametric Kruskal–Wallis tests (Kruskal & Allen Wallis, 1952) to determine if cumulative tree mortality (percent BA loss) was affected by the number and identity(ies) of bark beetle species present. Given a significant global difference among groups, we used Dunn tests (Dunn, 1964) to assess pairwise differences (all p values were Bonferroni-corrected). Both analyses were conducted in R using the rstatix package (Kassambara, 2021).

RESULTS

Susceptibility to individual bark beetle species

The RF models accurately predicted the occurrence of outbreaks of SB, MPB, and WBBB (Table 1). Performing spatial cross-validation on withheld data, the model produced AUC values ranging from 0.67 to 0.72 and sensitivity values ranging from 69% to 75%. The combination of ADS surveys and our models of stand susceptibility to individual bark beetle species suggested 71% of the study area was susceptible to outbreaks of either SB, MPB, or WBBB (or combinations thereof) (Figure 2b). Of the susceptible area, 69% experienced an outbreak by at least one of the three focal bark beetle species during the study period (49% of the total area) (Figure 2b). Stands susceptible to SB comprised 39% of the sampled stands, and of those stands, 44% experienced SB outbreaks during the study period (Figure 2a). Stands susceptible to MPB comprised 26% of the sampled stands, and of those stands, 85% were affected by MPB (Figure 2a). Finally, stands susceptible to WBBB comprised 33% of the sampled stands, and 55% of those stands experienced WBBB (Figure 2a).

TABLE 1 Model skill metrics from random forest models predicting the presence/absence of the spruce beetle (SB) in Engelmann spruce, mountain pine beetle (MPB) in lodgepole pine, and western balsam bark beetle (WBBB) in subalpine fir.

Species model	AUC	Sensitivity	Specificity
SB	0.70	0.77	0.48
MPB	0.62	0.69	0.47
WBBB	0.64	0.72	0.46

Note: Values are the mean accuracy statistics after 10-fold spatial cross-validation.
Abbreviation: AUC, area under the receiver operating characteristic curve.

Across the SRM, susceptible hosts and bark beetle outbreaks varied spatially. Susceptible lodgepole stands were concentrated at more northern locations, while susceptible spruce stands were most abundant at more southern locations, although they were also widespread in north and central locations (Figure 2c,d). Susceptible fir stands were distributed across the SRM (Figure 2e). While the distributions of MPB and WBBB outbreaks mirrored the spatial patterns of their susceptible hosts, SB activity was concentrated in the south, and to a lesser extent the northern part of the region, with more limited tree mortality in the central SRM (Figure 2c–e).

Susceptibility to multiple bark beetle species

Maps of host tree BA (USDA, 2019b) revealed that 54% of all sampled stands had presence of two or more host species. Based on spatial intersections of the single-species outbreak susceptibility maps, we found that 46% of those

