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Forest recovery following synchronous outbreaks of spruce and western balsam bark beetle is slowed by ungulate browsing

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Abstract. Understanding how severe disturbances and their interactions affect forests is key to projecting ecological change under a warming climate. Substantial increases in some biotic disturbances, such as bark beetle outbreaks, in temperate forest ecosystemsmay compromise recovery to a forest vegetation type (i.e., physiognomic recovery or resilience), especially if subsequent biotic disturbances (e.g., herbivory) alter recovery mechanisms. From 2005 to 2017, severe outbreaks (>90% mortality) of spruce bark beetles (SB, *Dendroctonus rufipennis*) affected Engelmann spruce (*Picea engelmannii*) across 325,000 ha of spruce and subalpine fir (*Abies lasiocarpa*) forest in the southern Rocky Mountains, USA. Concurrently, an outbreak of western balsam bark beetle (WBBB, *Dryocoetes confuses*) infested subalpine fir across at least 47,000 of these hectares. We explored the capacity of 105 stands affected by one or two bark beetle outbreaks and browsing of juvenile trees by ungulates to return to a forest vegetation type in the context of pre-outbreak forest conditions and topography. Nine initial forest trajectories (i.e., at least several decades) were identified from four pre-outbreak forest types affected by three biotic disturbances that occurred at different spatial scales and severities. Most stands (86%) contained surviving nonhost adult trees in the main canopy (fir and aspen [*Populus tremuloides*]) and many surviving juveniles of all species, implying that they are currently on a trajectory for physiognomic recovery. Stands composed exclusively of large-diameter spruce were affected by a severe SB outbreak and were most vulnerable to a transition to a low-density forest, below regional stocking levels (<370 trees/ha). Greater pre-outbreak stand structural complexity and species diversity were key traits of stands with a higher potential for physiognomic recovery. However, all multispecies stands shifted in relative composition of the main canopy to nonhost species, suggesting low potential for compositional recovery over the next several decades. Most post-outbreak stands (86%) exceeded regional stocking levels with trees taller than the browse zone (<2 m). As such, ungulate browsing on over half of all juveniles will primarily affect the rate of infilling of the forest canopy and preferential browsing of more palatable species will influence the composition of the future forest canopy.

Key words: compositional recovery; compound disturbances; Dendroctonus; Dryocoetes; *Engelmann spruce; physiognomic recovery; quaking aspen; southern Rocky Mountains; subalpine fir; subalpine fir decline; ungulate herbivory.*

Introduction

Disturbances are important catalysts for ecological change, particularly as climate warms (Turner 2010, Enright et al. 2015, Millar and Stephenson 2015). Losses in forest cover in some forest ecosystems are already occurring when severe disturbance (e.g., wildfire) is followed by unfavorable environmental conditions for recovery (Stevens-Rumann et al. 2018, Davis et al. 2019, Rodman et al. *a*). Interaction of multiple, overlapping disturbances also has the capacity to cause forest loss if a subsequent disturbance removes or alters necessary structures for recovery (i.e., compound disturbance interaction; Paine et al. 1998, Kane et al. 2017). Despite the widespread distribution of biotic disturbances, including insect outbreaks, pathogens, and impacts of large herbivores, in many forest ecosystems and their important effects on forest structure (Kautz et al. 2017), there are many uncertainties about how their interactions may influence forest recovery (Buma 2015). Given projected increases in intensity and extent of some biotic disturbances with climate warming (Seidl et al. 2017), understanding when severe biotic disturbances and their interactions compromise recovery is critical for projecting ecological change (Turner 2010, Johnstone et al. 2016) and the ensuing consequences for ecosystem services, like carbon stocks (Thom and Seidl 2015, Berner et al. 2017).

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Bark beetle outbreaks have recently caused widespread tree mortality across western North America (Meddens et al. 2012, Kautz et al. 2017) in habitats within the range of native ungulates, such as elk [*Cervus canadensis*; (Ivan et al. 2018)]. The growing consensus is that conifer forests possess relatively limited ability to resist bark beetle outbreaks (Raffa et al. 2008), particularly with the added stress of climate warming (Temperli et al. 2015, Seidl et al. 2017). Consequently, research is increasingly focused on understanding recovery or resilience of forest cover following these broad-scale tree mortality events (Hansen et al. 2010, Windmuller-Campione and Long 2015), and forest recovery is currently the source of intense management and policy concern (Vose et al. 2018). In this context, we distinguish *physiognomic recovery*, the return to a similar forest cover or stand structure, from *compositional recovery*, the return to a similar species composition and relative dominance. As most bark beetles attack a specific host tree species or genus (Raffa et al. 2008), physiognomic recovery is primarily supported by surviving adult trees of the nonhost species and the growth release of juvenile trees that established prior to bark beetle outbreaks (i.e., advanced regeneration) rather than seedling establishment post-disturbance (Veblen et al. 1991, Diskin et al. 2011). Spatial interaction of multiple, overlapping biotic disturbances (of the same or different type) that kill multiple species of adult trees may result in insufficient densities of surviving trees within a stand for physiognomic recovery (Kane et al. 2017). Additionally, persistent post-outbreak browsing by ungulates of some or all juvenile tree species may alter forest recovery, which has been observed following fire (Romme et al. 1995, Bailey and Whitham 2002). Alternatively, stands with greater forest complexity (i.e., higher diversity of species and tree sizes) prior to disturbance(s) may increase the probability for physiognomic recovery, depending on species-specific and size-specific differences in vulnerability to insect attack or browsing (Veblen et al. 1994, Peterson et al. 1998, Churski et al. 2016). Spatial variability in local outcomes of disturbance-related forest changes under climate warming is likely be mediated by variability in biophysical factors, often linked to topographic setting (Bretfeld et al. 2016, Redmond and Kelsey 2018). Thus, research is critically needed to determine whether co-occurring disturbances in forests influence the potential for physiognomic recovery, particularly in the context of pre-outbreak stand conditions and topographic variability.

