THESIS

INTERACTIONS AND IMPACTS OF MULTIPLE BARK BEETLE OUTBREAKS IN THE SOUTHERN ROCKY MOUNTAINS

Submitted by

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ABSTRACT

INTERACTIONS AND IMPACTS OF MULTIPLE BARK BEETLE OUTBREAKS IN THE SOUTHERN ROCKY MOUNTAINS

In conifer forests of western North America, outbreaks of native bark beetles are important biotic disturbances that influence forest structure and function. Subalpine forests in the southern Rocky Mountains (SRM) are home to multiple species of host-specific bark beetles that can affect the same stand concurrently or successively, potentially interacting to affect landscape patterns of tree mortality and subsequent disturbance dynamics. Despite their importance, the causes and consequences of interactions among bark beetle disturbances are poorly understood. To examine how outbreaks of different bark beetle species interact, we conducted two studies in the SRM. First, using broad-scale geospatial data, we explored the extent and severity of overlapping outbreaks of multiple bark beetle species across the SRM. We found that forest stand susceptibility to outbreaks of multiple bark beetle species is limited by host tree distributions, and that overlap of outbreaks was relatively uncommon. Furthermore, cumulative tree mortality was rarely higher in stands that experienced overlapping outbreaks compared to stands that experienced single-species outbreaks. These results suggest that forest trajectories in mixed-species stands will not be altered when multiple bark beetle outbreaks co-occur, compared to single-species outbreaks. Second, in a multi-scale study including both field and geospatial data, we explored how history of stand-replacing fires and a severe spruce beetle (*Dendroctonus rufipennis*) outbreak affected future susceptibility to subalpine fir (*Abies lasiocarpa*) decline (SFD) from outbreaks of the western balsam bark beetle (*Dryocoetes confusus*) and associated fungal pathogens. At the landscape scale, we found that disturbance history had limited effects on the susceptibility to future SFD, with a weak trend towards higher susceptibility in younger forests. At the stand scale, however, we found no effect of disturbance history on stand structure or composition traits that have been shown to influence susceptibility to SFD. Individual tree-scale analyses revealed that tree and local neighborhood traits were most important for determining likelihood of SFD. Weak connections between disturbance history, stand structure and composition, and SFD underscore the variability in forest recovery after disturbance, and highlight the need for future research. Together, these results from these studies indicate that, while climate change may be amplifying tree mortality events, subalpine forests in the SRM may be broadly resilient to co-occurring and successive disturbances.

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1.1 Introduction

Global change has altered disturbance regimes around the world, a trend that is likely to continue (Turner 2010, Sommerfeld et al. 2018). Changing disturbance regimes will alter forest ecosystem structure and function, including vegetation patterns (Anderegg et al. 2015), nutrient cycling (Turner et al. 2007, Edburg et al. 2012), 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 and further complicate our ability to forecast ecosystem change (Buma 2015, Johnstone et al. 2016). Consequently, understanding the causes and consequences of disturbance interactions remains a high research priority (Turner 2010, Trumbore et al. 2015, Kleinman et al. 2019).

Disturbance interactions occur when an ecosystem, which has not fully recovered from an initial disturbance, is affected by a secondary disturbance (Burton et al. 2020). Such interactions are expected to occur more frequently when disturbances share common drivers. For example, warm temperatures and dry conditions can lead to increases in both fire and bark beetle activity by lowering fuel moisture and increasing beetle population development rates, respectively (Bentz et al. 2010, Parks and Abatzoglou 2020). While overlapping disturbances may occur due to common drivers, 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, windthrown trees can initiate bark beetle outbreaks in subalpine forests (Veblen et al. 1991b, 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 eliminated mature trees that would have acted as seed sources (e.g. Andrus et al., 2021). While recent studies have examined interactions between abiotic disturbances (e.g., drought and wildfire) and between biotic and abiotic disturbances (e.g., windthrow and bark beetle outbreaks), interactions between two or more biotic disturbances have received relatively little study (Buma 2015, Kleinman et al. 2019). Given that many widespread biotic disturbances are facilitated by warming (Bentz et al. 2010), and these disturbances cover broad areas (Hicke et al. 2020), there is a particular need to understand their interactions.

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 in the western United States over the past two decades (Hicke et al. 2016, 2020). For many species of bark beetle, the development of outbreak is due to a set of common drivers, such as stand age and favorable climate conditions (Raffa et al. 2008, Bentz et al. 2010), which may lead to overlapping outbreaks (Andrus et al. 2020). As such, the United State Forest Service (USFS) estimates that almost 2 million ha of forested area across the West are at risk for outbreaks of more than one bark beetle species over the next 15 years and beyond (Krist et al. 2015, USDA 2019). Subalpine forests of the southern Rocky Mountains (SRM) have already experienced outbreaks of multiple species of bark beetles that have caused widespread mortality of Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*), and subalpine fir (*Abies lasiocarpa*), tree species that commonly co-occur across the subalpine zone. Critically, while the effects of single-species bark beetle outbreaks have been widely studied, little research has examined patterns of outbreak overlap or the effects of overlapping outbreaks on forest mortality (Kleinman et al. 2019).

In subalpine forests of the SRM, the spruce beetle (SB; *Dendroctonus rufipennis*), the mountain pine beetle (MPB; *Dendroctonus ponderosae*), and the western balsam bark beetle (WBBB; *Dryocoetes confusus*) are important drivers of tree mortality of Engelmann spruce, lodgepole pine, and subalpine fir, respectively (Bentz et al. 2009, Karel and Man 2017). These beetles 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 and Carroll 2006). Under these conditions, healthy trees can physically expel the beetles through resin exudation and/or repel and kill attacking beetles through the production of defensive compounds (Raffa et al. 2005). However, beetles can overcome tree defenses through pheromone-mediated mass attacks, at which point the extensive beetle colonization and introduction of associated fungal pathogens can kill even healthy trees (Wallin and Raffa 2004). Eruption to outbreak stages is complex but generally requires landscapes composed of large, abundant, susceptible hosts. 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, Kolb et al. 2016, Hart et al. 2017). Outbreak severity varies among the three beetle species in the SRM; host basal area mortality in SB and MPB (genus *Dendroctonus*) can be very severe (often >80%), whereas WBBB (genus *Dryocoetes*) is observed to be less aggressive (Wood 1982), causing dispersed fir mortality across the landscape (Stock 1991a, Johnson et al. 2014) .

For all three bark beetles, a stand's susceptibility to outbreak is strongly influenced by patterns in forest structure and composition, which often reflects past disturbance history (Windmuller-Campione et al. 2021). Outbreaks are more likely to develop in stands with larger trees and greater host abundance (Hart et al. 2014b, Buonanduci et al. 2020, Harvey et al. 2021). Larger host trees have thicker phloem that provides better nutrition for mass-attacking beetles (Graf et al. 2012), while higher host density allows for more successful within-stand beetle dispersal (Negrón 2020), both of which can increase the likelihood and severity of outbreaks (Fettig et al. 2007). Subalpine forests of the SRM are characterized by an infrequent (200-500 yr), high-severity fire regime (Buechling and Baker 2004, Sibold et al. 2006) that can create extensive areas composed of even-aged trees; similarly, widespread fire and logging activity in the 1800s may have increased susceptibility to bark beetle attacks (Veblen and Donnegan 2005, Windmuller-Campione et al. 2021). This abundance of large-diameter hosts of multiple species, along with shared climate drivers, may synchronize outbreaks of different bark beetle species. While outbreaks more readily develop in stands dominated by a preferred host (Safranyik and Carroll 2006), constraints of host abundance are less important during the eruptive phase of an outbreak (DeRose and Long 2012, Hart et al. 2014b), which can enable bark beetle activity in mixed-species stands. In those stands, activity from a single bark beetle species will typically be concentrated on one host species. However, if outbreaks of multiple species occur in the same stand, the combined mortality of both host species may be greater, with potential consequences for future forest trajectories. The way that these factors interact to influence the likelihood and severity of multi-species outbreaks are not well understood, particularly across heterogeneous forest landscapes such as the SRM.

In this study, we use broad-scale geospatial data to explore the frequency and severity of multi-species outbreaks of SB, MPB, and/or WBBB across susceptible subalpine forests in the SRM. Because multi-species outbreaks are not possible in monospecific stands, we used stand structure and composition to confine our analyses to forests susceptible to multiple 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) Given stand conditions susceptible to outbreaks of multiple bark beetles, how common is the overlap of outbreaks of multiple bark beetle species? (3) In areas susceptible to outbreaks of multiple bark beetles, is cumulative tree mortality greater in stands affected by overlapping outbreaks in comparison to single-species outbreaks? We expected that most forests were susceptible to at least one bark beetle species prior to the recent epidemics due to their existing size and age structures (Windmuller-Campione et al. 2021). Because most forests are composed of more than one host species, we expected that stands susceptible to multiple bark beetles would be similarly widespread, as would the occurrence of overlapping outbreaks. Alternatively, if dilution of host abundance in mixed-species stands limits susceptibility to individual bark beetle species, then stands susceptible to multiple bark beetles may be relatively rare, and 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.

1.2 Methods

1.2.1 Study area

The study area is the subalpine zone (2700-3600 m) of the southern Rocky Mountains (SRM), which extends from northern New Mexico to southern Wyoming, USA (Fig. 1.1). 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) (Romme et al. 2009, PRISM Climate Group 2020). 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 aristate*], 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 outbreaks of SB, MPB, and WBBB occurred across the SRM from 1999 to 2019, affecting 15%, 19%, and 14% of subalpine forests, respectively (USDA 2020) (Fig. 1.1). 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 Rio Grande and Colorado rivers, making them ecologically, economically, and socially important.

1.2.2 Data

To describe the distributions and densities of the three host tree species across the SRM, we used Individual Tree Species Parameter Maps (ITSPM) created by the National Insect and Disease Risk Mapping project (NIDRM; USDA 2019a). These maps use Forest Inventory and Analysis (FIA) data, 30-m resolution Landsat imagery, and biophysical predictors 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 x 240-m raster datasets of species basal area (BA) and stand density index (SDI), as well as total stand BA in ca. 2002 from the ITSPM (Table S1). Additionally, we used these data to calculate the relative abundance (percent BA contribution) of each host species to the stand. Host BA, SDI, and relative abundance have all been shown to be important predictors of outbreak occurrence and severity at a stand level (Shore and Safranyik 1992, Fettig et al. 2007, Harvey et al. 2021).

To describe patterns of outbreaks of the three focal bark beetle species in the SRM, we used vector data from the USFS Aerial Detection Survey (ADS) (USDA 2020). ADS data is 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 and 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 basal area loss due to bark beetles during the study period produced by Rodman et al. (2021). Briefly, these data were produced using the

Google Earth Engine implementation of LandTrendr (Kennedy et al. 2018), which quantifies declines in vegetation indices in Landsat image time series. These declines were compared with field data from bark beetle-affected forests to predict percent basal area loss across subalpine forests of the SRM. The resulting maps were strongly predictive of field-derived estimates of outbreak severity (Rodman et al. 2021).

1.2.3 Data processing

Percent BA loss was calculated at a 30 x 30-m resolution and aggregated to 240 x 240 m for this study using the mean value of all 30-m cells (Rodman et al. 2021). A resolution of 240 x 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 rasters with a resolution of 240 x 240 m, projected in Albers Equal Area projection. Specifically, we considered a cell to have bark beetle species presence if an ADS polygon intersected the centroid of a 240-m cell. Because our research questions do not focus on timing or order of disturbance, we combined all years of bark beetle presence data during the study period. We then created three binary raster datasets describing the presence or absence of each bark beetle species across all years. To increase the reliability of detection, grids of cumulative bark beetle presence were then multiplied by grids of host presence, defined here as >1 m^2ha^{-1} host BA, to obtain a grid of bark beetle activity (Chapman et al. 2012). Because our study focused solely on bark beetle disturbances, we excluded areas that experienced wildfire or logging within ~10 years of the study period from our analyses. Since data on forest management of private lands is unavailable or incomplete, we also restricted our study to public forest lands managed by the US Forest Service (Figure 1). Though these restrictions exclude ~30% of subalpine forests in the SRM, they were necessary to ensure that 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).

Because beetles disperse outward from eruption epicenters during outbreaks (Aukema et al. 2008), occurrence and severity in a given stand depends strongly on the presence and severity in an adjacent stand (*i.e.* beetle pressure *sensu* Preisler, 1993). To minimize the impact of this autocorrelation in our analyses, we used a systematic design to sample every third grid cell (1/9th of the total study area or 106,143 sample points), since beetles typically fly < 500 m during outbreaks (Schmid 1970, Turchin and Thoeny 1993). At each sample point, we extracted values for disturbance severity, presence/absence of each bark beetle species, and host characteristics (species-specific BA, SDI, and relative abundance; Windmuller-Campione et al., 2021).

1.2.4 Analyses

Defining susceptible host forest

Stand hazard ratings have been widely used to characterize the susceptibility of a stand to beetle outbreaks based on stand composition and structure (Schmid and Frye 1976, Shore and Safranyik 1992, Hart et al. 2014b). Hazard rating systems have been developed for SB and MPB, but to our knowledge do not exist for WBBB. To ensure our classification of stand susceptibility was consistent across our focal beetle species, we developed a unified statistical framework using Random Forest (RF) classification models (Breiman 2001), which are robust to correlated predictors and spatial autocorrelation in the response. We predicted stand susceptibility using BA, SDI, and relative abundance for each respective host, which are commonly included in stand hazard ratings (Fettig et al. 2007). Since the NIDRM host composition data is modeled and can include very low positive abundance values for a tree species in areas where they are likely to be absent, we restricted each RF model to points that had >1 m^2ha^{-1} host BA to ensure host presence. We fit our probability RF models (Malley et al. 2012) using the *ranger* package (Wright and Ziegler 2017) within a *tidymodels* framework (Kuhn and Wickham 2020). RF hyperparameters were optimized through cross-validation using the *tune* package (Kuhn 2021). To account for class imbalance of the response variable (beetle presence), we used a Synthetic Minority Over-sampling Technique (SMOTE; Chawla et al. 2002). We assessed our RF models using sensitivity (rate of accurately predicting beetle presence) and AUC (area under the receiver operating characteristic curve), two common metrics of model accuracy. Finally, after ensuring models accurately predicted outbreak presence/absence, we defined locations where the RF-predicted outbreak probability was greater than 40% to be susceptible, though we explored different thresholds using sensitivity analysis (Fig. S1.4).