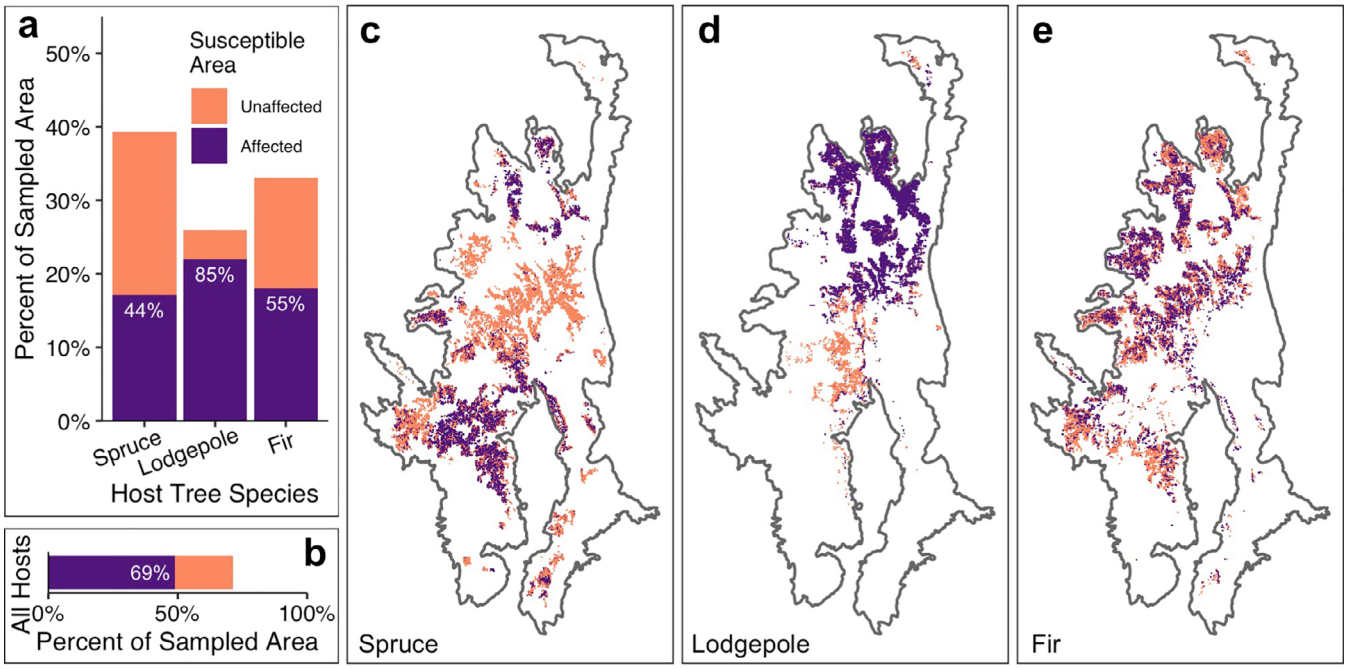


FIGURE 2 Host tree susceptibility to bark beetle outbreak and the occurrence of outbreak in the southern Rocky Mountains. Left column shows the percent of the sampled area susceptible to and affected by (a) each focal bark beetle species for their respective host tree species and (b) all beetle species for all hosts. Values within the bars indicate the percent of susceptible stands affected during the study period (1999–2019). Maps show the locations of unaffected and affected stands across areas with susceptible spruce (c), lodgepole (d), and fir (e).

stands were characterized by conditions suitable to outbreaks of multiple bark beetle species (25% of the total sampled area) (Figure 3a). Stands with both susceptible spruce and fir were most common (15% of the sampled area), followed by lodgepole and fir (6%). Susceptible spruce–lodgepole and spruce–lodgepole–fir forests were relatively uncommon, each representing less than 3% of the sampled area. Susceptible spruce–fir stands were distributed across most of the subalpine SRM (Figure 3b), while susceptible lodgepole–fir was concentrated in the northern part of the region (Figure 3c). Susceptible spruce–lodgepole stands were mostly in the central part of the region (Figure 3d), while stands where all three host species were susceptible were distributed throughout the central and northern SRM (Figure 3e). Lodgepole pine was absent across much of the southern SRM and therefore these areas were unsuitable for overlap of MPB with either of the other two bark beetle species (Figure 3c–e).

Extent of overlapping bark beetle outbreaks in susceptible stands

An outbreak of at least one species was observed in 83% of the area that was susceptible to two or more bark beetle species (Figure 3a). Within those overlap-susceptible forests, overlapping outbreaks were observed in 31% of stands (Figure 3a). Overlap occurred in 23% of spruce–fir susceptible stands, 40% of lodgepole–fir susceptible stands, and 18% of spruce–lodgepole susceptible stands. For stands where all three hosts were susceptible to bark beetle outbreak, the overlap of at least two species occurred in 71% of stands, and the overlap of all three beetle species occurred in 26% of stands (0.6% of all samples; Figure 3a). Spatial distributions of stands with multiple outbreaks largely mirrored the distributions of susceptible stands (Figure 3b–e). However, stands affected by outbreaks of all three bark beetle species were concentrated in the northern portion of the distribution of susceptible stands (Figure 3e).