Over the past 20 yr, outbreaks of spruce bark beetle (SB, *Dendroctonus rufipennis*) and western balsam bark beetle (WBBB, *Dryocoetes confusus* and associated agents [e.g., *Armillaria*]) have caused widespread mortality of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), respectively, across tens of thousands of hectares of spruce–fir forest in the southern Rocky Mountains (USDA 2018). Both of these beetles are native to the study area. Concurrent mortality of two co-occurring tree species may have important ecological consequences for recovery of spruce-fir forests. Following previous outbreaks of SB, subalpine fir has replaced spruce as the forest dominant (Schmid and Frye 1977, Veblen et al. 1991). This scenario may, however, be unlikely if severe WBBB outbreaks occur in the same stands as SB outbreaks. Additionally, use of spruce–fir forests by some ungulate species increases following tree mortality (Ivan et al. 2018), which may also result in high rates of juvenile browsing. Although Rocky Mountain forests commonly exhibit high potential for physiognomic recovery following individual and multiple disturbances, the recovery process from severe disturbances is slow (Veblen et al. 1994, Rodman et al. 2019*b*) and overlapping disturbances, such as blowdown then fire or bark beetle then fire, can cause unexpected shifts in vegetation trajectories (Kulakowski et al. 2013, Gill et al. 2017, Carlson et al. 2017).

In addition to the important effects of climate on bark beetle reproduction and host tree defenses (Hansen et al. 2001, Raffa et al. 2008, Reich et al. 2016, Hart et al. 2017), stand conditions in Engelmann spruce and subalpine fir forests influence susceptibility to SB and WBBB outbreaks (McMillin et al. 2003, Hart et al. 2014, Kulakowski et al. 2016) and may, therefore, also affect post-outbreak recovery. SBs preferentially attack large-diameter spruce trees (>20 cm dbh [diameter at breast height]) in landscapes with abundant suitable hosts (Schmid and Frye 1977, Hart et al. 2014). WBBB outbreaks generally occur in stands with greater fir density and basal area (McMillin et al. 2003). Significant reductions in tree density and basal area of host species (e.g., >60%) commonly result from SB and WBBB outbreaks. Following SB outbreaks, relative species composition in the canopy shifts toward nonhost species, such as fir and aspen (*Populus tremuloides*; Schmid and Frye 1977, McMillin et al. 2003, DeRose and Long 2007), reducing the potential for compositional recovery in the subsequent decades. The influx of light and other resources following mortality from SB and WBBB outbreaks commonly increases growth rates of non-arboreal understory species (i.e., shrubs and herbaceous species) and surviving trees that supplement or form the next forest canopy (Veblen et al. 1991, Parish et al. 1999). The initial mechanisms of recovery following both SB and WBBB are, therefore, influenced by the relative abundance of species and the size-class distribution of the pre-outbreak forest, whereas longer-term rates of recovery may vary with species-specific responses to post-disturbance environmental conditions and the effect of ungulate herbivory on juveniles. Though several studies examine the implications of individual insect outbreaks for forest recovery (DeRose and Long 2010, Redmond and Kelsey 2018), how ungulate herbivory affects forest recovery following tree mortality from two types of insects, separately and in combination, has not previously been examined.

The current study investigates forest recovery dynamics following a widespread, severe SB outbreak (>90% mortality of canopy Engelmann spruce) and a concurrent increase in WBBB-attributed subalpine fir mortality in the San Juan Mountains, southern Colorado, USA. From 2005 to 2017, nearly all forest types containing Engelmann spruce in the study area were affected by the SB outbreak (325,000 ha) and mortality of subalpine fir from WBBB co-occurred in 47,000 of these hectares (USDA 2018). Our objective was to evaluate how initial post-outbreak forest trajectories (i.e., at least several decades) and the potential for physiognomic recovery is influenced by pre- and post-outbreak forest composition and structure, topography, the co-occurrence of SB with WBBB, and ungulate herbivory. We expect (1) recovery to be compromised when monotypic stands are host to a severe bark beetle outbreak and high proportions of juveniles are heavily browsed, or when mixed-species stands (spruce and fir) are affected by concurrent bark beetle outbreaks and high proportions of juveniles are heavily browsed, (2) ungulates to influence initial forest trajectories by preferentially browsing more palatable species (i.e., fir and aspen; DeRose and Long 2010), and (3) juvenile density and height growth rates to be greater at topographically moister sites and beneath more open forest canopies.

Methods

Study area

The study area is located across the elevation gradient of the subalpine zone (2,800–3,600 m) in the eastern San Juan Mountains, southern Rocky Mountains, USA (Fig. 1). The subalpine zone of southern Colorado is characterized by a cool and moist climate (Romme et al. 2009). Average annual temperatures range from 1.3° (northern plots) to 2.2°C (southern plots; 1970–2017, PRISM Climate Group 2018) and temperatures have increased by about 1°C over the past three decades (1975–2012; Kelsey et al. 2018). Total mean annual precipitation ranges spatially from 510–1,300 mm with about 65% of precipitation falling as snow from October–April. Subalpine forests are dominated by Engelmann spruce and interspersed with subalpine fir and aspen (Romme et al. 2009).

Field data collection

In summers of 2016 and 2017, we used a stratified random sample design to survey stand structure and composition, ungulate herbivory impacts on juvenile trees, and environmental characteristics in 105 plots affected by SB outbreaks or SB and WBBB outbreaks. To identify suitable plot locations, we first used aerial detection survey data (ADS; USDA 2018) to locate accessible stands (within 5 km of a trailhead) affected by SB outbreaks or SB and WBBB outbreaks. In the field, stands identified by ADS were sampled if spruce or spruce and fir experienced >~20% loss of basal area from the SB outbreak or the SB and WBBB outbreak, respectively. Starting from a location >100 m from the selected stand edge, roads, or water bodies (e.g., lakes, streams), we randomly located a 20 × 20 m plot in stands with pre-outbreak communities composed of spruce, spruce–fir, or aspen–spruce–fir. Subsequent plots were systematically spaced >400 m away. Reliable spatial data of bark beetle outbreak severity was not available to stratify sampling across disturbance severities. All plots were in areas without evidence of livestock grazing (dung) or direct recent forest management (e.g., cut stumps, tree planting). For each plot, we recorded aspect (°), slope (°), elevation (m), and topographic shape (concave, convex, flat).