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

Once we modeled stand susceptibility to each beetle individually, we defined overlap susceptibility by identifying stands that were susceptible to more than one bark beetle species (i.e., the predicted probability of outbreak was greater than 40% for two or more bark beetle species). To understand how frequently outbreaks of multiple bark beetle species overlapped, we then calculated the percent of all overlap-susceptible forests with presence of multiple beetles identified by ADS data. Within stands that were susceptible to outbreaks of multiple beetle species, we used non-parametric Kruskal-Wallis tests to determine if cumulative tree mortality (percent BA loss) of stands was affected by the identity of bark beetle species present (Kruskal and Wallis 1952). Given a significant global difference among groups, we used Dunn tests to assess pairwise differences (Bonferroni corrected) (Dunn 1964). Both analyses were conducted in R using the *rstatix* package (Kassambara 2021). We limited our analyses to stands where beetle presence matched susceptibility. All analyses were performed in R v. 4.0.2 (R Core Team 2020).

1.3 Results

1.3.1 Forest stand susceptibility to individual bark beetle species

RF models accurately predicted the occurrence of outbreaks of WBBB, SB, and MPB (Table 1.1). Both sensitivity and AUC were between 68 and 72% for models of each beetle species. Models of stand susceptibility to individual bark beetle species suggested 67% of the study area was susceptible to outbreaks of SB, MPB, and/or WBBB (Fig. 1.2b). Stands susceptible to SB comprised 37% of the sampled points, and of those points 40% experienced SB outbreaks during the study period (Fig. 1.2a). Stands susceptible to MPB comprised 26% of the sampled points, and of those points, 71% were affected by MPB (Fig. 1.2a). Finally, stands susceptible to WBBB comprised 28% of the sampled points, and 49% of those points experienced WBBB (Fig. 1.2a). Across all subalpine forests in the SRM, 67% were susceptible to outbreaks of at least one bark beetle species, and 61% of this area experienced bark beetle disturbance of some kind over the study period (42% of the total area) (Fig. 1.2b).

Across the SRM, patterns of susceptible hosts and bark beetle outbreak demonstrated clear spatial patterns. Susceptible lodgepole was concentrated at more northern locations, while susceptible spruce was more abundant at more southern locations (Fig. 1.2c-d). Susceptible fir was distributed across the SRM (Fig. 1.2e). 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 (Fig. 1.2c-e).

1.3.2 Forest stand susceptibility to outbreaks of multiple bark beetle species

Based on spatial intersections of single-species RF model predictions, 22% of sampled area was characterized by stand conditions suitable for outbreak overlap (Fig. 1.3a). Stands with both susceptible spruce and fir were most common (13% of the sampled area), followed by lodgepole and fir (5%). Susceptible spruce-lodgepole and spruce-lodgepole-fir forests were relatively uncommon, each constituting less than 2% of the sampled area. Susceptible spruce-fir stands were distributed across most of the subalpine SRM (Fig. 1.3b), while susceptible lodgepole fir was concentrated in the northern part of the region (Fig. 1.3c). Stands where both spruce and lodgepole were susceptible were concentrated in the central part of the region (Fig. 1.3d), while stands where all three host species were susceptible were sparsely distributed throughout the central and northern SRM (Fig. 1.3e); lodgepole pine was absent across much of the southern SRM and therefore these areas were unsuitable for overlap of the three bark beetle species (Fig. 1.3c-e).

1.3.3 Extent of overlapping bark beetle outbreaks in susceptible stands

Overlapping outbreaks were observed in 28% of the area that was susceptible to two or more bark beetle species (Fig. 1.3a). Overlap occurred at 21% and 31% of spruce-fir and lodgepole-fir susceptible stands, respectively; however, overlap only occurred in 6% of spruce-lodgepole stands. For stands where all three hosts were susceptible to bark beetle outbreak, the overlap of at least two species occurred in 50% of stands, but the overlap of all three beetle species only occurred in 15% of stands (0.2% of all samples; Fig. 1.3a). Spatial distributions of stands with multiple outbreaks largely mirrored the distributions of susceptible stands (Fig. 1.3b-e). However, stands affected by outbreaks of all three bark beetle species were concentrated in the northern portion of the distribution of susceptible forests (Fig. 1.3e).

1.3.4 Severity of tree mortality in single-species outbreaks vs. overlapping multi-species 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 and SB and/or MPB, cumulative BA loss was lowest when WBBB was the only bark beetle species present (Fig. 1.4). In stands susceptible to both MPB and WBBB (lodgepole-fir), cumulative BA loss was similar between stands with the presence of MPB only and stands with the presence of both MPB and WBBB (Fig. 1.4b,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 (Fig. 1.4a). In stands susceptible to SB and MPB (spruce-lodgepole), cumulative BA loss was greatest when outbreaks of both MPB and SB occurred (Fig. 1.4c). In stands susceptible to all three beetles (spruce-lodgepole-fir), cumulative BA loss was generally greater when SB was present (Fig. 1.4d).

1.4 Discussion

When outbreaks of multiple bark beetle species overlap in time and space, we hypothesized that mixed-species forests would experience elevated tree mortality compared to single-species outbreaks. However, we found that forest stands susceptible to outbreaks of multiple bark beetle species were relatively uncommon throughout the southern Rocky Mountains, and of all susceptible stands, less than one third experienced mortality from multiple beetle species. When overlap did occur, patterns of stand-scale severity reflected the identity of the bark beetle and host tree species involved. Outbreaks of both SB and MPB led to more severe tree mortality when compared to overlap-susceptible stands that experienced a single outbreak. However, stands susceptible to both SB and MPB were rare in the SRM; the majority of mixed-species stands included subalpine fir, often as a relatively minor component relative to spruce or lodgepole. In these stands, the overlap of WBBB with other species did not cause higher cumulative tree mortality when compared to outbreaks of SB or MPB alone. Overall, our results indicate that subalpine forests of the SRM are rarely at risk of elevated tree mortality due to overlapping bark beetle outbreaks, compared to single-species outbreaks.

1.4.1 Forest stand susceptibility to outbreaks of multiple bark beetle species

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). Our RF modeling of host abundance accurately predicted forest stand susceptibility to individual bark beetle species, yet despite the widespread distributions of each host species across our study area, we found a relative scarcity of stands susceptible to outbreaks of multiple beetles. Moreover, susceptibility to outbreak overlap was not evenly distributed among the three bark beetle/host species: 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 (Fig. S1.1), as it is across much of the SRM (Alexander 1985, Romme et al. 2009). Previous research on subalpine fir decline in the SRM lends support for lower thresholds of susceptibility to WBBB (McMillin et al. 2003, Harvey et al. 2021), though these studies examined the severity of fir mortality, not the occurrence. Susceptibility to SB and MPB, on the other hand, is favored by higher abundances of spruce and lodgepole, respectively (Schmid and Frye 1976, Shore and Safranyik 1992) (Fig. S1.1). The scarcity of stands susceptible to SB and

MPB is amplified by the largely non-overlapping distributions of spruce and lodgepole in the SRM, which occupy stands of different ages and moisture availability (Veblen 1986). This asymmetric distribution of tree species among mixed species stands is a key factor that limits simultaneous susceptibility to multiple bark beetle outbreaks. Other forest systems with uneven distribution of tree species may show similar resistance to disturbance from multiple host-specific agents.

1.4.2 Extent of overlapping bark beetle outbreaks in susceptible stands

Even within the relatively limited number of stands susceptible to multi-species outbreaks, less than one third experienced outbreaks of multiple species during the study period. While stand hazard ratings are widely used by managers to assess susceptibility to outbreak, we found that outbreaks occurred even in stands that would be classified as low/moderate hazard (Schmid and Frye 1976, Shore and Safranyik 1992) (Fig. S1.1). This supports research showing that local constraints of stand structure are relaxed once beetle populations reach epidemic levels, especially under warmer climate conditions (Klutsch et al. 2009, DeRose and Long 2012, Hart et al. 2014b). The relatively infrequent occurrence of overlapping outbreaks in susceptible stands shows that, even with these relaxed constraints, most mixed-species forest stands in the SRM have a composition that makes them more resistant to multi-species outbreaks, and able to persist when such outbreaks occur.

1.4.3 Severity of tree mortality in single-species outbreaks vs. overlapping multi-species outbreaks

Given that a stand is susceptible to multiple beetles, we expected that outbreak severity would increase when multiple outbreaks occurred because mortality would not be limited to one host species. Since the survival of non-host 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. The majority of overlap-susceptible stands did not experience higher BA loss when compared to single-species outbreaks. This is likely also due to differences in abundance between the three host species: stands with a small contribution of fir may still experience an outbreak of WBBB, but the mortality may not meaningfully contribute to cumulative severity when an outbreak of SB or MPB also occurs. Moreover, WBBB-caused mortality is known to be less severe than SB or MPB, even when fir dominates the stand (Stock 1991, McMillin et al. 2003, Harvey et al. 2021; Fig. S1.2).

Interestingly, severity in spruce-fir stands was lower when both SB and WBBB occurred, compared to the occurrence of SB alone. This counterintuitive result may be due 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 (Fig. S1.3). Thus, the majority of SB and WBBB overlap most likely occurred in areas with less severe SB outbreaks, whereas spruce-fir stands with only SB were abundant in the severe southern outbreaks. Taken together, these results highlight the importance of tree distributions in driving the outbreak patterns of host-specific bark beetle species (Koontz et al. 2021). Other forest systems that experience mortality from multiple biotic agents may have similar mortality responses if there are asymmetries in the distribution of hosts or the severity of disturbance agents.

1.4.4 Implications for management and future research

The most widespread bark beetle species in the SRM are driven by similar climate conditions and shared disturbance history, which may suggest that forecasting and management should incorporate the compounded effects of multiple bark beetle outbreaks. Our results suggest, however, that most mixed-species stands are not at risk for elevated mortality from multiple bark beetle species, compared to single-species outbreaks. The exception is spruce-lodgepole forests, where future research should investigate the potential compounded effects of multiple outbreaks on recovery (Andrus et al. 2020). The comparatively low severity of WBBB outbreaks could suggest that management that promotes subalpine fir may buffer against severe outbreaks, though this may be complicated given that subalpine fir also experiences widespread mortality from drought and fungal pathogens (Bigler et al. 2007, Lalande et al. 2020). Thus, while severe mortality due to overlapping bark beetle outbreaks is not expected to be widespread in the SRM, our framework can help managers identify the most vulnerable forests.

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, these data suffer from some spatial inaccuracies (Coleman et al. 2018). Especially relevant is the common practice of “lumping” patchy and heterogeneous WBBB-caused tree mortality (often <5 m in diameter) into single large polygons (Parish et al. 1999, Johnson and Ross 2008). These lumped polygons may include forested area unaffected by WBBB, potentially leading to an overestimation of the presence of WBBB across the landscape. Additionally, the ITSPM host data was modeled across the region, meaning our classifications of bark beetle susceptibility are based on predicted values (Krist et al. 2007), which may have led to over- or under-estimation of host presence or abundance in some areas. Lastly, Landsat-derived measures of cumulative BA loss, though largely accurate

(Rodman et al. 2021), also had a degree of predictive error that, when added to the aforementioned data sources, likely resulted in noisy data signals.

Future research should examine the stand-scale severity of multi-species outbreaks in the field to support our region-wide analyses. Because our focal beetle species were host-specific, 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 level. 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. Systems with a greater richness and diversity of host tree species may experience different outcomes, so further research could use our framework to address this knowledge gap in other regions with multiple biotic disturbance agents, such as California, USA (Stephenson et al. 2019, Dudney et al. 2020). However, though the potential for synergistic effects of multiple outbreaks has been largely ignored in forest management, our analyses suggest that management aimed at mitigation of single-species outbreaks, rather than overlapping outbreaks, is appropriate under most circumstances in the SRM.

1.5 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 consequences of overlapping bark beetle outbreaks in susceptible forest stands across broad extents. Our findings indicate that elevated tree mortality caused by co-occurring outbreaks of two or more bark beetle species is limited to a relatively small extent of subalpine forests in the SRM, highlighting the importance of forest structure in determining the patterns of occurrence and severity of multiple host-specific insect herbivores. 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 most affected by biotic disturbance interactions.

1.6 Tables

Table 1.1. Accuracy statistics 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. AUC is the area under the receiver operating characteristic curve.

	AUC	Sensitivity	Specificity
SB	0.71	0.70	0.60
MPB	0.72	0.69	0.73
WBBB	0.68	0.70	0.55

1.7 Figures

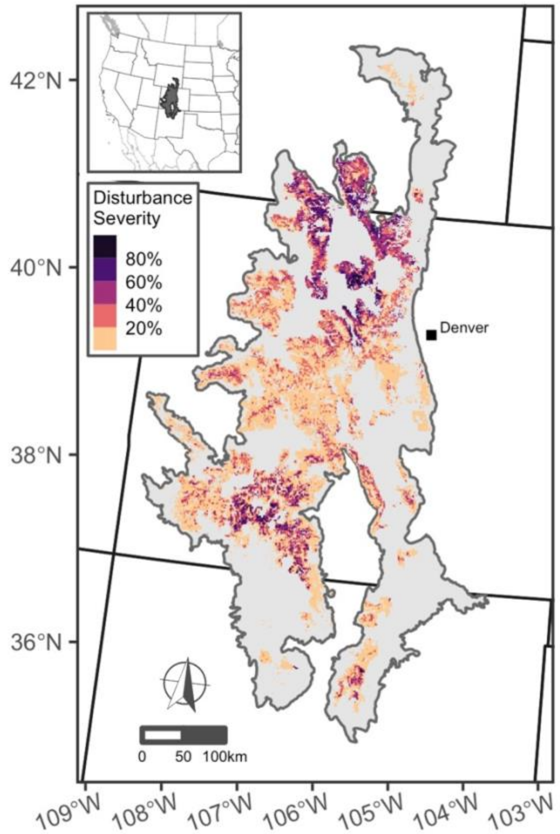

Figure 1.1. The extent of subalpine forest within US Forest Service lands within the Southern Rocky Mountains (SRM), USA (gray). Colored areas show the cumulative disturbance severity (percent of pre-outbreak tree basal area killed by bark beetles) during the 1999-2019 study period (Rodman et al. 2021).