Severity of tree mortality in single-species outbreaks versus overlapping multispecies outbreaks

In stands susceptible to outbreaks of multiple bark beetle species, the effect of overlapping outbreaks on cumulative tree mortality depended on bark beetle species identities. In stands susceptible to WBBB as well as SB and/or MPB, cumulative BA loss was lowest when WBBB was the only bark beetle species present (Figure 4). In stands susceptible to both MPB and WBBB (lodgepole–fir),

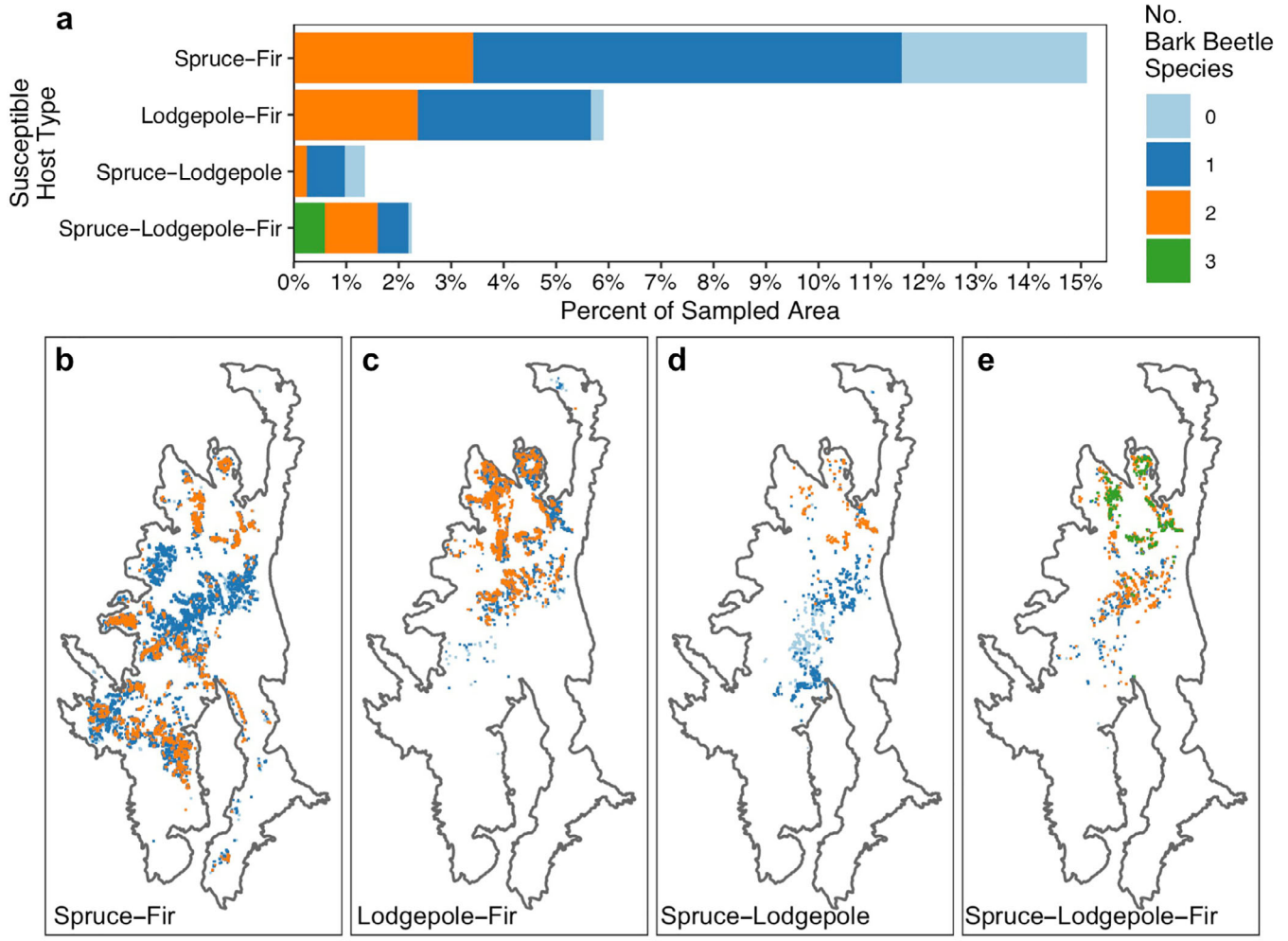


FIGURE 3 Susceptibility and occurrence of bark beetle outbreak overlap in the southern Rocky Mountains. (a) Percent of each susceptible host type affected by one or multiple bark beetle species during the study period (1999–2019). (b–e) Locations of single- and multispecies outbreaks in stands with conditions susceptible to overlap.

cumulative BA loss was similar between stands with the presence of MPB only and stands with the presence of both MPB and WBBB (Figure 4b,d). In contrast, in stands susceptible to both SB and WBBB (spruce–fir), cumulative BA loss was lower with the presence of both SB and WBBB than with SB only (Figure 4a). In stands susceptible to SB and MPB (spruce–lodgepole), cumulative BA loss was greatest when outbreaks of both MPB and SB occurred (Figure 4c). In stands susceptible to all three beetles (spruce–lodgepole–fir), cumulative BA loss was greatest when all three beetles were present (Figure 4d).