To characterize stand structure and composition, we recorded species, status (live or dead), and diameter at breast height for all trees >4 cm dbh in the plot. For all recently dead spruce and fir trees (standing and fallen), we estimated time since beetle infestation (Appendix S1) and recorded mortality agents by stripping the bark to identify bark beetle galleries by species (USDA 2010). We sampled juvenile conifers (>5 cm height and <4 cm dbh) in a minimum of four 4 × 10 m belt transects (160 m^2) arranged in four orthogonal directions from plot center. If juvenile conifer density was <6 individuals per 20 m^2 in the first four transects, we sampled an additional four 2 × 10 m transects parallel to the existing transects until a density of >6 individuals/20 m^2 was reached or the entire 400-m^2 plot had been sampled. Given that aspen commonly regenerate asexually in dense clusters, aspen juveniles were sampled separately. We counted aspen juveniles in two 4 × 10 m transects extending in opposite directions. If <8 individuals/20 m^2 were encountered, then we sampled an additional two transects until aspen juvenile density was >8 individuals/20 m^2 or the entire 400-m^2 plot had been sampled. For each seedling or sapling encountered, we recorded species, status (live, dead), subplot number (five 4 m^2 subplots per transect), height class (seedlings: HC1, 5–20 cm; HC2, 20–80 cm; HC3, 80–140 cm; saplings: HC4, >140 cm but <4cm dbh). We also recorded a browse rating that included the following two categories: (1) light, < 10% of juvenile browsed, main leader not browsed; (2) heavy, 10–100% of juvenile browsed, main leader browsed (i.e., release into main canopy unlikely unless browsing ceases). To assess the rate of height growth release, we measured the 5-yr height growth increment (determined by bud-scar counts; Urza and Sibold 2013) for the five live spruce and fir saplings (10 total) that were nearest to plot center and on a trajectory to enter the canopy (i.e., rapid growth rates, no damage to leader).

Characterizing potential for stand recovery from multiple biotic disturbances according to pre-outbreak forest type

Similar to other studies examining the effects of mortality from disturbances on forest recovery

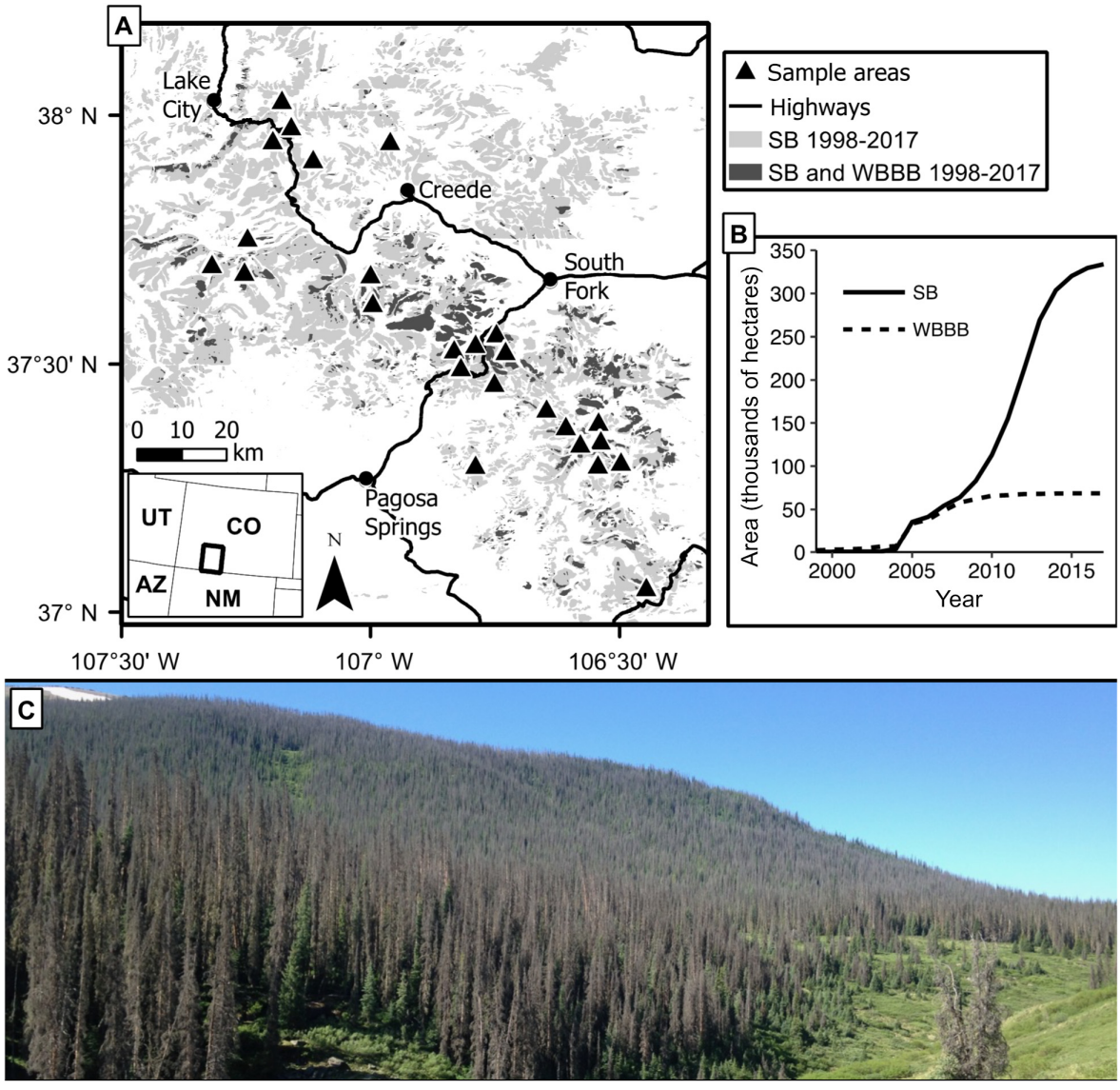

FIG. 1. (A) Study area map illustrating sampling areas (collections of plots, triangles), spruce beetle (SB) activity, and spatial overlap of SB and western balsam bark beetle (WBBB) activity from 1998 to 2017 in the southern Colorado Rocky Mountains, USA. (B) Time series of cumulative area with presence of SB or WBBB from 1998–2017 in the study area extent in Panel A. SB and WBBB activity spatial data from the USDA Aerial Detection Survey (USDA 2018). (C) Photo showing extent and severity of spruce beetle outbreaks in San Juan Mountains.

(Windmuller-Campione and Long 2015, Campbell et al. 2019), we assess the potential for recovery to a forest vegetation type (i.e., physiognomic recovery) following SB and WBBB outbreaks and herbivory, rather than recovery to the same relative species dominance prior to the outbreaks (i.e., compositional recovery), using a minimum tree density threshold. We characterize the potential for recovery of forest cover based on the assumption that higher live tree densities, especially of individuals >1.4 m tall, will likely lead to more rapid recovery. For each plot, we first quantified the density of post-outbreak live trees and *potential juvenile successors* (see Appendix S2: Fig. S1 for flowchart describing method). Potential juvenile successors within each subplot (4 m^2) were defined as the tallest juvenile with light browsing, and the tallest juvenile within each subplot was identified as potential seedling successors (5–140 cm tall) or potential sapling successors (>140 cm tall but <4 cm dbh). We only selected one juvenile per subplot to ensure that potential juvenile successors were spatially distributed throughout the plot rather than clustered at the spatial scale of the subplot (following Windmuller-Campione and Long 2015). The tallest juvenile per subplot has a greater chance for survival to the

main canopy because it likely has a competitive advantage over smaller juveniles and a greater chance of escaping the browse zone (Runkle and Yetter 1987).