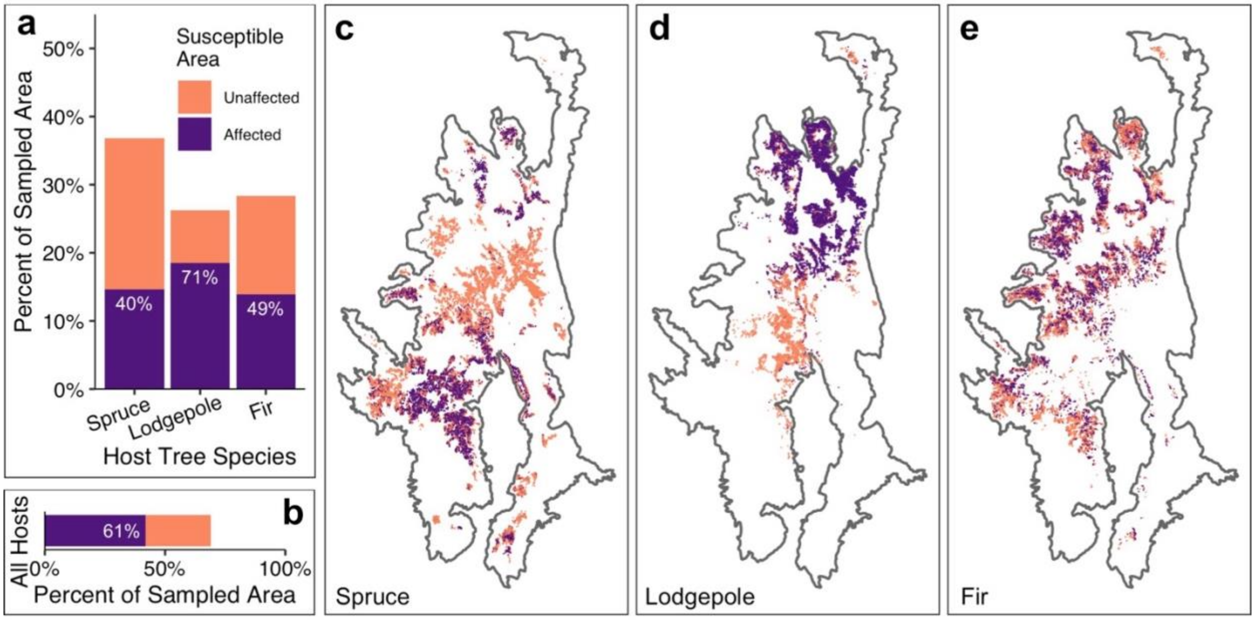

Figure 1.2. Host tree susceptibility to bark beetle outbreak and occurrence of outbreak in the SRM. Percent of sampled area susceptible to and affected by (a) each focal bark beetle species for their respective host tree species, and (b) all beetle species for all hosts. Darker portions with white text indicate the percent of susceptible stands affected during the study period (1999-2019). (c-e) Locations of susceptible and affected stands for each host.

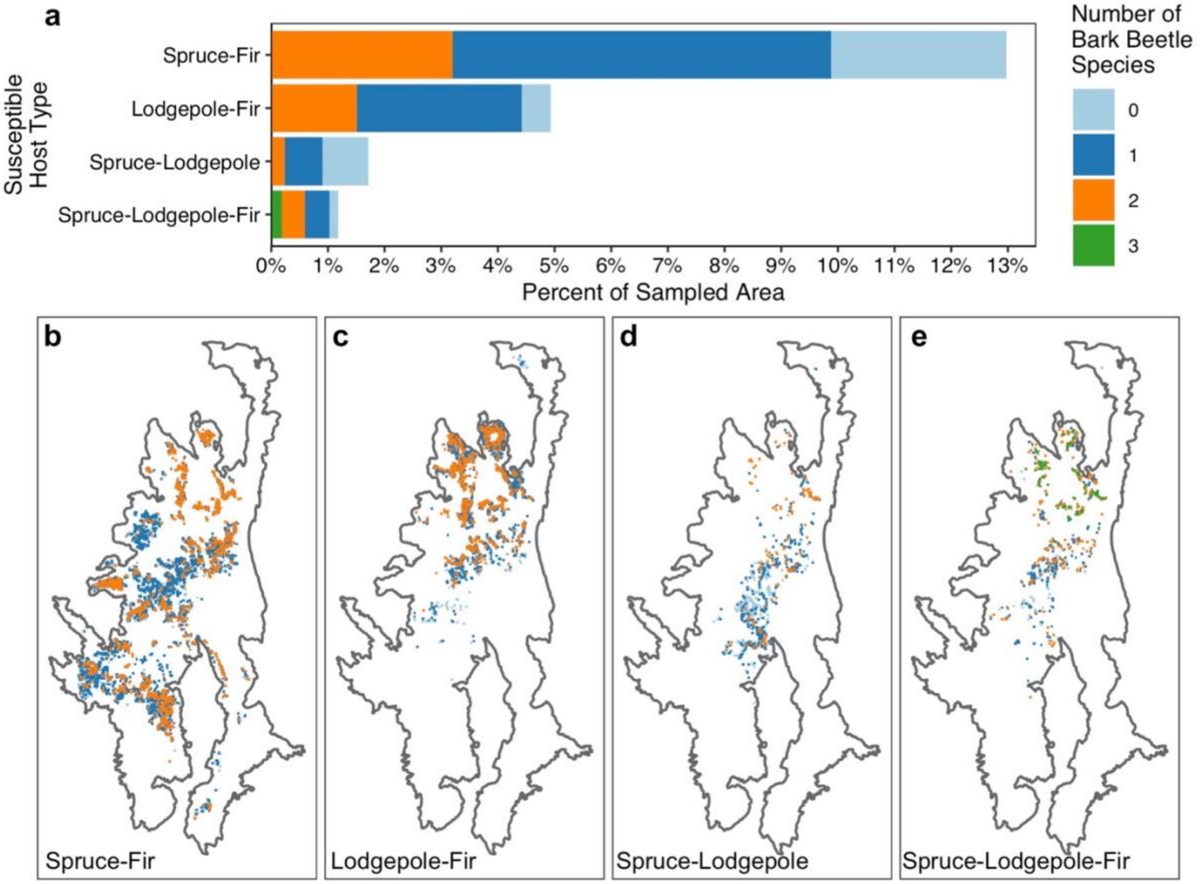

Figure 1.3. Susceptibility and occurrence of bark beetle outbreak overlap in the SRM. (a) Percent of sampled area susceptible to outbreak overlap by the number of species of bark beetles present. Darker portions indicate the percent of each affected by one or multiple bark beetle species during the study period (1999-2019). (b-e) Locations of single-outbreak and outbreak overlap in stands with conditions susceptible to overlap.

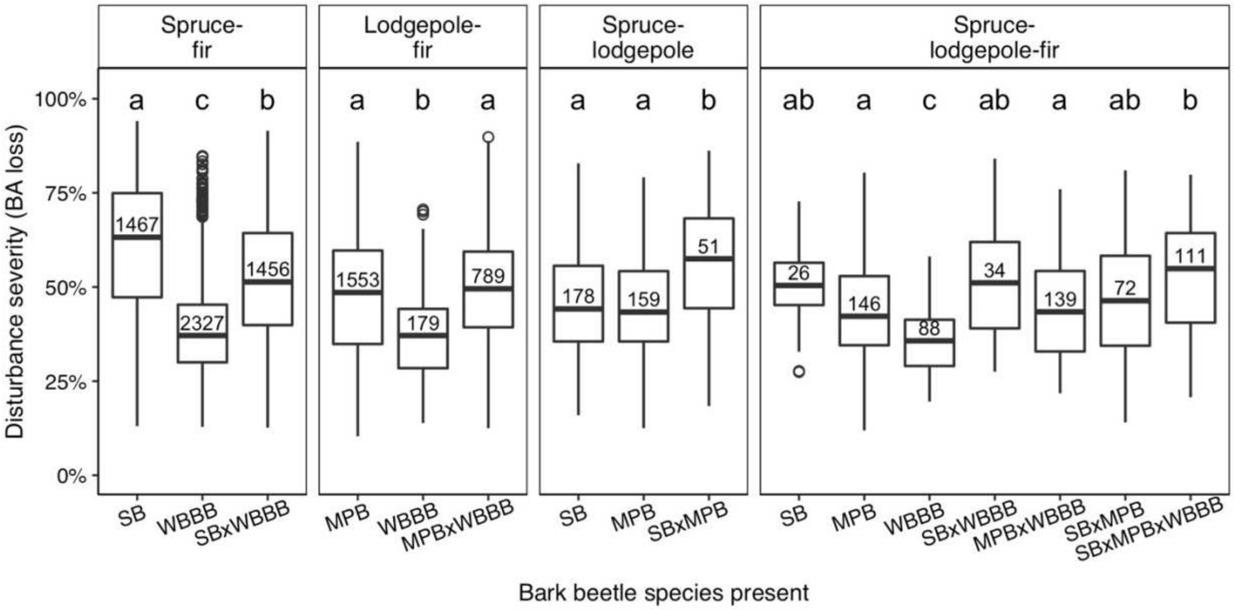

Figure 1.4. Severity of single-species outbreaks and multi-species outbreaks in susceptible (a) spruce-fir, (b) lodgepole-fir, (c) spruce-lodgepole, and (d) spruce-lodgepole-fir forests. Disturbance severity is expressed as percent basal area mortality at each sampling location, cumulative over the study period (1999-2019). X-axis shows the bark beetle(s) active in those areas during the study period. Values within each box show the number of sampling locations in each group. Letters across the top of each plot display the results of pairwise comparisons using a Dunn test (alpha = 0.05, Bonferroni corrected), conducted after a Kruskal-Wallis test indicating significant differences between groups.

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CHAPTER 2: DISTURBANCE HISTORY HAS LIMITED INFLUENCE ON SUBSEQUENT SUBALPINE FIR DECLINE

2.1 Introduction

Disturbances are important drivers of structure, composition, and function in forested ecosystems across the Earth (Turner 2010). Disturbance regimes, the cumulative effects of disturbance events through space and time (Sousa 1984), are shaped by topography, climate, and biota, and their interactions. Thus, changes in climate are expected to alter disturbance regimes through the direct effects of warming on disturbances and biota, but also by changing the ways in which disturbance events interact in space and time (Seidl et al. 2017). Disturbances may interact when one disturbance alters the attributes of (*i.e.*, ‘linked effects’; *sensu* Simard et al. 2011) or ecosystem recovery following (*i.e.*, ‘compound effects’; Paine et al. 1998) a secondary disturbance. Spatial and temporal heterogeneity in disturbances across a landscape creates a mosaic of biological legacies (Johnstone et al. 2016) that structure forest community trajectories and subsequent disturbance interactions (Sommerfeld et al. 2018). As many disturbances are likely to be altered by a changing climate, uncovering the ways that past disturbances affect subsequent ones is crucial for predicting future forest dynamics.

Over the past two decades (ca. 2000-2020), outbreaks of native bark beetles and associated fungal pathogens have affected tens of millions of hectares of conifer forest area in western North America, in many places causing severe tree mortality (Hicke et al. 2020). While pine species (e.g., *Pinus contorta*) have been most widely affected by these recent outbreaks, mortality of subalpine fir (*Abies lasiocarpa*) has also been widespread (Howe et al. 2022). Subalpine fir is a key component of stand development and disturbance regimes in subalpine forests throughout western North America (Veblen et al. 1991a). Disturbance regimes in subalpine forests are characterized by infrequent, stand-replacing fires, after which the affected areas are colonized by early-seral trees such as pines or spruce (Whipple and Dix 1979). After ca. 100 years, shade-tolerant subalpine fir proliferates in the understory, and acts as a key mechanism for structural recovery following overstory mortality of pines or spruce from subsequent bark beetle outbreaks (Veblen et al. 1991b, Lloret et al. 2012). Because subalpine fir are important for the persistence of subalpine forests, mortality could have consequences for forest trajectories (Diskin et al. 2011, Andrus et al. 2020). However, in comparison to tree species with higher economic value, disturbance interactions involving subalpine fir have received relatively little study.

In the southern Rocky Mountains (SRM), subalpine fir is a common component of subalpine forest stands, where it has experienced widespread mortality from biotic disturbance agents starting in the late 1990s (Duda et al. 2015, USDA 2020). This mortality has been attributed to a combination of fungal pathogens, bark beetles, and drought, collectively known as subalpine fir decline (SFD; Lalande et al. 2020). While due to a combination of stressors, western balsam bark beetle (WBBB; *Dryocoetes confusus*) has been observed in up to 78% of dead fir trees, suggestive of a key role (Lalande et al. 2020, Harvey et al. 2021). Similar to other bark beetles, WBBB kill host trees by feeding and reproducing in the phloem, disrupting nutrient transport and introducing an associated blue stain fungus (*Ceratocystis dryocoetidis*) (Gibson et al. 1997). Endemic populations of WBBB infest dying or recently dead trees, but climate conditions can trigger outbreaks in susceptible forests, where they target large, old, slow-growing trees (Bleiker et al. 2003). Additionally, SFD is associated with two fungal pathogens that also predominantly affect larger trees, Armillaria root rot (*Armillaria* spp.) and Annosus root disease (*Heterobasidion parviporum*), which can infect subalpine fir separately or concurrently with WBBB (Lalande et al. 2020). Last, subalpine fir is susceptible to direct mortality from prolonged drought due to low stomatal conductance during moisture stress (Bigler et al. 2007).