DISCUSSION

Contrary to expectations, we found that forest stands susceptible to outbreaks of multiple bark beetle species were relatively uncommon throughout the SRM, and of all susceptible stands, less than one third experienced mortality from multiple beetle species (1999–2019). When overlapping outbreaks did occur, stand-scale severity depended on the identity of the bark beetle and host tree species. Overlapping outbreaks of SB and MPB led to more severe tree mortality when compared with overlap-susceptible stands of spruce–lodgepole that experienced a single outbreak. However, stands susceptible to both SB and MPB were rare (<4% of the sampled area). The majority of mixed-species stands included subalpine fir, often as a minor component of BA relative to spruce or lodgepole. In stands including subalpine fir, the overlap of WBBB with other bark beetle species did not cause higher cumulative tree mortality when compared with outbreaks of SB or MPB alone. While species assemblages and disturbance dynamics may shift due to future climate change, our results indicate that, currently, subalpine forests of the SRM are rarely at risk of elevated tree mortality due to overlapping bark beetle outbreaks, compared with single-species outbreaks. This study builds on

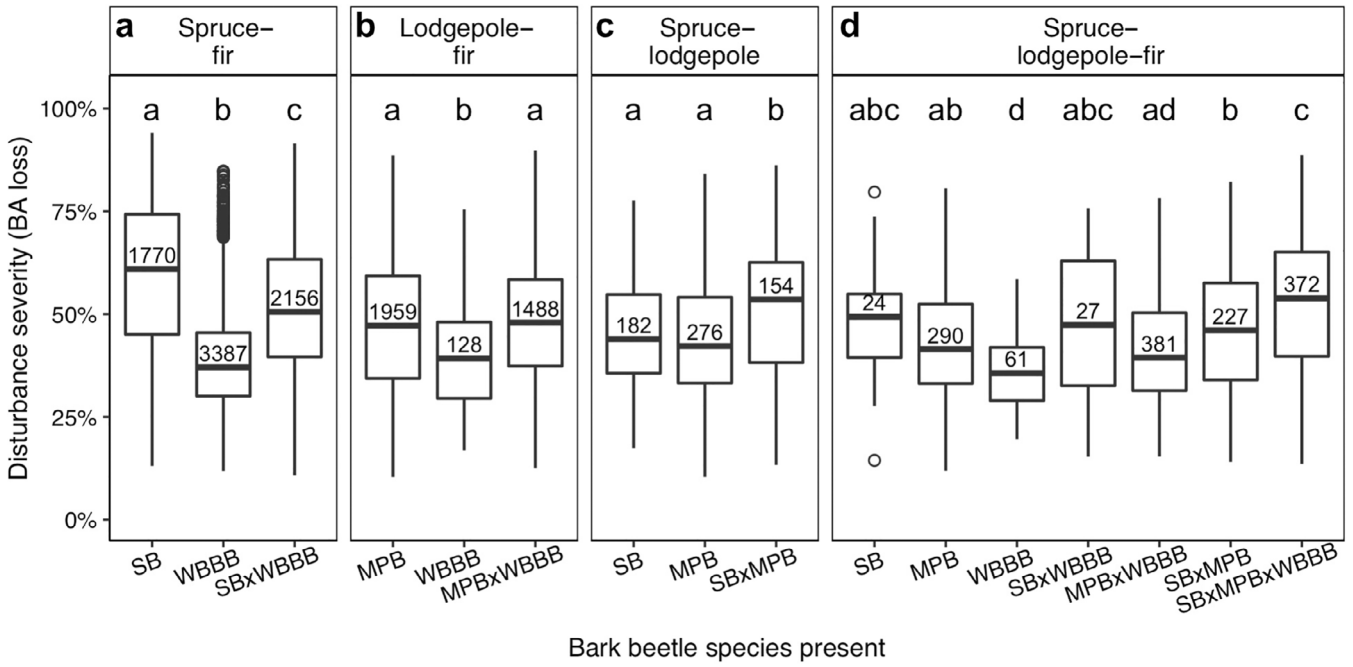


FIGURE 4 Severity of single-species and multispecies outbreaks in susceptible (a) spruce–fir, (b) lodgepole–fir, (c) spruce–lodgepole, and (d) spruce–lodgepole–fir forest types. MPB, mountain pine beetle; SB, spruce beetle; WBBB, western balsam bark beetle; abbreviations separated with an "x" indicate multiple species were present. Disturbance severity is expressed as percent basal area (BA) mortality at each sampling location, cumulative over the study period (1999–2019). Lower and upper limits of each box represent the first and third data quartiles, respectively, and the midlines show the median. Whiskers extend to the smallest and largest values 1.5 × the interquartile range, and circles represent outliers. Values within each box indicate the number of sampled stands in each group. Letters across the top of each plot display the results of pairwise comparisons using a Dunn test (Dunn, 1964; $\alpha = 0.05$, Bonferroni-corrected), conducted after a Kruskal–Wallis test indicating significant differences between groups (Kruskal & Allen Wallis, 1952).

previous research suggesting that tree diversity can buffer against severe effects from bark beetle outbreaks.

Susceptibility to multiple bark beetle species

Despite the widespread distributions of each host species across our study area, we found a relative scarcity of stands susceptible to outbreaks of multiple bark beetle species. Analysis of the NIDRM data showed that almost half of all sampled stands only included one of our three focal species, meaning those stands were either largely monospecific or included contribution of nonfocal species. This meant that, while almost half of all stands with multiple focal species were susceptible to outbreak overlap, that amounted to only a quarter of the sampled area. Moreover, susceptibility to overlap was not evenly distributed: stands susceptible to both SB and MPB were much less widespread than stands susceptible to WBBB and one or both of the others. This