We classified the potential for physiognomic recovery for each stand into one of three categories (high, moderate, low) by comparing different size classes of trees to the minimum density threshold, defined here as 370 trees or juveniles/ha for conifers (spruce and/or fir) and 740 trees or juveniles/ha for aspen. Classes were defined as (1) *high*, stands where the combined density of main canopy and subcanopy trees (including potential sapling successors, >1.4 m tall) exceeded the minimum density threshold; (2) *moderate*, stands where the combined density of main canopy and subcanopy trees and potential sapling successors was less than the minimum density threshold, but the combined density of trees and potential juvenile (saplings and seedlings) successors exceeded the threshold; and (3) *low*, stands where combined density of tree and potential juvenile successors (saplings and seedlings) was less than the minimum density threshold. When stands were composed of conifers and aspen, the minimum density threshold was adjusted based on the proportion of live conifers and aspen post-outbreak.

Our thresholds (see previous paragraph) follow recommendations for minimum silvicultural restocking of seedlings (at least one growing season in age) for suitable timberlands in federally managed forests in the study area (USDA 2017). For comparison, the lowest pre-SB outbreak stand density assessed in the present study and Andrus et al. (2016) in the San Juan Mountains was 425 conifers/ha for trees >4 cm dbh. By including adults and well-established juveniles (mostly much older than one growing season) with a higher probability of survival, the minimum stocking threshold used here represents a conservative threshold for assessing physiognomic recovery to disturbance.

To understand how pre-outbreak forest composition affects recovery to outbreaks of SB and WBBB, we classified pre-outbreak composition based on tree density (stems/ha) and basal area (m^2/ha). Pre-outbreak stand density and basal area were reconstructed by adding trees killed by SB and WBBB within the past 15 yr to the live tree density and basal area. We used relative species density to assign each plot to one of four forest composition types: (1) *spruce*, where ≥90% of tree density was spruce; (2) *spruce–fir*, where spruce density was <90% and fir density was ≥10%; (3) *aspen–spruce*, where spruce density was <90% and aspen density was ≥10%; (4) *aspen–spruce–fir*, where spruce density was <90% and both aspen and fir density were >5%.

Analysis

Comparing ungulate herbivory by juvenile species and height class.—We divided the density of heavily browsed juveniles for each species into the four previously defined height classes by total juvenile density in each plot. We statistically compared whether the proportion of spruce browsed (expected to be less palatable) was less than fir or aspen (expected to be more palatable) within each size class and whether saplings were browsed less frequently than seedlings using a non-parametric, one-way Mann-Whitney U test ($\alpha = 0.05$).

Drivers of pre-outbreak juvenile density and post-outbreak growth rates.—To explore the biophysical drivers of variability in pre-outbreak density of juveniles, we modeled pre-outbreak juvenile density and juvenile height growth rate as a function of topographic variables (elevation, heat load [McCune and Keon 2002], slope, topographic position index [Zevenbergen and Thorne 1987], topographic wetness index [Beven and Kirby 1979] from 30 m DEM) and stand structure (pre- and post-outbreak stand density and basal area). The topographic wetness index is a commonly used static measure of soil moisture that integrates the amount of water input from upslope areas and the loss of water due to the local slope. We modeled juvenile density using a negative binomial generalized linear model and constructed models for all species combined and individually by species. To understand the drivers of variability in the rate of juvenile height growth, we modeled juvenile height growth rate (cm/yr) using a generalized linear model with the same variables as well as species, percentage of basal area lost to bark beetle mortality (indicator of increase in light or other resource availability), and mean average juvenile height by plot. All predictor variables were standardized to allow comparison of model coefficients by subtracting the mean and dividing by the standard deviation. Beginning with a saturated model of uncorrelated variables, we iteratively trimmed the model until it only included significant terms ($P < 0.10$) and minimized AIC (Akaike information criterion).

Results

Forest trajectories and recovery from multiple biotic disturbances

Nine initial forest trajectories were interpreted from four pre-outbreak forest types affected by SB or SB and WBBB outbreaks and ungulate herbivory (Figs. 2, 3). The WBBB outbreak affected 60% of stands in the spruce–fir pre-outbreak forest type and 65% of the stands in the aspen–spruce–fir pre-outbreak forest type (Fig. 2). Ungulate browsing on juveniles occurred in 95% of plots (Appendix S3: Fig. S2). We found 100% mortality of main canopy spruce in 60% of stands, but 100% mortality of main canopy fir in only 30% of stands. The combined effects of the SB and WBBB outbreaks caused 100% mortality of main canopy trees in < 10% of stands affected by both bark beetle species (Fig. 3; Appendix S3). Following only SB outbreak (i.e., exclusive of plots affected by both SB and WBBB), species composition by stand density and basal area shifted