Because the biotic agents that cause SFD are most active in areas with abundant, large, fir (Bleiker et al. 2003), stands are expected to be most susceptible to SFD when they are mature (>100 years since last stand-replacing fire; (Maclauchlan 2016). Furthermore, mortality of co-occurring tree species (e.g., pine or spruce) from outbreaks of other bark beetle species may also increase future susceptibility by facilitating high relative abundance of fir (McMillin et al. 2003). While the associated competition release may increase a tree's resistance to biotic agents in the short term, the resulting thick phloem may increase susceptibility to WBBB once growth slows (Bleiker et al. 2005). However, despite the ecological importance and potential vulnerability of subalpine fir, the effects of prior disturbances on the occurrence and severity of SFD have not been explored.

In the late 1940s, spruce-fir forests on the White River plateau in northwestern Colorado, USA experienced a severe spruce beetle (SB; *Dendroctonus rufipennis*) outbreak that caused over 90% mortality of large Engelmann spruce (Cahill 1951) across an area of ca. 47,000 ha (Bebi et al. 2003). About 70 years prior, in ca. 1879, stand-replacing fires affected about 11% of spruce-fir forests in the region (Bebi et al. 2003, Kulakowski et al. 2003). These disturbances shaped the geography of future disturbances: areas burned by the ca. 1879 fires were not affected by the 1940s SB outbreak because of a lack of mature spruce (Bebi et al. 2003). Furthermore, areas that were affected by the 1940s SB outbreak did not experience subsequent SB activity during widespread synchronous outbreaks from 2000-2014 (Hart et al. 2015b). However, research has yet to explore how these different disturbance histories may have influenced the recent (ca. 2000-2020) SFD episode observed throughout the region.

In this study, the overarching goal was to understand how disturbance history influences tree mortality due to SFD at the tree, stand, and landscape scales. Specifically, we asked: 1) How does disturbance history affect landscape-scale susceptibility to recent SFD? 2) How does disturbance history influence stand-scale susceptibility to SFD by altering structure and composition? And 3) How do host tree characteristics, stand structure, topography, and disturbance history affect tree-scale susceptibility to SFD? Because SFD is responsive to host size and abundance (Harvey et al. 2021), we expected these individual- and stand-level drivers to be the strongest predictors of occurrence and/or severity at all three scales. At the landscape scale, we expected that forests that were unburned by a ca. 1879 fire and forests that experienced the 1940s SB outbreak would have more widespread occurrence of recent SFD. At the stand scale, we expected stands that were unburned and stands that experienced the SB outbreak to have larger and more abundant subalpine fir trees, making them more susceptible to SFD. At the individual tree scale, we expected that larger trees in close proximity to previous or concurrent SFD, within stands composed of larger and more abundant fir, would have the highest probability of being affected by SFD.

2.2 Methods

2.2.1 Study area

The study area consists of the Flat Tops Wilderness Area and surrounding subalpine forests, located in the White River National Forest, northwestern Colorado, USA (Fig. 2.1). These forests cover a total of 81,550 ha, at elevations ranging from 2800-3250 m. Subalpine forests in the study area are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir, with some lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*). The climate in this region had a mean January temperature of -8.2°C, a mean July temperature of

13.9°C, and a mean total annual precipitation of 946 mm from 1991 to 2020 (PRISM Climate Group 2020). In ca. 1879, this area experienced large, stand-replacing fires, followed by a severe spruce beetle outbreak that occurred in the 1940s. These historical disturbance events created a mosaic of disturbance histories across the region, consisting of older (No ca. 1879 fires) and younger (Yes ca. 1879 fires) stands that were either affected or unaffected by a severe 1940s SB outbreak (Yes 1940s SB and No 1940s SB, respectively). The combination of these conditions created four distinct disturbance histories: 1) Yes ca. 1879 fires; Yes 1940s SB (4% of subalpine forests), 2) No ca. 1879 fires; Yes 1940s SB (37%), 3) Yes ca. 1879 fires; No 1940s SB (7%), and 4) No ca. 1879 fires; No 1940s SB (51%). (Fig. 1). SFD occurrence has been reported across much of Colorado since the late 1990s, including in our study area (USDA 2020, Lalande et al. 2020).

2.2.2 Geospatial data

To investigate how historical disturbance events in subalpine forests affect susceptibility to recent SFD on the landscape, we compared the areas of aerially observed locations of SFD with maps of past SB and wildfire. To map occurrence of SFD, we acquired annual maps (1999-2019) of the area affected by SFD from the USFS Aerial Detection Survey (ADS) program (USDA 2020) (Fig. S2.1). ADS data are gathered annually via aerial sketch mapping, where experts record 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 of individual biotic agents (Coleman et al. 2018). We utilized maps of ca. 1879 fires and 1940s SB produced by Bebi et al. (2003). Briefly, these maps were produced using historical surveys that described the area burned in the late 1800s (Sudworth 1900) and visual interpretation of aerial photographs collected in 1971 and 1984

(Bebi et al. 2003). Spatial information on disturbance history were then translated to USFS maps of the distribution of subalpine forest across the study area. Finally, maps were then validated using field data collected in a subset of stands within the study area. Given our interest in the effects of disturbance history on patterns of recent SFD, we removed areas affected by recent (1984-2019) fires using data from Monitoring Trends in Burn Severity (USDA and USGS 2017).

2.2.3 Field data

Site selection

To determine if disturbance histories in spruce-fir forest affect subsequent severity of SFD, we used a factorial sampling design to capture four disturbances histories listed above. From each disturbance history category, we randomly selected 10 sites using maps of disturbance history produced by Bebi et al. (2003). Because we aimed to measure severity of SFD in our field sampling, we restricted our sampling to areas with observed SFD since 1997 using ADS data. We also randomly selected nearby locations that could be used as alternate sampling sites in case the initially chosen site did show evidence of the targeted disturbance history or SFD. To limit potential effects of forest edges, we restricted our sampling to the interior (>100 m from polygon edge) of large forest stands (>5 ha). To ensure sites were accessible, we limited sampling to areas <1 km from a road or <500 m from a trail, and to slopes with <30% grade. Lastly, to limit climate variation among sites, we used maps of actual evapotranspiration and climatic water deficit norms (1981-2010) produced by (Rodman et al. 2020) to exclude any sampling locations with outlying climate conditions, defined here as values outside of the interquartile range.

Sampling protocol

We sampled 27 sites in summer 2021 (Fig. 2.1). To establish a site, we walked to a pre-determined GPS point and assessed past and current disturbance of the surrounding area to ensure that it matched the GIS-predicted disturbance history category. At each site, we cored large trees to estimate stand age, examined the soil for charcoal evidence of fire, and searched for evidence of past SB mortality (e.g., old standing spruce snags with evidence of bark beetle galleries) and recent SFD. Spruce snags from the 1940s outbreaks still remain standing in many parts of the study area (Veblen et al. 1991). When evidence of the targeted disturbance history was not present or the stand was unaffected by SFD, we moved to a nearby randomly generated site within the polygon. Ultimately, we sampled eight Yes ca. 1879 fires and Yes 1940s SB, nine No ca. 1879 fires and Yes 1940s SB, six Yes ca. 1879 fires and No 1940s SB, and four No ca. 1879 fires and No 1940s SB sites (Table 1).

At each site, we established a 20 m x 20 m square plot and recorded the plot center location, elevation, slope angle, slope aspect, topographic position (basin/mid-slope/ridgetop), and topographic configuration (concave/flat/convex). For each tree > 5 cm diameter at breast height (DBH; 1.37 m above ground level), we recorded the species, status (live/dead), DBH (cm), canopy position (suppressed/intermediate/co-dominant/dominant), health of live trees (healthy/yellowing), and structural condition of dead trees. Because we aimed to quantify stand susceptibility to SFD prior to recent outbreaks, we used structural condition classes following Harvey et al. (2021) to determine if a tree died during the recent SFD event. In subalpine fir trees that were dead or yellowing, we looked for evidence of WBBB galleries and *Armillaria* spp. root fungi by removing bark at the bole and base, respectively, and recorded the presence of each biotic agent. Because SFD exhibits strong patterns of fine-scale spatial aggregation, we also recorded the distance to the nearest fir affected by SFD in three classes (<3 m, 3-5 m, >5 m) for all fir trees (Harvey et al. 2021). If the original 20 m x 20 m plot did not have 25 live or recently killed subalpine fir trees, we extended the north-south edge of the plot by 5 m and inventoried the additional area; this was repeated until 25 fir trees were recorded, or until the north-south edge reached 50 m.

Data processing

We used our field measurements to describe stand structure and topography at a stand level. We summarized tree abundance using basal area (BA), stand density index (SDI), relative abundance (species BA proportion of total BA), and trees per ha. We summarized tree size using quadratic mean diameter (QMD), a commonly used metric of tree size that more heavily weights larger trees (Curtis and Marshall 2000). Because BA, SDI, and relative abundance are highly correlated with each other, we only included BA, QMD, and trees per ha in our analyses (Fig. S2.2). To describe site moisture, we used topographic relative moisture index (TRMI), a measure that incorporates topographic shape, topographic position, slope angle, and slope aspect (Parker 1982).

2.2.4 Statistical analysis

Disturbance history effects on landscape-scale presence of SFD

We assessed how disturbance history affected the landscape-scale presence of SFD using a spatial overlay analysis (O'Sullivan and Unwin 2014), an approach that has been widely used for investigating linkages between disturbances (Hart et al. 2015a, Cole et al. 2022). Briefly, spatial overlay analysis compares the observed intersection of two spatial datasets with an expected area of intersection under a random spatial distribution. In this study, the independent variable was the disturbance history category, and the dependent variable was the occurrence of SFD from 1999-2019, derived from ADS. We calculated the expected area by multiplying the proportion of spruce-fir forest (all disturbance histories) that had experienced SFD by the area of each disturbance history. Thus, if the observed area of SFD is greater than the expected area, a positive linkage exists between that disturbance history category and SFD occurrence. Because our spatial overlays assessed the entire populations within our study area and not samples, all departures of observed values from expected values are viewed as true differences and no additional statistical comparisons were performed. Given the combined spatial error in the datasets (Bebi et al. 2003, Johnson and Ross 2008), we considered deviations of over 10% to be ecologically meaningful.

Stand scale effects of disturbance history on factors influencing SFD susceptibility

To understand how stand structure and topography differed with disturbance history, we used linear regression models. Specifically, we built separate models for the following response variables: mean fir DBH, fir BA, fir QMD, fir trees per ha, total BA, total trees per ha, elevation, and TRMI. For each model, we included the presence/absence of the ca. 1879 fires and 1940s SB outbreak, and their interaction as predictors. Because we were interested in comparing all disturbance histories with each other, we conducted linear contrasts for the interaction models, with a Bonferroni correction for multiple comparisons. All data processing and analyses were conducted in R version 4.1.2 (R Core Team 2020).

Tree-scale factors influencing susceptibility to SFD

To determine tree- and site-level factors that influence SFD, we built generalized linear mixed regression models (logistic regression, binomial family) using lmerTest in R (Bates et al. 2014, Kuznetsova et al. 2017). Our models tested the probability that a given subalpine fir tree was affected by WBBB and/or fungal pathogens as a function of tree size, proximity to SFD mortality, stand structure, topography, and disturbance history with a random intercept for site identity. Because our potential predictors of SFD occurrence spanned a range of spatial scales we built a series of models (e.g., Burton et al., 2014) in a multi-step process (Table 1).

Step 1: Tree-level predictors

To first account for the tree-level drivers of SFD, we used a model selection approach to identify the most parsimonious model of SFD occurrence. Predictor variables included tree size (DBH) and proximity to a neighboring tree affected by SFD, which have both been shown to influence SFD occurrence (Harvey et al. 2021). To meet the assumption of normality, we used a natural logarithm transformation of DBH. We built models that included all ecologically plausible combinations of the two predictor variables and their interactions (4 models total). We then selected the most parsimonious model using AIC (Akaike 1973) for this and all subsequent steps in our hierarchy (Burnham et al. 2011).

Step 2: Stand structure predictors

We then added stand-scale predictors of SFD to the best model from Step 1. Predictor variables included fir abundance (BA) and density (trees per ha), which have been linked with stand-scale patterns of SFD occurrence (McMillin et al. 2003, Lalande et al. 2020). We also included fir size (QMD), which is associated with SFD at a tree scale (Bleiker et al. 2003, Harvey et al. 2021), and is an important stand-scale predictor of other bark beetle-driven disturbances (Raffa et al. 2008). We generated ten more models similarly to Step 1, testing for individual, combined, and interaction effects of the three stand structure variables. We selected the best model from all those generated in Steps 1 and 2.

Step 3: Disturbance history

To determine if disturbance history affects SFD occurrence, we added variables indicating the presence/absence of 1940s SB and ca. 1879 fires to the best selected model from

Step 2. We generated three additional models testing the effects of each disturbance individually, and together as an interaction term and identified the best model.

Step 4: Topographic predictors

Because we expected topography to have the least proximal effect of SFD occurrence, topographic predictors were added as the final step in our hierarchical process. We augmented the previously selected model by including terms for site elevation and TRMI. We tested models with both predictors individually, together, and with their interaction. For the final model, we assessed residual distributions using the DHARMa package in R (Hartig 2022).

2.3 Results

2.3.1 Disturbance history effects on landscape presence of SFD

Of the 81,550 ha of spruce-fir forest in our study area, ADS data indicated that 57% had experienced at least some tree mortality due to SFD over the 1999-2019 period. Areas that established following the ca. 1879 fires were characterized by a greater area of SFD than expected, although the 1940s outbreak further altered this relationship; the observed areas of SFD-affected forest were 20% (654 ha) and 5% (324 ha) greater than a random spatial distribution for areas with presence and absence of 1940s SB, respectively (Fig. 2.2). The area of SFD in forests that established prior to the ca. 1879 fires did not differ from a random distribution (3% less; Fig. 2.2).