is likely because stands are susceptible to WBBB even when fir is a relatively minor component of the stand's BA (Appendix S1: Figure S1), as it is across much of the SRM (Alexander, 1985; Romme et al., 2009). Previous research on WBBB in the SRM lends support for lower thresholds of host abundance for susceptibility to WBBB outbreaks (Harvey et al., 2021; McMillin et al., 2003), although these studies examined the severity of fir mortality, not the occurrence. Susceptibility to SB or MPB, on the other hand, is favored by higher abundances of large individuals of their host trees than are likely required by WBBB (Schmid & Hs Frye, 1976; Shore & Safranyik, 1992). The scarcity of stands susceptible to both SB and MPB is largely the result of nonoverlapping distributions of Engelmann spruce and lodgepole pine in the SRM, which most often occupy stands with different disturbance histories, ages, and topographic positions (e.g., moisture availability and elevation) (Veblen, 1986). Even in areas suitable to establishment of both spruce and lodgepole, serotinous lodgepoles may more readily repopulate a postfire landscape, preventing shade-intolerant spruce trees from reaching a susceptible size while those lodgepole are also susceptible (Farris et al., 1998; Whipple & Dix, 1979). For all three of our focal tree species, asymmetric distributions of tree age, size, and presence across the landscape are likely key factors that limited simultaneous susceptibility to multiple bark beetle outbreaks. Other forest systems with

asymmetric spatial overlap of host tree species may experience a similarly limited extent of biotic disturbance overlap from multiple host-specific agents.

Our approach to mapping susceptibility in unaffected stands allowed us to assess the potential for overlapping bark beetle outbreaks, as well as their effects. However, because we defined susceptibility based on stand conditions quantified early in the study period, our method did not consider the possibility that tree mortality from an initial outbreak of one bark beetle species might shift a stand's susceptibility to another species later in the study period. Linked biotic disturbance interactions (sensu Simard et al., 2011), where an initial disturbance affects the likelihood or severity of a subsequent disturbance, have been observed in the SRM when two biotic disturbance agents affect the same host (e.g., Cole et al., 2022), but to our knowledge, this has not been observed for host-specific agents affecting separate hosts. Since bark beetle outbreaks are mainly driven by climate and the abundance of large-diameter hosts, a change in species composition from mortality of one host species is unlikely to significantly change the susceptibility of another host species, especially within a short study period. Outbreaks unfold across landscapes over the course of many years, and in slow-growing systems like the subalpine SRM, it could take many decades for surviving trees to reach large enough size and density for increased stand hazard (Aplet et al., 1988; Veblen, 1986). While outside the scope of this study, investigating the potential for linked short-interval bark beetle disturbances, both negative and positive, will be an important avenue for future research (Harvey et al., in review).