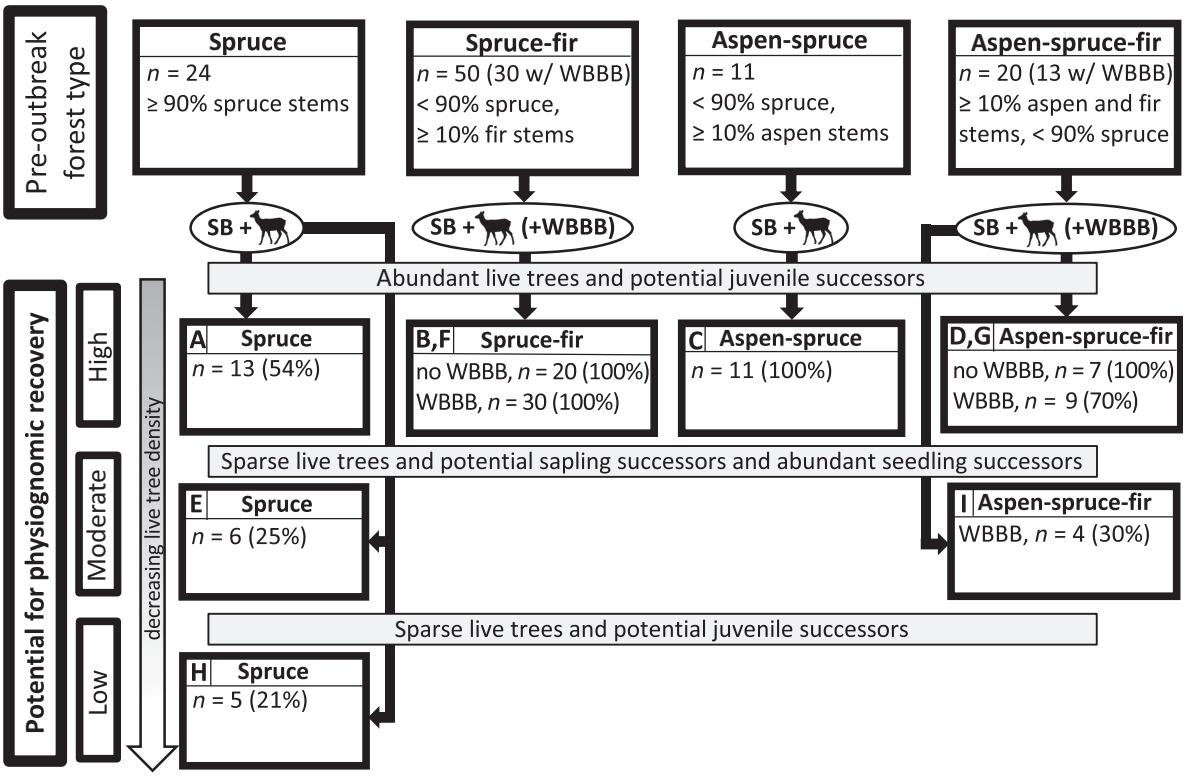

FIG. 2. Summary of observed initial forest trajectories (i.e., at least several decades) and potential for physiognomic recovery to forest following spruce bark beetle outbreaks (SB), western balsam bark beetle (WBBB), and ungulate herbivory in the San Juan Mountains, southern Colorado, USA. The top row describes stand structure and composition of the pre-beetle outbreak forest type (trees > 4 cm dbh only). The subsequent rows illustrate the number and percentage of plots transitioning to each physiognomic recovery class (high, moderate, low) and the letter in the upper left corner of each box corresponds with the figure letter for each trajectory in Fig. 3. Tree density decreases from high to low potential for physiognomic recovery. The potential for physiognomic recovery for each stand was assessed by comparing densities of main canopy and subcanopy trees (>1.4 m tall, includes potential sapling successors) and trees in all sizes-classes to a minimum density threshold. Ungulate browsing only affected the potential for physiognomic recovery when juveniles were heavily browsed (>10% foliage and leader loss) and when densities of main canopy and subcanopy trees were insufficient to meet the minimum density threshold (i.e., low and moderate).

toward fir and/or aspen depending on pre-outbreak forest type (Fig. 3, Appendix S3: Table S1). In stands also affected by WBBB, species composition by stand density and basal area shifted toward aspen in aspen–spruce–fir stands. The lower severity of the WBBB outbreak compared to the SB outbreak (Fig. 3, Appendix S3: Table S1) resulted in smaller shifts in species composition by stand density and basal area away from fir than spruce in spruce–fir stands.

Most stands (86%, 90 out of 105) achieved minimum density thresholds with main canopy and subcanopy trees (i.e., "high" potential for recovery) when subjected to the combined effects of two (SB and herbivory) or three (SB and WBBB outbreaks and herbivory) biotic disturbances (Figs. 2, 3). This included all spruce–fir (n = 50) and aspen–spruce (n = 11) stands, whether affected by two (only SB and herbivory) or all three disturbances (SB, WBBB, and herbivory). All aspen–spruce–fir stands without WBBB (n = 7) also exceeded the minimum density thresholds with main canopy and subcanopy trees (Figs. 2, 3). The additional effect of WBBB reduced densities of main canopy and subcanopy trees (but not all trees and seedlings) below the minimum density threshold (i.e., "moderate" potential for recovery) in 31% of aspen–spruce–fir stands (4 out of 13 stands). Most spruce stands met the minimum density threshold with main canopy and subcanopy trees (13 out of 24) or all trees and seedlings combined (6 out of 24 spruce plots), despite >89% tree mortality of main canopy trees (Appendix S3: Table S1). Spruce stands that did not meet the minimum density threshold (5 out of 24 spruce stands; i.e., "low" potential for recovery) were dominated by large-diameter spruce; median dbhs pre-outbreak were 14.5 cm and 34.5 cm for spruce stands in the high and low potential for recovery classes, respectively (Appendix S4: Fig. S2).

Ungulate herbivory by species and juvenile size class

Ungulates heavily browsed >55% of all juveniles (Fig. 4) and 35% (median) of juveniles across all plots were heavily browsed (Appendix S3: Fig. S2).