2.3.2 Stand-scale effects of disturbance history on factors influencing SFD susceptibility

Modeling of pre-outbreak stand characteristics and topographic conditions as a function of disturbance history type revealed limited connections. The presence of neither the 1940s SB outbreak nor the ca. 1879 fires showed significant relationships with characteristics of host trees (Fig. 2.3a), stand structure (Fig. 2.3b-f), or topography (Fig. 2.3g-h), either separately or together

(Table 2.1). Within each disturbance history category, all measures of stand structure and topography showed considerable variability among sites, which exceeded any effects of historical disturbances (Table S2.2).

2.3.3 Tree-scale factors influencing susceptibility to SFD

At our field sites, subalpine fir comprised 56% of all live or recently dead trees. (Table S2.3) About 24% of all subalpine fir had died in the last ca. 20 years, 50% of which had evidence of SFD (12% of all subalpine fir; Table S2.3). Of the subalpine fir affected by SFD, 87% had evidence of WBBB, 23% had evidence of *Armillaria* root rot, and 10% had evidence of both (Table S2.3).

Step 1 of our hierarchical modeling process revealed that both diameter and distance to nearest affected fir were strong predictors of SFD occurrence. Probability of SFD increased with diameter (Fig. 2.3a) and decreased with distance to nearest affected fir (Fig. 2.3b). We found that an interaction effect between diameter and distance to nearest fir did not improve model fit (Table S2.4). Step 2 revealed that model fit was not improved by the inclusion of any stand structure variables (Table S2.4). Step 3 revealed that presence of 1940s SB led to lower probability of SFD (Fig. 2.3c), but presence/absence of ca. 1879 fires did not improve the model (Table S2.4). Finally, Step 4 revealed a negative relationship between elevation and probability of SFD with all other significant predictors in the model (Fig. 2.3d). Model diagnostics showed no violation of assumptions (Fig. S2.4).

2.4 Discussion

The order and timing of disturbances, rate of stand development, and biological legacies that persist post-disturbance all influence the nature of disturbance interactions (Johnstone et al. 2016). Here, we found that the occurrence and severity of SFD was not strongly linked to either stand-replacing wildfires that occurred ca. 120 years earlier or outbreaks of spruce beetles that occurred ca. 60 years earlier. Instead, the probability of SFD occurrence was more strongly related to tree-scale predictors such as diameter and proximity to a neighboring tree with SFD. These results suggest that variability in post-disturbance trajectories and recovery rates, driven by abiotic factors and stand conditions, may create heterogeneity at local to landscape-scales that outweigh the overall effects of prior disturbance occurrence on SFD (Bakaj et al. 2016, Seidl et al. 2016). This indicates that management for SFD mitigation should prioritize areas based on tree traits rather than disturbance history.

2.4.1 Disturbance history effects on landscape presence of SFD

At the landscape level, differences between observed and expected areas affected by SFD were relatively minimal in each disturbance history. Counter to expectations that older stands would have a higher abundance of subalpine fir and consequently higher susceptibility to SFD (Veblen 1986, McMillin et al. 2003), we found that younger forests initiated following the ca. 1879 fires had more area affected by SFD than would be expected under a random spatial distribution. Though stand development in spruce-fir forests can be highly variable, spruce, lodgepole pine, or five-needle pines are typically the initial colonizer following stand-replacing fire, while abundant regeneration of subalpine fir may not occur until 50-100 years later (Whipple and Dix 1979, Veblen 1986, Coop et al. 2010). However, in more mesic areas such as the Flat Tops plateau, fir may establish more readily (Romme and Knight 1981, Veblen 1986, Rebertus et al. 1992). Thus, stands that initiated ca. 120 years ago likely have enough large fir to support SFD activity (Maclauchlan 2016). Further, this more rapid stand development may cause individuals to experience high levels of competition, making them more susceptible to drought and SFD (Bleiker et al. 2005). Previous studies show that infestation by WBBB, a primary component of SFD, is more likely to occur in smaller host trees than other bark beetle species, supporting the hypothesis that relatively young forests could be susceptible to SFD (McMillin et al. 2003, Lalande et al. 2020). Moreover, research on outbreaks of other bark beetle species has shown that the dampening effect of stand replacing fires on subsequent outbreaks only persists for several decades (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003, Hart et al. 2014b). Alternatively, in stands that established prior to the late 1800s (*i.e.* did not experience the ca. 1879 fires), the initial cohort of subalpine fir, which is relatively short-lived, may have already died, leading to transitions back towards longer-lived species such as spruce. It is notable, however, that the landscape effects we observed were small and could be due to spatial error in our datasets, since the most notable effects that we observed were present across a relatively small area.

2.4.2 Stand-scale effects of disturbance history on factors influencing SFD susceptibility

While landscape analyses suggested a potential effect of disturbance history on the occurrence of SFD, field data suggested that there were only limited differences in fir size or abundance among stands with differing disturbance histories. A very weak trend for smaller fir trees and higher stand density was observed for stands with ca. 1879 fires and no 1940s SB outbreak, which may support our interpretation of the landscape-level analysis that smaller fir stressed by competition may be increasing SFD susceptibility. However, these relationships were not statistically meaningful in stand-scale analyses, and no other measure of stand structure or topography varied significantly with disturbance history. Thus, disturbance history relationships with landscape patterns of SFD and stand attributes that drive SFD are apparently contradictory. This may be due to our limited field dataset not sufficiently describing the high variability in stand attributes across the region, or because of the relatively small area of spruce-fir forest that established following the ca. 1879 fires. Further research should aim to characterize the among- and within-stand variability of spruce-fir forests in order to draw out the effects of disturbance history.

2.4.3 Tree-scale factors influencing susceptibility to SFD

At the tree scale, the occurrence of SFD was most strongly related to tree size and local neighborhood effects. The results of our mixed-effects model supported previous research, demonstrating that larger trees located near other SFD-caused tree mortality were more likely to experience SFD (Lalande et al. 2020, Harvey et al. 2021). The importance of tree-neighborhood effects further aligns with previous observations of within-stand distribution SFD, which most often occurs in small patches of a 5 m radius (Stock 1991). However, we found that individual trees in stands composed of larger fir or greater fir basal area were not more susceptible to SFD, counter to previous research (Bleiker et al. 2003, McMillin et al. 2003, Maclauchlan 2016, Harvey et al. 2021). This was also counter to our results at the landscape scale, which may suggest that stand structure and composition have a stronger effect on SFD occurrence than severity. Disturbance history did have a minor effect on the probability of a tree experiencing SFD; trees in stands unaffected by the 1940s SB outbreak were slightly more likely to experience SFD, counter to expectations that 1940s SB would increase dominance of subalpine fir, and therefore susceptibility to SFD. Because we did not see an effect of 1940s SB on SFD in our stand-level analyses, its inclusion in our tree-level model suggests it may capture a lurking variable of SFD not accounted for in our analyses. It is possible that the areas most heavily affected by the 1940s SB outbreak are characterized by climate conditions that are more suitable to spruce than to fir (Jaime et al. 2022), perpetuating a disturbance and succession regime that does not include abundant establishment and subsequent mortality of fir. For example, areas with lower soil moisture availability may limit fir establishment (Andrus et al. 2018, Chai et al. 2019) and fungal abundance, making those areas less susceptible to both WBBB and root rot. Alternatively, the fir cohort that was released by the overstory spruce mortality may still be experiencing release from competition, making them individually more resistant to the agents that cause SFD (Bleiker et al. 2005). Taken together, these results support previous research showing that the drivers of SFD differ across spatial scales (Harvey et al. 2021). The inconsistent effects of disturbance history on susceptibility to SFD in our study underscores the need for further research.

2.4.4 Limitations and future directions

The lack of consistent support for a linkage between disturbance history and SFD occurrence or severity was surprising, and highlights both the variable dynamics of spruce-fir forests and the relatively limited scope of our field data. Studies on the effects of fire or SB outbreaks on the likelihood of subsequent SB outbreaks show strong negative feedbacks (Kulakowski et al. 2003, Hart et al. 2015b), suggesting there may be similar relationships with SFD that our study did not uncover. These relationships of prior disturbance on stand susceptibility to biotic agents may be most apparent in the initial decades following a disturbance. Future studies should sample more sites within each disturbance history category to separate the within- and among-site variability from the potential effects of disturbance history. Additionally, while the ca. 1879 fires were mostly high severity, the presence of large enough trees to support the 1940s SB outbreak in some burned areas suggest that some areas burned with moderate to low severity, which may have influenced our results, especially in Yes ca. 1879 fire and Yes 1940s SB sites. Reliable information on stand structure and composition across the landscape would also improve landscape-scale analyses, but the modeling used to produce broad-scale geospatial datasets on forest composition do not necessarily incorporate the influence of historical disturbances, making them unreliable for this study (Krist et al. 2007, Riemann et al. 2010). Data on SFD occurrence from ADS are comparatively more reliable (Coleman et al. 2018) but may overestimate SFD area due to the common practice of "lumping" the patchy mortality into single large polygons (Johnson and Ross 2008). Nevertheless, this study represents the first multiscale analysis of disturbance history effects on SFD, a driver of substantial tree mortality throughout western North America, providing a foundation for further investigation.

Though many forest disturbances are known to influence the likelihood and severity of future disturbances, our results suggest that recent SFD may be occurring independently of fire and bark beetle disturbances that occurred in the 19th and 20th centuries, respectively. This implies that many spruce-fir forests, regardless of past disturbance history, are susceptible to widespread SFD given suitable climate conditions (Harvey et al. 2021). While susceptibility to SFD is widespread, mortality from SFD has been observed to be less severe than mortality from other biotic disturbances such as SB or mountain pine beetle (Wood 1982, Johnson et al. 2014). Because mortality from biotic disturbances is governed by dynamics at the tree, stand, and landscape levels, multi-scale analyses such as ours are crucial for understanding how disturbances manifest across complex landscapes (Raffa et al. 2008). Management of spruce-fir forests in the SRM has primarily focused on the effects of SB outbreaks and wildfire, and our results suggest that SFD should not necessarily be considered a main priority, especially given that management aimed at modifying stand structure is unlikely to affect subalpine fir resistance to mortality.

2.5 Conclusion

Subalpine fir is an important component of subalpine forests in the SRM and understanding how previous disturbances might influence subalpine fir decline is integral for predicting future forest conditions. Here, we utilized unique maps of multiple historical disturbances to investigate how patterns of occurrence and severity of subalpine fir decline are affected by past fires and SB outbreak. Analyses spanning multiple spatial scales revealed limited connections between disturbance history, stand structure, and fir mortality, suggesting that most forests with the presence of subalpine fir are susceptible to SFD. We found only weak trends associating landscape SFD presence with younger stands, while occurrence of SFD at tree-level was more common in areas unaffected by SB, highlighting a need for future research to elucidate these potential relationships. The uniform nature of SFD susceptibility despite forest heterogeneity suggests that climate may play an outsized role in driving episodes of SFD (Reich et al. 2016, Harvey et al. 2021), similar to other bark beetle disturbances (Hart et al. 2014a, Kolb et al. 2016). As forest disturbances become more frequent and severe (Millar and Stephenson 2015), understanding the effects of their interactions on future forest dynamics is critical for both management and conservation.

2.6 Tables

Table 2.1. Number of field sites sampled in the White River National Forest, CO for each disturbance history category.

ca. 1879 fires	**1940s SB**	**Number of field sites**
Yes	Yes	8
No	Yes	9
Yes	No	6
No	No	4

2.7 Figures

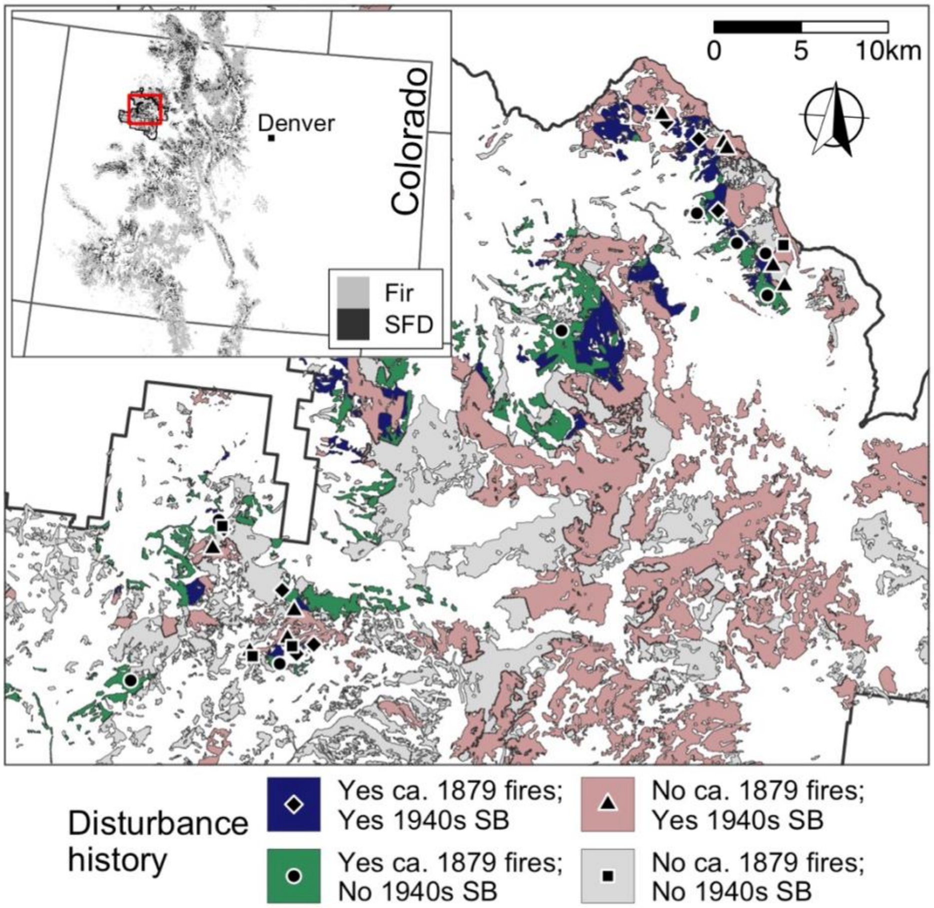

Figure 2.1. Map of the study area and study sites in the White River National Forest, Colorado, USA. The red rectangle in the inset map in the upper left corner displays the study area extent. Shading in the inset map shows the distribution of subalpine fir and subalpine fir decline (1999-2019) in the southern Rocky Mountains. The main map displays the areas affected by the 1940s SB outbreak, the ca. 1879 fires, their overlap, and the unaffected forested area. Black icons show field sampling locations; their shapes correspond the disturbance histories.