Extent of overlapping bark beetle outbreaks in susceptible stands

Of the stands susceptible to multispecies outbreaks, over 80% experienced an outbreak of at least one bark beetle species during the study period, but less than one third experienced outbreaks of multiple species. This could suggest that even when mixed-species stands have structure and composition that could support outbreaks of multiple beetle species, conditions often favor one species over another. Locally, this could be due to the influence of the surrounding forest composition on the species of beetle that erupts to outbreak nearby, resulting in dispersal of one beetle species into a stand, but not another (Howe et al., 2022; Simard et al., 2012). More broadly, however, overlap may be relatively uncommon because conditions at different spatial and temporal scales must combine for population eruptions to occur, conditions that can vary between beetle species. Despite broadscale climate conditions being generally favorable for outbreaks of all three focal bark beetle species during the study period, stand-level conditions are likely to favor outbreaks of one species over another, even in stands with host compositions suitable to overlap. For example, more severe WBBB outbreaks are expected in more mesic areas (Harvey et al., 2021), whereas susceptible populations of lodgepole often occupy drier sites (Veblen, 1986; Whipple & Dix, 1979). In this way, the degree of susceptibility to each bark beetle species likely exists on a gradient in mixed-species stands, which could have contributed to the relative scarcity of co-occurring outbreaks in our relatively short study period. Nevertheless, continued warming may facilitate future outbreaks in stands already affected by one beetle species, so researchers and managers should continue to monitor overlap-susceptible stands.

Severity of tree mortality in single-species outbreaks versus overlapping multispecies outbreaks

Given that a stand is susceptible to multiple beetle species, we expected that outbreak severity would increase when multiple outbreaks occurred because mortality would not be limited to one host species (Guo et al., 2019). Since the survival of nonhost trees is a key mechanism for forest recovery after an outbreak (Lloret et al., 2012), severe mortality of multiple tree species could drive shifts in forest trajectories or vegetation types (Andrus et al., 2020). Contrary to expectations, we found that elevated mortality due to outbreak overlap was limited to the rare occurrences of overlapping SB and MPB outbreaks and the overlap of all three beetle species. The majority of overlap-susceptible stands did not experience higher BA loss when compared with single-species outbreaks. This is likely due to differences in abundance between the three host species: stands with a relatively small proportion of fir BA may still experience an outbreak of WBBB, but the mortality of fir may represent a small proportion of total mortality when an outbreak of SB or MPB also occurs. Moreover, WBBB outbreaks are known to result in less host BA loss than SB or MPB, even when fir dominates the stand (Maclauchlan et al., 2003; McMillin et al., 2003; Stock, 1991; Appendix S1: Figure S2). Taken together, this suggests that the inclusion of subalpine fir as a component of mixed-species stands may help to buffer against severe tree mortality, even in the event of overlapping outbreaks.

Interestingly, severity in spruce–fir stands was lower when both SB and WBBB occurred, compared with the occurrence of SB alone. This counterintuitive result may

be due not only to WBBB outbreaks being generally less severe than SB outbreaks, but also to the spatial patterns of severe SB outbreaks in the SRM. Generally, mortality due to SB was most severe in the southern portion of the SRM, where WBBB was relatively uncommon despite the availability of susceptible hosts (Appendix S1: Figure S3). Thus, the majority of SB and WBBB overlap likely occurred in areas with less severe SB outbreaks, whereas spruce–fir stands that only experienced SB occurred where outbreaks were more severe. This further highlights the importance of tree distributions in driving the outbreak patterns of host-specific bark beetle species (Koontz et al., 2021).