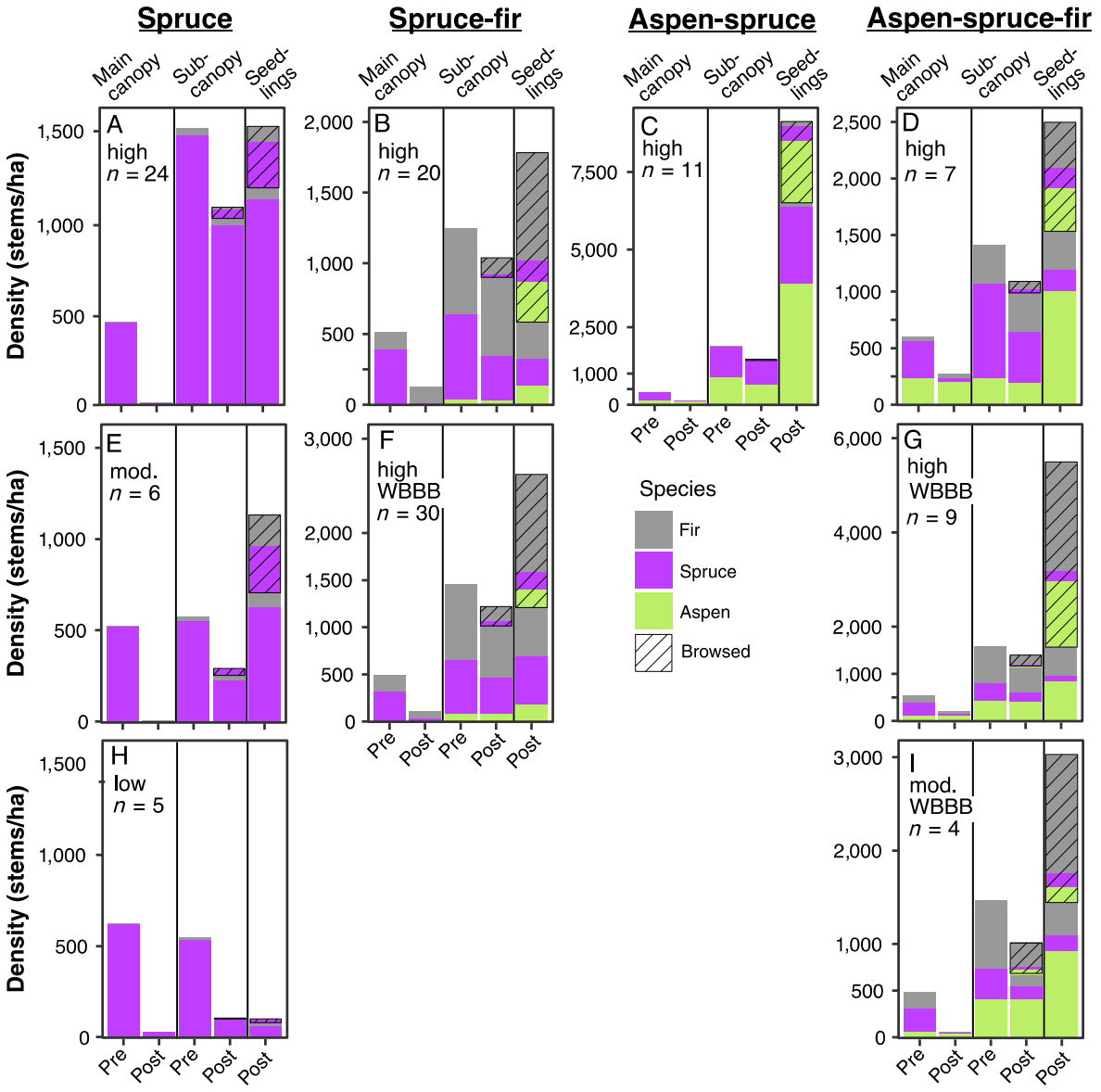

FIG. 3. Average density by species pre- and post-outbreak in size classes of main canopy (>20 cm dbh), subcanopy (>1.4 m tall but <20 cm dbh), and seedlings (<1.4 m in height) by initial forest trajectory (trajectories correspond to Fig. 2). One hundred and five sampled plots were first grouped by forest type (column headers) and then plots were grouped based on biotic disturbances and the post-disturbance recovery rating (low, moderate, and high; see *Methods*). All plots were affected by spruce bark beetle (SB) outbreak and ungulate herbivory and plots with WBBB were also affected by western balsam bark beetle (WBBB). Cross-hatching indicates >10% foliage and leader loss to browsing on saplings in the subcanopy and on seedlings. Note different *y*-axis scales.

The proportion of heavily browsed seedlings (<140 cm height, HC1-3) was greater than saplings (>140 cm but <4 cm dbh, HC4) across all species (Fig. 4; Mann-Whitney, $P < 0.001$). Fir and aspen were more heavily browsed than spruce in juveniles 20–80 cm and 80–140 cm tall (Fig. 4; all pairwise Mann-Whitney U, $P < 0.03$,). For example, the median percent of aspen (10.8%) and fir (13.1%) browsed was more than three times greater than spruce (3.6%) in HC3 (Fig. 4).

Effect of topography and stand structure on juvenile abundance and height growth rates

Variability in juvenile density (<4 cm dbh) was primarily explained by pre-outbreak stand structure (basal area, Fig. 5A), whereas juvenile growth rates were influenced by post-outbreak stand structure, topography, juvenile species, and juvenile height (Fig. 5B). Across all species, juvenile density increased as pre-outbreak basal area decreased (Fig. 5A; see Appendix S5: Table S1 for

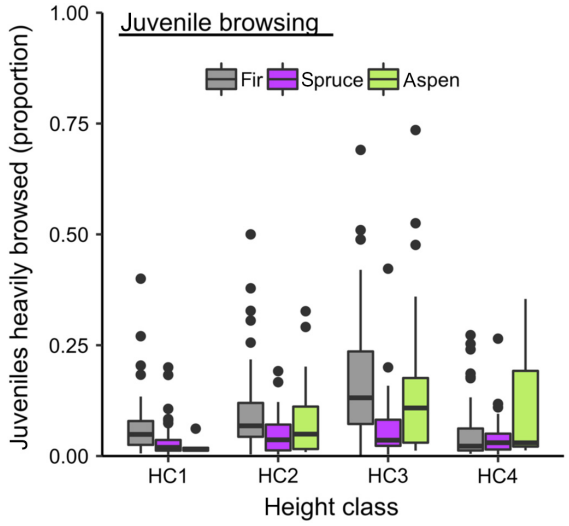

FIG. 4. Proportion of total juveniles heavily browsed (>10% foliage and leader loss) by height class and species in each plot. Proportion is computed as number of juveniles heavily browsed in each height class by species divided by total juveniles in all height classes (HC1–4) by plot. Height of juveniles in each height class is as follows: HC1, 5–20 cm; HC2, 20–80 cm; HC3, 80–140 cm; HC4, >140 cm and <4 cm dbh. In the boxplots, the thick horizontal line within the box is the median, the lower and upper hinges represent the interquartile range (IQR, 25th–75th percentiles) of the distribution. The whiskers extend ±1.5 times the IQR to form the limit for outliers (black dots).