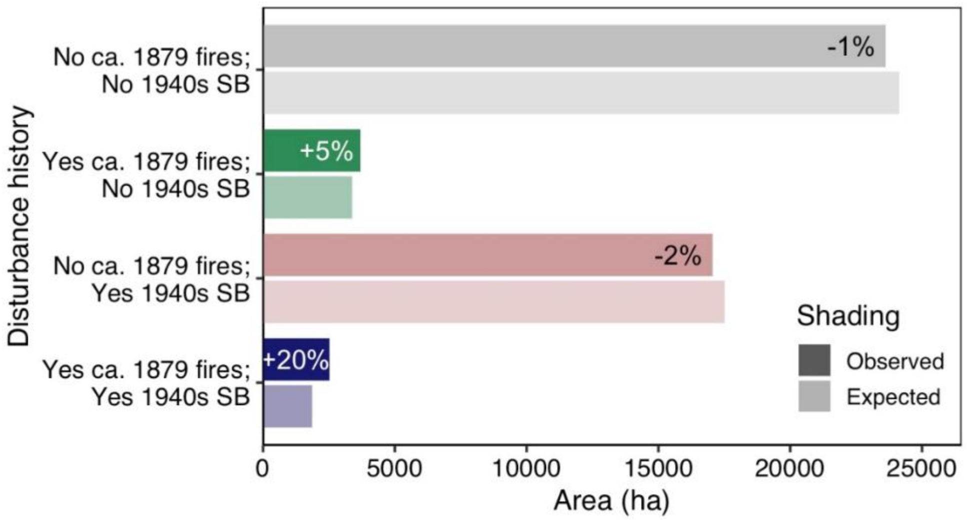

Figure 2.2. Area of each disturbance history affected by SFD. Text within bars shows the percent deviation from the expected area affected. Expected area was calculated from the fraction of total spruce-fir forest affected by SFD in the study area.

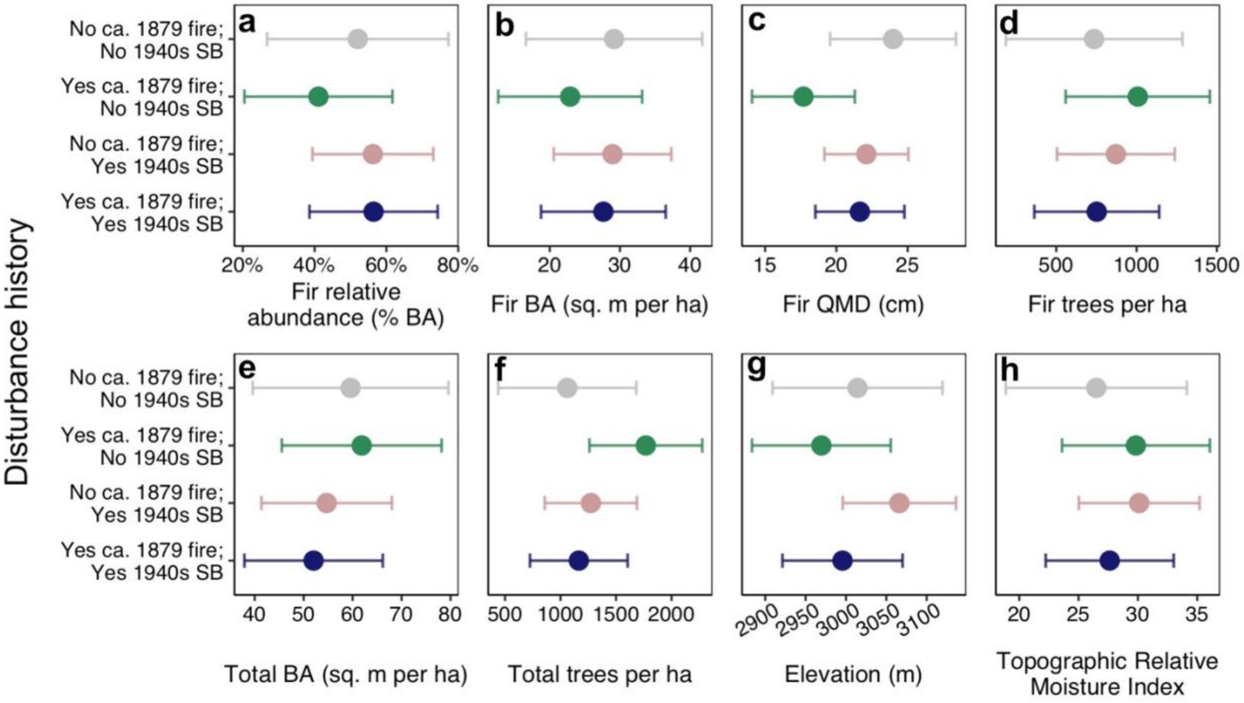

Figure 2.3. Modeled relationships of disturbance history type with stand structure and topography. Model coefficients of each disturbance history are presented for (a) fir relative abundance, (b) basal area of fir, (c) QMD of fir, (d) fir density, (e) total stand BA, (f) total stand density, (g) site elevation, and (h) TRMI. No significant relationships between disturbance history and stand characteristics were found. Error bars show 95% confidence intervals.

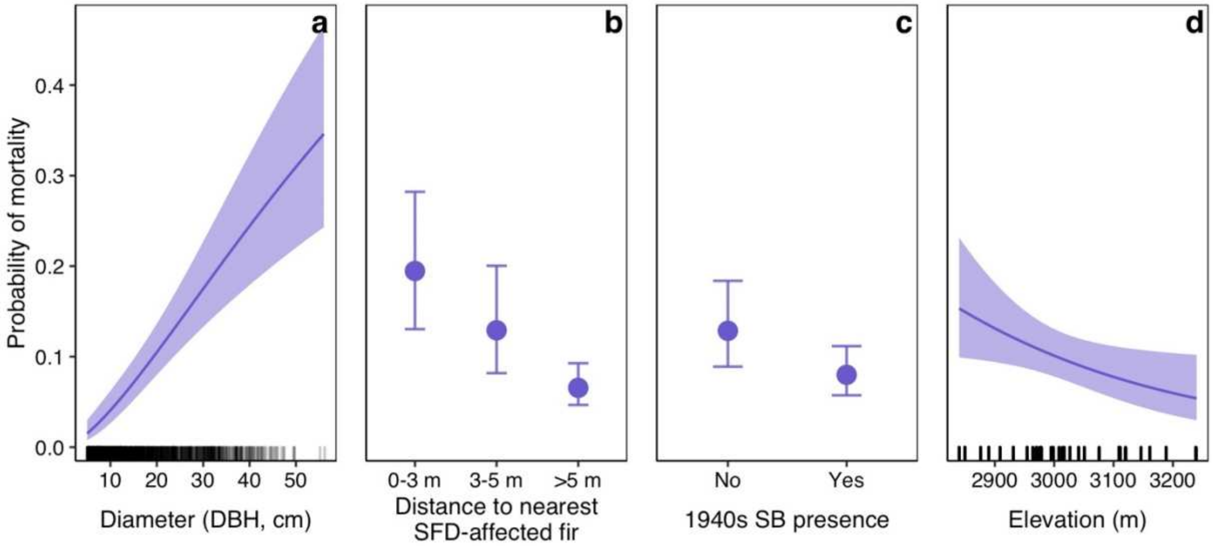

Figure 2.4. Effects of individual predictors included in the final generalized linear mixed model of tree-scale susceptibility to mortality from subalpine fir decline. Model estimates and 95% confidence intervals give the marginal effects of (a) diameter (diameter at breast height [DBH]), (b) distance to nearest fir affected by SFD, (c) the presence of 1940s SB, and (d) elevation, assuming the mean values of other predictors and the random intercept term of site.

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APPENDICES

Appendix S1

S1.1 Tables

Table S1.1. Data sources and descriptions.

Data	**Description**	**Source**	**Type**	**Year(s)**	**Resolution**
Bark beetle disturbances					
Aerial Detection Survey	Identification and mapping of forest pests causing damage	USFS and its partners (USDA 2020)	Polygon	1999-2019	Compiled at 1:100,000 scale
Disturbance Severity	Modeled percent cumulative basal area mortality due to bark beetles	Rodman et al. (2021a)	Raster	1997-2019	30 x 30 m
Host species data					
Host Basal Area (BA)	Individual Tree Species Parameter Maps (ITSPM) (Krist et al. 2007, 2010)	National Insect and Disease Risk Maps (NIDRM) (Krist et al. 2015, USDA 2019)	Raster	2002	240 x 240 m
Host Stand Density Index (SDI)	ITSPM	NIDRM	Raster	2002	240 x 240 m
Total forest BA	ITSPM	NIDRM	Raster	2002	240 x 240 m

S1.2 Figures

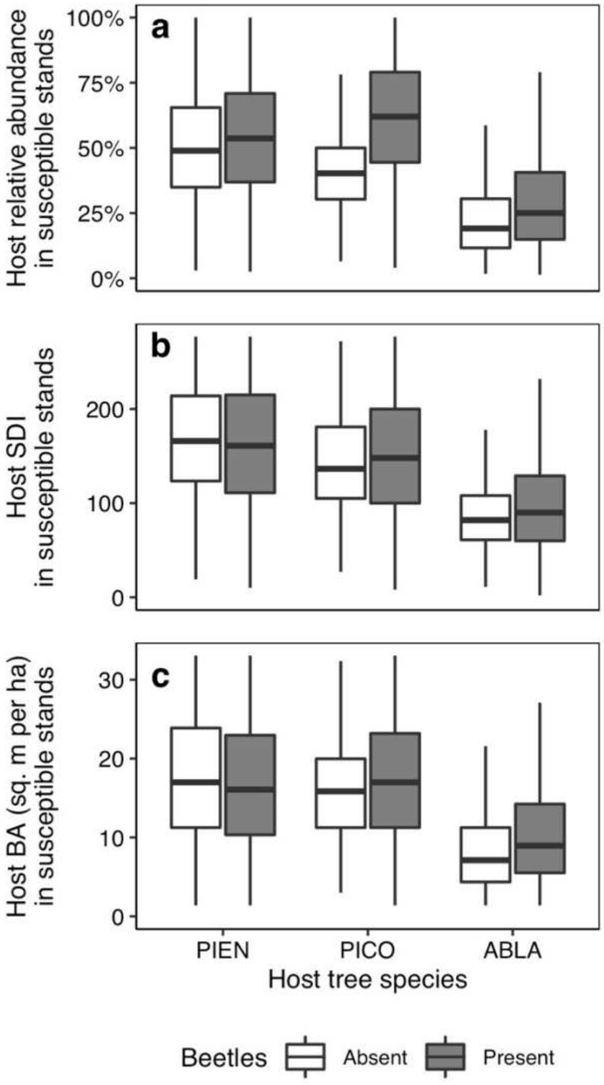

Figure S1.1. Values of host abundance measures (a) relative abundance (percent host basal area [BA] of total stand BA) (b) stand density index (SDI), and (c) BA in stands classified as susceptible by our Random Forest models. Box represents first and third quartiles; thick line represent median value.

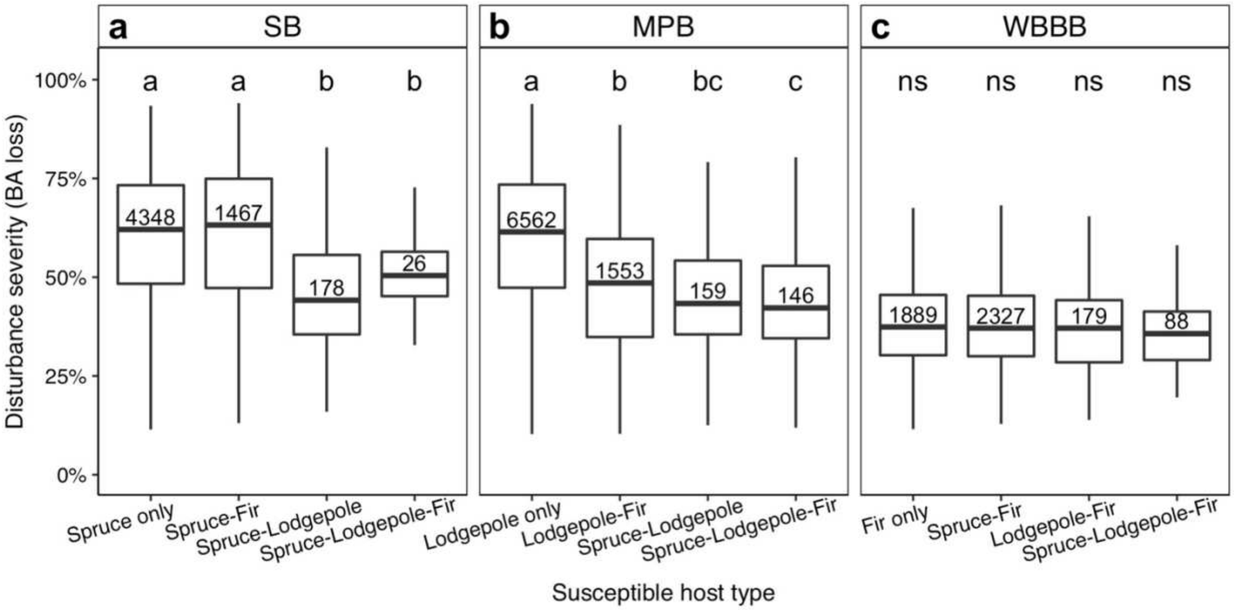

Figure S1.2. Severity of single-species outbreaks. Disturbance severity is expressed as percent basal area mortality, cumulative over the study period. X-axis shows susceptible host type defined by random forest analyses. Results are presented for (a) SB, (b) MPB, and (c) WBBB. Values within each box show the number of sample locations in each group. Letters across the top of each plot display the results of pairwise comparisons using a Dunn test (alpha = 0.05, bonferroni corrected), conducted after a Kruskal-Wallis test indicating significant differences among groups (alpha = 0.05).