Implications for management and future research

Since higher diversity of plants is expected to increase the diversity of insect herbivores (Strong et al., 1984), interactions between biotic disturbances are expected where preferred host abundance is high for multiple disturbance agents. This is particularly important for forests of western North America, where many of the most important biotic disturbance agents are host specific (Bentz et al., 2009). Outbreaks of the most widespread bark beetle species in the SRM are driven by similar climate conditions and shared disturbance history, and our results show that outbreaks of multiple bark beetle species can co-occur within the same stand within two decades. However, we also show that most mixed-species stands in the SRM are not at risk for elevated mortality from multiple bark beetle species when compared with single-species outbreaks. This is consistent with previous research that suggests that greater tree diversity contributes to lower-severity outbreaks by diluting the abundance of any given host (Connor et al., 2014; Guo et al., 2019; Jactel & Brockerhoff, 2007). Our results thus lend broad support to management strategies that promote resilience through increased tree diversity, which may help reduce stand-scale severity and increase the chances for recovery (Long et al., 2018).

The exception to this finding may be spruce–lodgepole forests, where we found increased outbreak severity when multiple outbreaks occurred. Future research should investigate the potential compounded effects of overlapping SB and MPB outbreaks on recovery. Forests that are susceptible to both SB and MPB may present a challenge for managers, since both monospecific and mixed-species stands may be susceptible to severe outbreaks. Furthermore, continued climate warming may help MPB outbreaks transition into forests of five-need pine species that co-occur with spruce at high elevation (Howe et al., 2021). The comparatively low severity of WBBB outbreaks suggests that management promoting subalpine fir may buffer against severe outbreaks, although this may also have unintended effects given that subalpine fir also experiences widespread mortality from drought and fungal pathogens (Bigler et al., 2007; Lalande et al., 2020). In general, however, host tree distributions and stand structure, as presented in our framework, can help managers identify the forests most vulnerable to overlapping outbreaks from multiple bark beetle species.

Despite the benefits, there are inherent limitations when describing stand-scale patterns over broad extents. While ADS data remain the most effective and widely used way to map the timing of tree mortality due to specific biotic agents, spatial inaccuracies are present in the ADS data (Coleman et al., 2018). Especially relevant is the common practice of "lumping" patchy WBBB-caused tree mortality (often <5 m in diameter) into single large polygons (Johnson & Ross, 2008; Parish et al., 1999). These lumped polygons may include forested areas unaffected by WBBB, potentially leading to an overestimation of its presence across the landscape. Additionally, the NIDRM host data were modeled across the region, meaning that our classifications of bark beetle susceptibility are based on predicted values (Krist et al., 2007), which may have led to over- or underestimation of host presence or abundance in some areas. Lastly, Landsat-derived measures of cumulative BA loss, although largely accurate (Rodman et al., 2021), also had a degree of predictive error that, when added to potential errors in the aforementioned data sources, likely resulted in noisy data signals. However, by systematically subsampling the data, using an RF modeling approach, and conducting our analyses across a broad extent, we were able to sufficiently mitigate these issues.

Future research that examines the relative contributions of individual bark beetle species to overall mortality is needed to support our region-wide analyses. Because our focal beetle species were host-specific specialists, we expected them to act independently of each other, but future research could additionally consider the temporal dynamics of successive outbreaks to investigate the potential for linked interactions at the stand and tree levels. Furthermore, our results from subalpine forests of the SRM are greatly influenced by region-specific bark beetle and host dynamics, especially the low contribution of subalpine fir in mixed stands and the scarcity of stands with both spruce and lodgepole. Forested regions with greater tree species richness and diversity may experience different outcomes, so further research could use our framework to address this knowledge gap in other areas affected by multiple biotic disturbance agents, such as California, USA (Stephenson et al., 2019).

CONCLUSION

Biotic disturbance agents play an integral role in disturbance regimes across the globe, and the SRM is no exception. This study presents a novel framework for investigating the impacts of overlapping bark beetle outbreaks in susceptible forest stands across a large forest ecosystem. Although tree mortality from bark beetles has been widespread and severe in the SRM and other forests in the western United States, our findings suggest that co-occurring outbreaks of two or more bark beetle species rarely result in severity than single-species outbreaks. Forest composition, especially the contribution of subalpine fir, was particularly important for diminishing the additive severity of multispecies outbreaks. Interacting bark beetle outbreaks can result in novel shifts in species composition, but surviving trees of all host species in the SRM indicate that tree species distributions and vegetation types are likely to persist. As biotic disturbances become more common in a changing climate, these results and the further application of our framework can help ecologists and managers identify the areas more likely to be affected by biotic disturbance interactions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Datasets utilized for this research are found in Rodman et al. (2021), USDA (2019a, 2019b, 2020), and USDA Forest Service and USGS (2017).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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