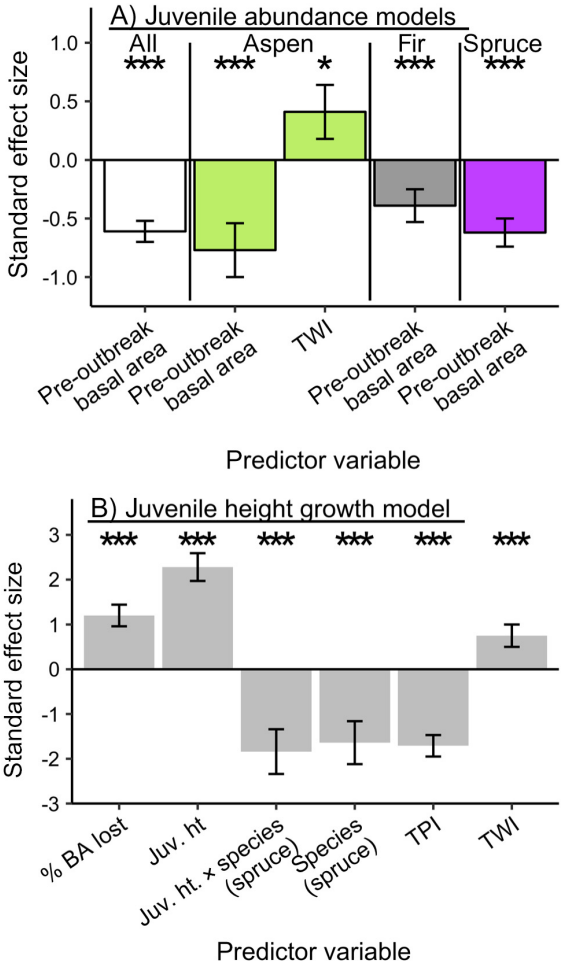

FIG. 5. (A) Negative binomial model effects (i.e., coefficients) testing the influence of pre-outbreak basal area and topographic predictor variables on juvenile (<4 cm dbh) density in four separate models: (1) all species (spruce, fir, and aspen), (2) aspen (green), (3) fir (gray), and (4) spruce (purple). TWI stands for topographic wetness index. (B) Generalized linear model effects (i.e., coefficients) testing the influence of topography (TWI; TPI, topographic position index), tree species (Engelmann spruce and subalpine fir), average juvenile height (juv. ht.), and percentage of total basal area lost to bark beetles (% BA lost) predictor variables on juvenile height growth rates. Bars represent mean standardized effect size and error bars represent standard errors. Only predictor variables with a $P < 0.1$ were included in models. Predictor significance levels are indicated by $*P < 0.1$; $**P < 0.05$; and $***P < 0.01$. See Appendix S5 for model results.

model results). Topographic variables were poor predictors of juvenile conifer densities, but juvenile aspen density increased with topographic wetness. Growth rates were faster for fir than spruce (Fig. 5B; see Appendix S5: Table S2 for model results). Growth rates of both species increased with the percent of basal area lost and topographic wetness (i.e., greater soil moisture availability) and decreased with topographic position index (i.e., greater growth at lower hillslope positions; Fig. 5B). Though growth rates of both species increased with juvenile height, the rate of height growth increase with juvenile height was greater for fir than spruce (height and species interaction term, Fig. 5B).

DISCUSSION

Most subalpine forests exhibited a high potential for recovery to a forest vegetation type (physiognomic recovery or resilience) following multiple coincident biotic disturbances in southern Colorado. Despite severe tree mortality (>90% of forest canopy) from two bark beetle outbreaks and widespread ungulate herbivory (Fig. 2, 3), survival of some adult trees of the nonhost species and many juveniles of all species were important indicators of a post-outbreak forests currently on a trajectory for physiognomic recovery (Fig. 3). However, ungulate browsing on over half of all juveniles could slow the rate of recovery and affect the composition of the future forest canopy (Fig. 4). The spatial overlap of two bark beetle outbreaks did cause important shifts in species composition, but did not appear to compromise mechanisms of physiognomic recovery to forest, which supports findings from studies examining forest recovery after single-species bark beetle outbreaks (Diskin et al. 2011, Redmond and Kelsey 2018, Campbell et al. 2019).

Forest recovery following multiple biotic disturbances

Forest recovery depended on the density of post-outbreak, unbrowsed survivors, with higher densities of larger trees supporting more rapid physiognomic recovery to forest. As most stands (86%) achieved the minimum density threshold with main canopy and subcanopy trees (>1.4 m tall; Fig. 2), initial forest trajectories should be relatively unaffected by high seedling depletion rates and the effects of ungulate browsing on juveniles <2 m tall. This also implies that our results are likely valid for at least the next several decades, unless a subsequent disturbance occurs. We expected physiognomic recovery to be compromised under two scenarios, either concurrent outbreaks of SB and WBBB in mixed-species stands or severe SB outbreaks in monotypic spruce stands. We found little evidence to support the first scenario as mixed-species stands (spruce–fir or aspen–spruce–fir) affected by concurrent outbreaks of SB and WBBB contained more than sufficient quantities of canopy-sized trees and unbrowsed juveniles to meet the minimum density threshold when all size classes were considered. Severe outbreaks of SB in some monotypic stands did, however, result in very low densities of survivors (21% of spruce stands with <370 survivors/ha, Fig. 3). Based on the nine initial trajectories we interpreted, monotypic stands of spruce was the pre-outbreak forest type most vulnerable to a transition to a low-density forest (i.e., open woodlands), but only when dominated by large-diameter spruce. Low-density conditions may persist for decades, because new seedling establishment is uncommon following SB outbreaks (DeRose and Long 2010). In the context of future tree mortality expected from internal stand dynamics (Oliver 1980) and increasing temperatures (van Mantgem et al. 2009), the density of survivors in most stands appears more than sufficient to absorb some additional mortality without shifting to a non-forest state.

The use of a minimum silvicultural restocking criterion as a benchmark for post-disturbance resilience is a common technique among ecological studies (Windmuller-Campione and Long 2015, Welch et al. 2016). Whereas the primary goal of these criteria is to assess future timber resources, the goals of ecological studies tend to focus on whether forests will recover to a similar forest ecosystem type and maintain similar ecosystem services (e.g., watershed protection or habitat; Welch et al. 2016). Future research is needed to develop finer resolution measures to gauge the potential for forest recovery that account for the regional to local-scale spatial variability in forest dynamics, species composition, and disturbance type (e.g., beetle outbreaks vs. wildfire) and that better address ecosystem function and ecosystem services (Thom and Seidl 2015).

Recovery of the forest canopy

Shifts in species composition toward nonhost species (e.g., fir) are common following SB outbreaks in other mountain ranges in the southern Rocky Mountains (present study; Schmid and Hinds 1974, Veblen et al. 1991, DeRose and Long 2007), but the trend toward increased aspen abundance following the spatial overlap of two bark beetle outbreaks is a key new finding with important ecological consequences for subalpine forests. The competitive exclusion of aspen in aspen–spruce–fir stands was delayed in both the present study and when blowdown was followed by wildfire (Kulakowski et al. 2013), suggesting that aspen forest cover may increase with expected increases in the area affected by spruce beetle outbreaks (Temperli et al. 2015) and fires in subalpine forests as climate warms. However, this finding must be considered in the context of recent, extensive mortality of aspen in Colorado (Worrall et al. 2015) and a predicted reduction in suitable climate space for aspen (Rehfeldt et al. 2009). Projecting future forest conditions and susceptibility to subsequent disturbances under a warmer climate needs to consider the long-lasting effects of these shifts in species composition and stand structure. For example, increased aspen dominance is likely to buffer against both fire spread and future SB or WBBB outbreaks (Shinneman et al. 2013) and the reduction in large live spruce has been shown to diminish the potential for SB outbreak for many decades (Hart et al. 2015).