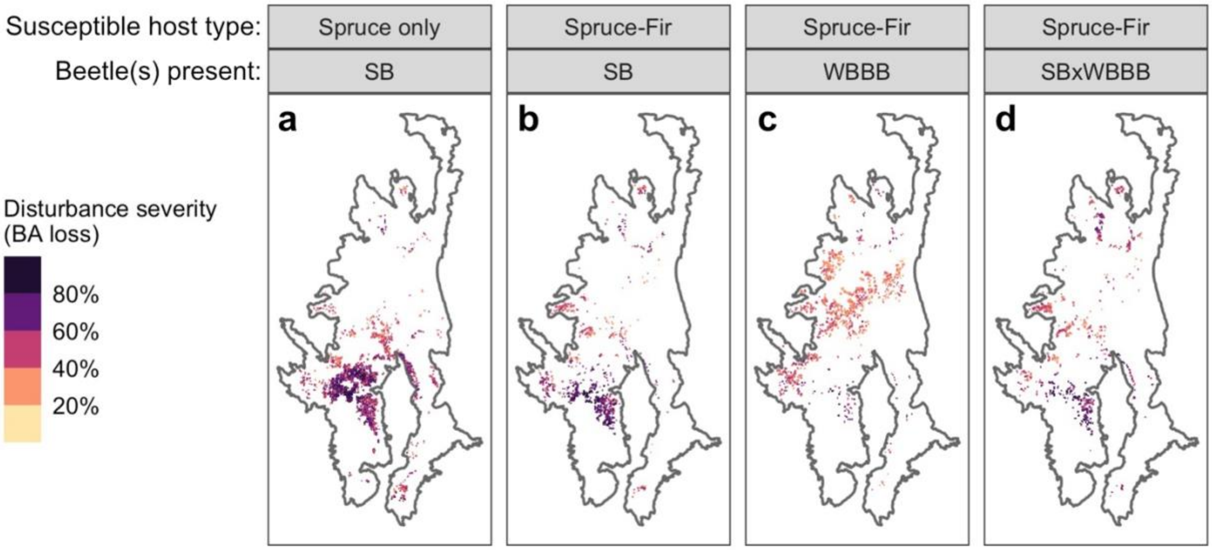

Figure S1.3. Distributions of SB and WBBB outbreak severity in spruce and spruce-fir forests. Disturbance severity is expressed as percent basal area mortality, cumulative over the study period.

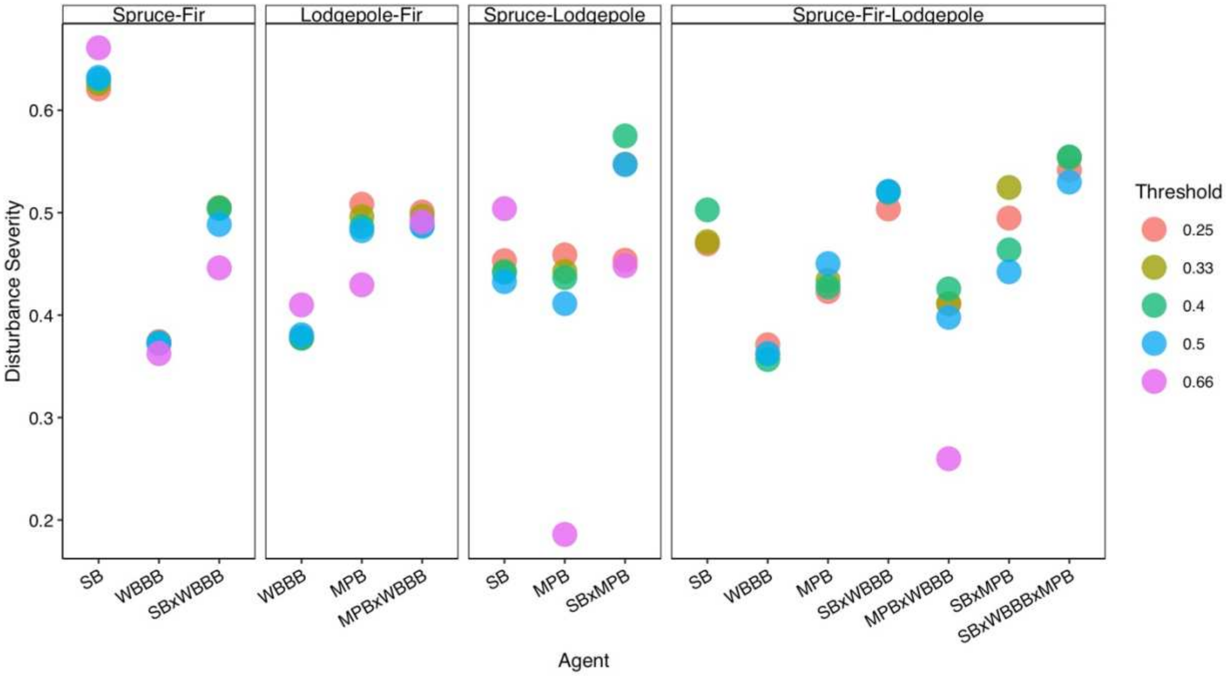

Figure S1.4. Sensitivity analysis for susceptibility thresholds. Thresholds represent the probability of beetle occurrence predicted by our Random Forest models above which a stand was considered susceptible to outbreak. Disturbance severity is expressed as percent basal area mortality, cumulative over the study period. We used a threshold of 0.4 in the main text.

Appendix S2

S2.1 Tables

Table S2.1. Linear model attributes for disturbance history effects on stand structure. Interactions between predictors are denoted by an asterisk, random effects are denoted by (1|Predictor).

Response	**Predictor(s)**	**R-squared**	**Significance**
Fir relative abundance	1940s SB	0.05046	none
Fir relative abundance	ca. 1879 fires	0.01185	none
Fir relative abundance	1940s SB * ca. 1879 fires	0.0700	none
Fir QMD	1940s SB	0.03357	none
Fir QMD	ca. 1879 fires	0.09424	none
Fir QMD	1940s SB * ca. 1879 fires	0.2134	none
Fir BA	1940s SB	0.01513	none
Fir BA	ca. 1879 fires	0.02195	none
Fir BA	1940s SB * ca. 1879 fires	0.04366	none
Fir trees per ha	1940s SB	0.006488	none
Fir trees per ha	ca. 1879 fires	0.001016	none
Fir trees per ha	1940s SB * ca. 1879 fires	0.04151	none
Total BA	1940s SB	0.03951	none
Total BA	ca. 1879 fires	< 0.001	none
Total BA	1940s SB * ca. 1879 fires	0.04424	none
Total trees per ha	1940s SB	0.04356	none
Total trees per ha	ca. 1879 fires	0.03133	none
Total trees per ha	1940s SB * ca. 1879 fires	0.1686	none
Elevation	1940s SB	0.04724	none
Elevation	ca. 1879 fires	0.105	none
Elevation	1940s SB * ca. 1879 fires	0.1404	none
TRMI	1940s SB	0.0009379	none
TRMI	ca. 1879 fires	0.0009475	none
TRMI	1940s SB * ca. 1879 fires	0.04138	none

Table S2.2. Means and standard error of stand characteristics for each disturbance history category.

ca. 1879 fires:	Yes		No		Yes		No	
1940s SB:	Yes		Yes		No		No	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Fir % BA (cm)	56.4	9.86	56.2	6.96	41.0	10.52	51.2	11.00
Fir QMD (cm)	21.6	1.37	20.2	1.51	17.1	1.26	22.5	2.91
Fir BA (m^2ha^{-1})	27.6	4.12	28.9	3.76	22.9	5.97	30.5	5.43
Fir trees (ha^{-1})	752	113	871	188	1008	307	736	183
Total BA (m^2ha^{-1})	52.0	4.8	54.7	6.0	61.9	11.6	59.6	7.5
Total trees (ha^{-1})	1165	130	1273	246	1768	293	1061	193
Elevation (m)	9829	105	10060	115	9743	123	9890	212
TRMI (0-100)	27.6	3.0	30.1	1.9	29.8	3.9	26.5	1.4

Table S2.3. Summary of subalpine fir and subalpine fir decline (SFD) at 27 field sites in the White River National Forest, CO, USA. Potential biotic agents included *Armillaria* spp. root rot fungus and western balsam bark beetle (WBBB; *Dryocoetes confusus*).

Site	**Fir trees (% total)**	**Dead fir (% fir)**	**Affected by SFD (% fir, % dead fir)**	**Affected by WBBB (% SFD)**	**Affected by fungus (% SFD)**	**Affected by WBBB and fungus (% SFD)**
ChineseWall-A1	22 (69%)	6 (27%)	4 (18%, 67%)	4 (100%)	2 (50%)	2 (50%)
ChineseWall-B1	19 (83%)	3 (16%)	3 (16%, 100%)	2 (67%)	1 (33%)	0 (0%)
CliffLakes-A1	28 (85%)	3 (11%)	1 (4%, 33%)	1 (100%)	0 (0%)	0 (0%)
CliffLakes-B1	19 (41%)	6 (32%)	1 (5%, 17%)	1 (100%)	0 (0%)	0 (0%)
DeepCreek-A1	30 (46%)	8 (27%)	2 (7%, 25%)	1 (50%)	1 (50%)	0 (0%)
DeepCreek-B1	19 (58%)	8 (42%)	4 (21%, 50%)	4 (100%)	0 (0%)	0 (0%)
DeepCreek-C1	20 (42%)	4 (20%)	2 (10%, 50%)	2 (100%)	0 (0%)	0 (0%)
DeepCreek-D1	16 (42%)	9 (56%)	2 (12%, 22%)	1 (50%)	1 (50%)	0 (0%)
EastMarvine-C1	26 (57%)	15 (58%)	12 (46%, 80%)	10 (83%)	5 (42%)	3 (25%)
LilyPond-A1	39 (78%)	1 (3%)	0 (0%, 0%)	0 (0%)	0 (0%)	0 (0%)
LilyPond-B1	22 (81%)	3 (14%)	2 (9%, 67%)	1 (50%)	1 (50%)	0 (0%)
LilyPond-C1	61 (78%)	21 (34%)	8 (13%, 38%)	8 (100%)	0 (0%)	0 (0%)
LostLakes-B1	44 (72%)	5 (11%)	3 (7%, 60%)	2 (67%)	1 (33%)	0 (0%)
LostLakes-B2	85 (75%)	5 (6%)	0 (0%, 0%)	0 (0%)	0 (0%)	0 (0%)
LostLakes-C1	35 (52%)	0 (0%)	0 (0%, 0%)	0 (0%)	0 (0%)	0 (0%)
MeadowLake-A1	16 (34%)	1 (6%)	0 (0%, 0%)	0 (0%)	0 (0%)	0 (0%)
MeadowLake-B1	19 (56%)	6 (32%)	4 (21%, 67%)	2 (50%)	2 (50%)	0 (0%)
MeadowLake-D1	30 (68%)	9 (30%)	8 (27%, 89%)	6 (75%)	2 (25%)	0 (0%)
NorthElk-A1	46 (88%)	16 (35%)	9 (20%, 56%)	7 (78%)	4 (44%)	2 (22%)
NorthElk-B1	49 (64%)	13 (27%)	2 (4%, 15%)	2 (100%)	0 (0%)	0 (0%)
NorthElk-C1	90 (93%)	38 (42%)	24 (27%, 63%)	24 (100%)	2 (8%)	2 (8%)
NorthElk-D1	45 (76%)	7 (16%)	6 (13%, 86%)	6 (100%)	0 (0%)	0 (0%)
Pagoda-A1	20 (38%)	5 (25%)	3 (15%, 60%)	2 (67%)	2 (67%)	1 (33%)
Pagoda-B1	39 (68%)	16 (41%)	8 (21%, 50%)	8 (100%)	1 (12%)	1 (12%)
PicketPin-A1	29 (42%)	9 (31%)	0 (0%, 0%)	0 (0%)	0 (0%)	0 (0%)
PicketPin-C1	34 (13%)	5 (15%)	2 (6%, 40%)	2 (100%)	0 (0%)	0 (0%)
PicketPin-D1	33 (73%)	2 (6%)	1 (3%, 50%)	1 (100%)	0 (0%)	0 (0%)
Total	**935 (56%)**	**224 (24%)**	**111 (12%, 50%)**	**97 (87%)**	**25 (23%)**	**11 (10%)**

Table S2.4. AIC values from tree-scale model selection. Response variable for all models was the presence/absence of subalpine fir decline (SFD). † Indicates the model selected at each hierarchy; ‡ indicates final selected model. An asterisk in the model represents an interaction, and the convention (1|*Predictor*) represents a random effect. "SFD Dist." refers to the distance to the nearest SFD-affected fir; "Fir TPH" refers to fir trees per ha; "SB" refers to presence of the 1940s SB outbreak; "Fire" refers to presence of the ca. 1879 fires.