Based on our findings, recovery of the main tree canopy to pre-disturbance densities will likely occur more rapidly in stands with greater pre-outbreak species diversity (i.e., greater compositional diversity) and higher pre-outbreak frequencies of smaller-diameter individuals (i.e., greater structural complexity). In comparison to monotypic stands, canopy tree mortality was generally lower in mixed-species forest types affected by SB or SB and WBBB (Fig. 3). Consequently, mixed-species forest types have greater abundances of live main canopy trees post-outbreak to initiate forest recovery. Greater species diversity and more open forest canopies pre-outbreak (i.e., lower basal area) also resulted in greater abundances of juveniles, a key recovery and reorganization mechanism following outbreaks. As aspen produces high abundances of root suckers (Romme et al. 1995) and fir is abundant in dense spruce–fir forests (Veblen 1986), pre-outbreak forest types with these species had high abundances of juveniles to support forest recovery.

Whereas higher species diversity was generally associated with higher potential for physiognomic recovery, some stands of aspen–spruce–fir affected by SB and WBBB outbreaks contained insufficient densities of main canopy and subcanopy trees to meet the minimum density threshold (i.e., moderate potential for recovery). In these stands, conifers meet their portion of the minimum density threshold, but spatial aggregation of juvenile aspen resulted in insufficient densities to meet their portion of the minimum density threshold. The greater minimum density threshold for aspen

is likely based on lower rates of survival and high rates of juvenile browsing (Baker et al. 1997), but these rates probably vary with life stage and may represent a potential short-coming of the minimum density threshold framework.

Effect of ungulate herbivory on forest recovery and future canopy composition

Heavy ungulate browsing on >50% of juveniles will primarily slow the rate of infilling of the forest canopy rather than the capacity for physiognomic recovery to forest, because most post-outbreak stands (86%) meet the minimum density threshold with trees taller than the browse zone (2 m, Figs. 2, 3). If frequent browsing of juveniles persists, then many juveniles may die or be prevented from escaping the maximum browsing zone of ungulates, likely slowing forest recovery and possibly creating a "browse trap" (Staver and Bond 2014). However, preferential browsing of more palatable species like aspen and fir in our study (Fig. 4) will likely influence the composition of the future forest canopy (Churski et al. 2016). The greater abundances of aspen and fir than spruce (Fig. 3) and faster growth rates of fir than spruce (Fig. 5a) suggests both fir and aspen may outcompete spruce leading to a future forest canopy dominated by fir and aspen in mixed-species stands. However, the higher proportion of heavily browsed fir and aspen than spruce (Fig. 4) may negate this apparent advantage, favoring higher rates of spruce recruitment into taller height classes.

Variability in the rates of forest recovery

Consistent with other studies following bark beetle outbreaks (Veblen et al. 1991, DeRose and Long 2010, Campbell et al. 2019), height growth release of surviving advance regeneration, rather than new establishment, will likely supplement surviving adult trees in forming the next forest canopy (Fig. 3). However, we found evidence for important variation in the rate of forest recovery (Fig. 5a, b). In stands experiencing less mortality of main canopy trees, juvenile growth rates are slower, but fewer replacements are needed (Fig. 5a). Conversely, stands with greater losses of main canopy trees exhibited faster rates of juvenile height growth, which are known to persist for decades following SB outbreaks (Veblen et al. 1991). The effect of topographic variability on growth rates will add an additional layer of complexity to spatial patterns in recovery (Fig. 5b). After accounting for the percent of basal area lost, juveniles were growing faster in topographically wetter sites and sites at lower slope positions where temperatures are presumably warmer. However, faster growth rates of juvenile fir than spruce may be short-lived if the effects of warming on adult fir growth are more deleterious than the effects on spruce growth (Kelsey et al. 2018).

Importance of recovery mechanisms following disturbance under climate warming

Sufficient abundances of live trees for forest recovery is commonly observed following individual (DeRose and Long 2010, Diskin et al. 2011, Redmond and Kelsey 2018, Campbell et al. 2019) or multiple bark beetle outbreaks (present study), which strongly contrasts with very low densities of trees for postfire forest recovery in many recently burned dry forests (Stevens-Rumann et al. 2018, Davis et al. 2019, Rodman et al. *a*). Key differences in recovery mechanisms between wildfire and bark beetle outbreaks may buffer outbreaks from the effects of climate warming for the next several decades. Recovery following bark beetle outbreaks is much less dependent on new seedling establishment, a life stage highly vulnerable to climatic limitations (Conlisk et al. 2017), than recovery following wildfire. The presence of nonhost species and of understory populations of juveniles not killed by bark beetles provide more robust mechanisms of post-disturbance recovery and maintenance of forest cover under climate warming. Though increases in severity and spatial extent of bark beetle outbreaks are expected (Raffa et al. 2008, Temperli et al. 2015, Reich et al. 2016, Foster et al. 2018), currently available evidence indicates that individual and multiple, simultaneous bark beetle outbreaks are much less effective at converting forest to non-forest vegetation types than wildfire.

Conclusion

Studies examining the consequences of overlapping biotic disturbances are a key knowledge gap, particularly in the context of recent widespread bark beetle outbreaks and expected increases in some biotic disturbances with climate warming. In this study, we showed that tree mortality from two bark beetle species and impacts of ungulate herbivory on juveniles were generally insufficient to compromise mechanisms for physiognomic recovery to forest. Instead, survival of some canopy-sized nonhost trees and abundant juveniles of host and nonhost species imply that most stands are currently on a trajectory for forest recovery. We identified that greater pre-outbreak stand structural complexity and species diversity were key traits that provided stands with a high potential for physiognomic recovery, which supports the long-standing idea that diversity enhances ecological resilience. Though the immediate impacts of the bark beetle outbreaks on canopy species composition are clear, differences in juvenile abundance and preferential browsing of some tree species create uncertainty about rate of canopy infilling and the composition of the future forest canopy. Unlike recent evidence documenting failed seedling establishment in some postfire landscapes, forests experiencing mortality from one or

more beetle outbreaks and ungulate herbivory of juveniles are more likely to recover.

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