Model	**AIC**
Tree-level predictor selection	
SFD ~ log(DBH) + SFD Dist. + (1|Site)	581.9†
SFD ~ log(DBH) + (1|Site)	593.7
SFD ~ SFD Dist. + (1|Site)	626.5
SFD ~ log(DBH)*SFD Dist. + (1|Site)	584.5
Stand structure predictor selection	
SFD ~ log(DBH) + SFD Dist. + Fir BA + Fir QMD + scale(Fir TPH) + (1|Site)	587.2
SFD ~ log(DBH) + SFD Dist. + Fir BA + Fir QMD + (1|Site)	585.5
SFD ~ log(DBH) + SFD Dist. + Fir BA + scale(Fir TPH) + (1|Site)	585.8
SFD ~ log(DBH) + SFD Dist. + Fir QMD + scale(Fir TPH) + (1|Site)	585.4
SFD ~ log(DBH) + SFD Dist. + Fir BA + (1|Site)	583.9
SFD ~ log(DBH) + SFD Dist. + Fir QMD + (1|Site)	583.5
SFD ~ log(DBH) + SFD Dist. + scale(Fir TPH) + (1|Site)	583.9
SFD ~ log(DBH) + SFD Dist. + Fir BA*Fir QMD + (1|Site)	587.4
SFD ~ log(DBH) + SFD Dist. + scale(Fir TPH)*Fir QMD + (1|Site)	587.2
SFD ~ log(DBH) + SFD Dist. + scale(Fir TPH)*Fir BA + (1|Site)	587.6
Disturbance history predictor selection	
SFD ~ log(DBH) + SFD Dist. + SB + (1|Site)	578.6†
SFD ~ log(DBH) + SFD Dist. + Fire + (1|Site)	583.9
SFD ~ log(DBH) + SFD Dist. + Fire*SB + (1|Site)	581.6
Topographic predictor selection	
SFD ~ log(DBH) + SFD Dist. + SB + scale(Elevation) + TRMI + (1|Site)	576.6
SFD ~ log(DBH) + SFD Dist. + SB + scale(Elevation) + (1|Site)	576.1‡
SFD ~ log(DBH) + SFD Dist. + SB + TRMI + (1|Site)	579.9
SFD ~ log(DBH) + SFD Dist. + SB + scale(Elevation)*TRMI + (1|Site)	578.4

S2.2 Figures

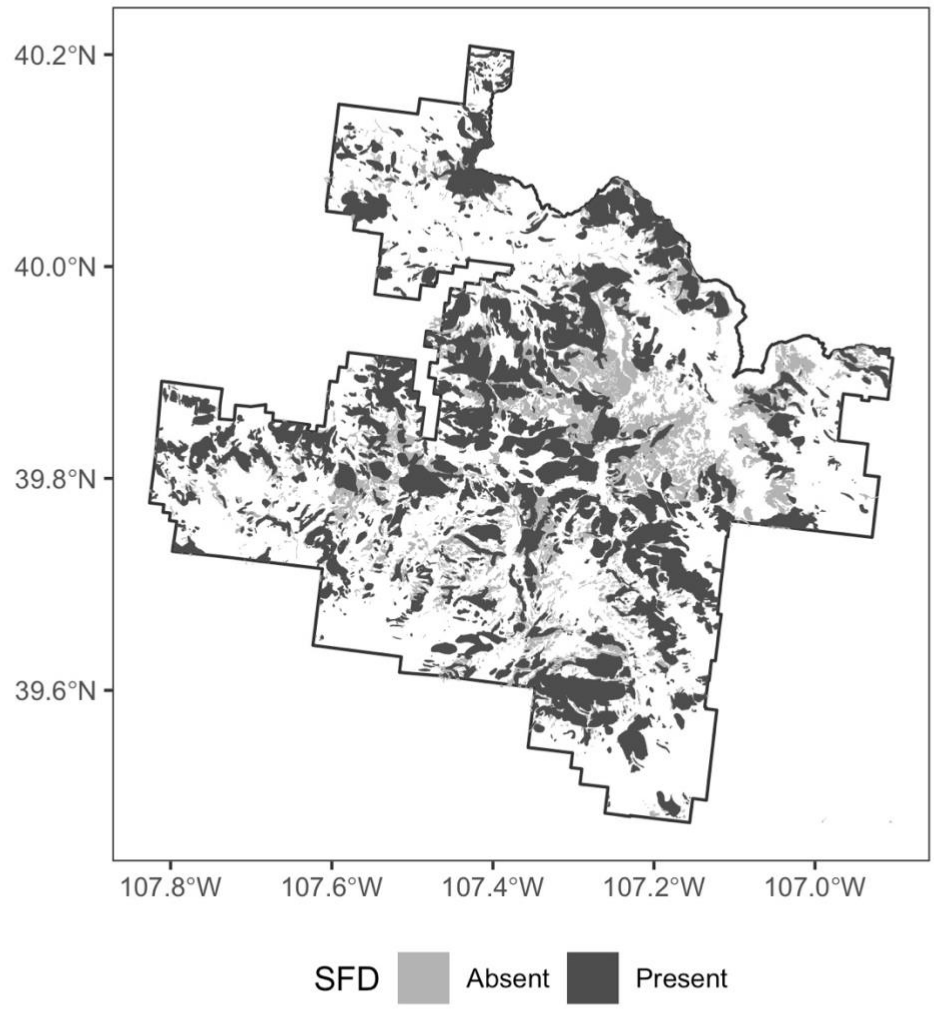

Figure S2.1. Map of subalpine fir decline (SFD) in the White River Plateau, Colorado, USA. Border represents the White River National Forest. Unshaded areas show non-susceptible forest or non-forest.

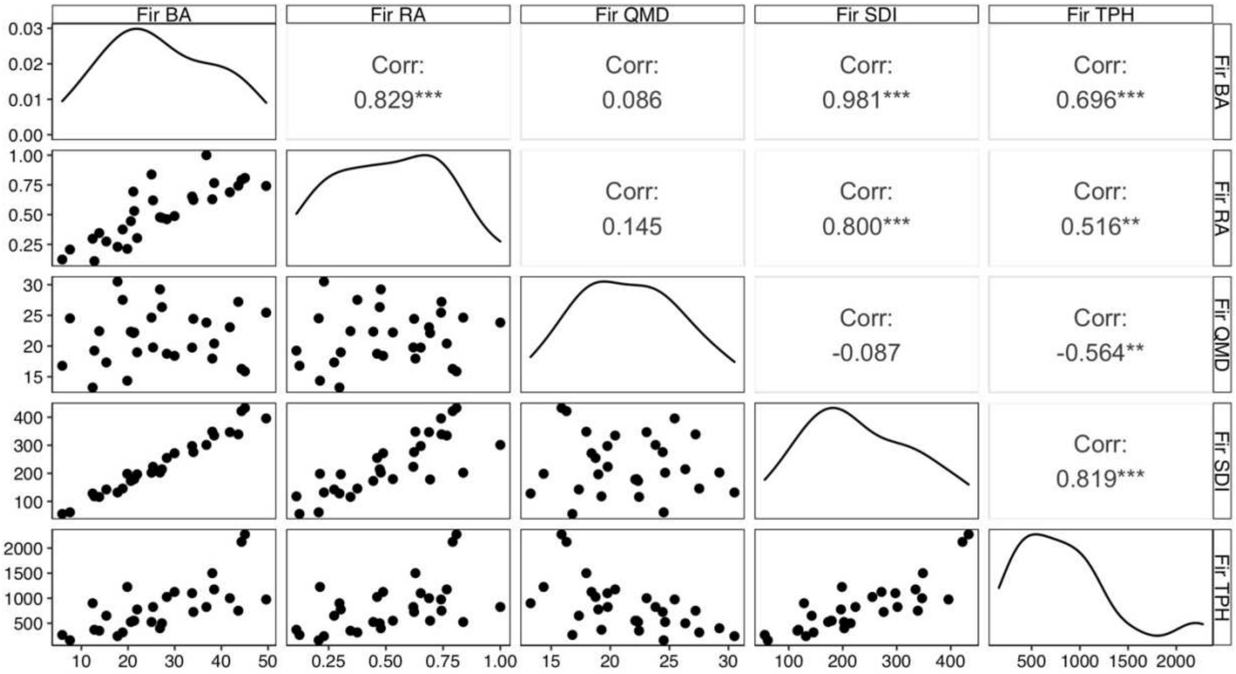

Figure S2.2. Pairwise correlations between stand structure summaries. Boxes to the right display Pearson correlation coefficients with asterisks denoting statistical significance. Boxes to the left display scatterplots of values, and middle boxes show density distributions of each variable.

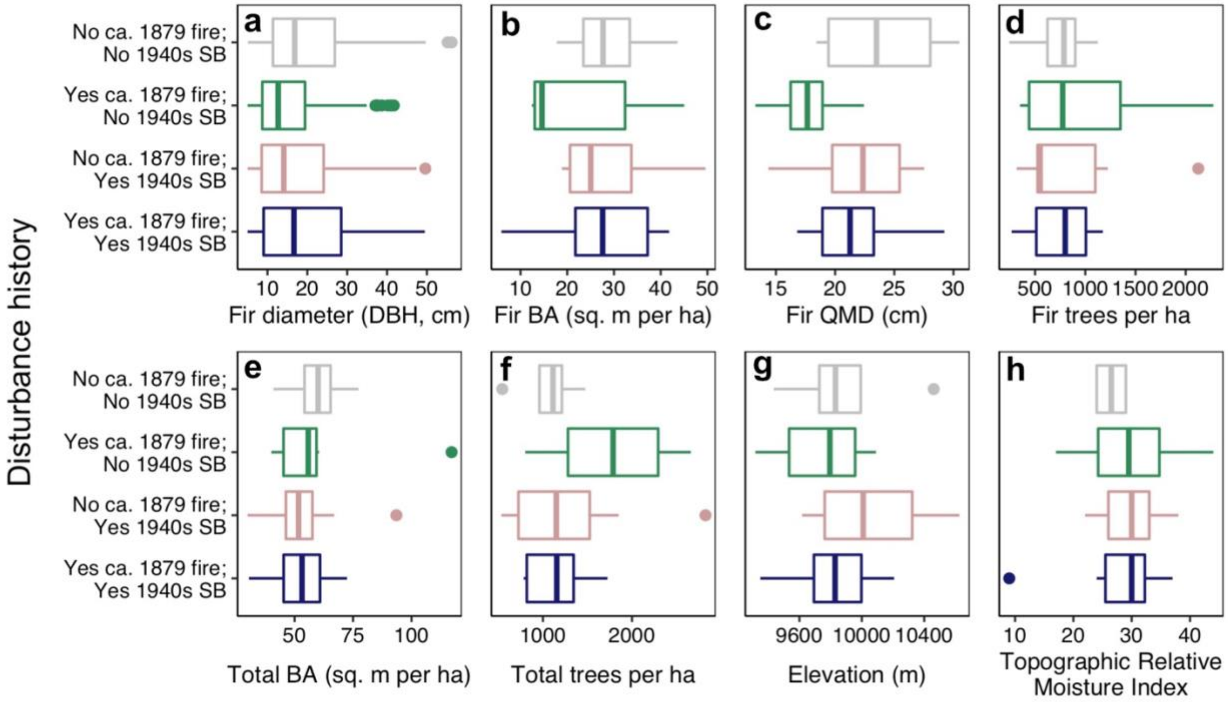

Figure S2.3. Stand structure and topography in each disturbance history. (a) Fir DBH (tree-level) did not vary with disturbance history in a mixed effects model (alpha = 0.5). Stand structure variables (b) fir BA, (c) fir QMD, (d) fir trees per ha, (e) total stand BA, and (f) total stand trees per ha, as well as topographic variables (g) elevation and (h) TRMI did not vary significantly with disturbance history in linear models (alpha = 0.5).

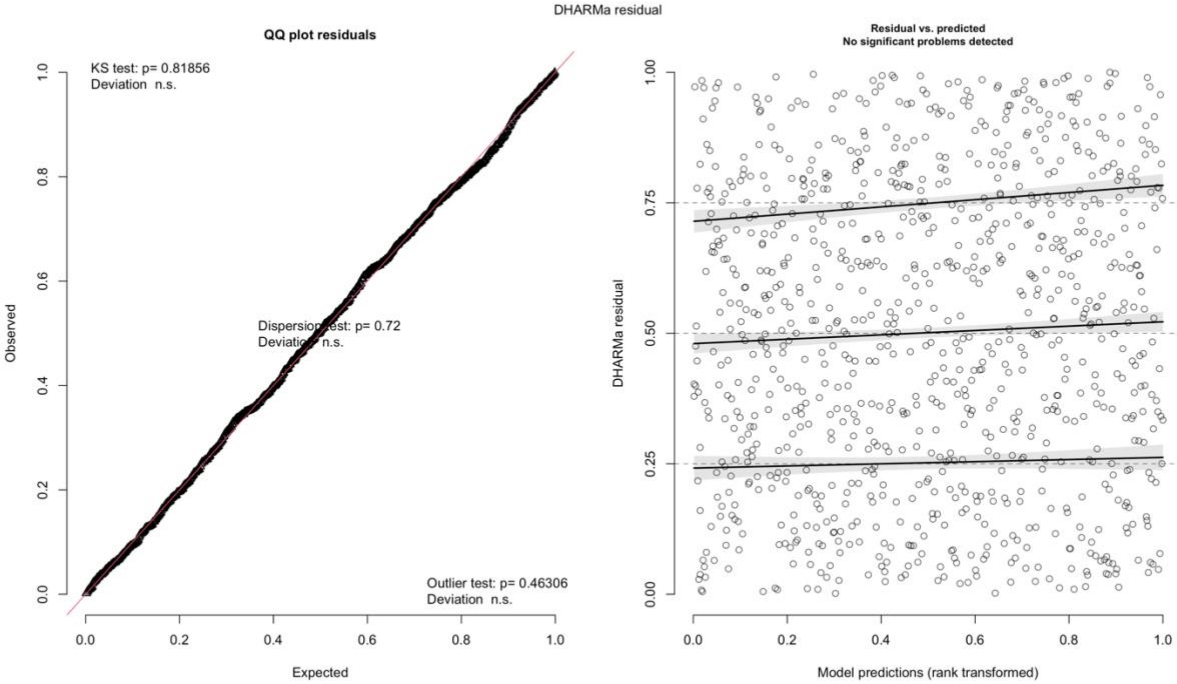

Figure S2.4. Diagnostics of final tree-level model. Diagnostic tests were performed using the R package DHARMa (Hartig 2022).