Does the legacy of historical thinning treatments foster resilience to bark beetle outbreaks in subalpine forests?

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Abstract. Promoting ecological resilience to increasing disturbance activity is a key management priority under warming climate. Across the Northern Hemisphere, tree mortality from widespread bark beetle outbreaks raises concerns for how forest management can foster resilience to future outbreaks. Density reduction (i.e., thinning) treatments can increase vigor of remaining trees, but the longevity of treatment efficacy for reducing susceptibility to future disturbance remains a key knowledge gap. Using one of the longest-running replicated experiments in old-growth subalpine forests, we measured stand structure following a recent (early 2000s) severe mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak to examine the legacy of historical (1940s) thinning treatments on two components of resilience. We asked: 'How did historical thinning intensity affect (1) tree-scale survival probability and stand-scale survival proportion (collectively "resistance" to outbreak) for susceptible trees (lodgepole pine [*Pinus contorta*] ≥ 12 cm diameter) and (2) post-outbreak stand successional trajectories?' Overall outbreak severity was high (MPB killed 59% of susceptible individuals and 78% of susceptible basal area), and historical thinning had little effect on tree-scale and stand-scale resistance. Tree-scale survival probability decreased sharply with increasing tree diameter and did not differ from the control (uncut stands) in the historical thinning treatments. Stand-scale proportion of surviving susceptible trees and basal area did not differ from the control in historically thinned stands, except for treatments that removed nearly all susceptible trees, in which survival proportion approximately doubled. Despite limited effects on resistance to MPB outbreak, the legacy of historical treatments shifted dominance from large-diameter to small-diameter lodgepole pine by the time of outbreak, resulting in historically thinned stands with ~2× greater post-outbreak live basal area than control stands. MPB-driven mortality of large-diameter lodgepole pine in control stands and density-dependent mortality of small-diameter trees in historically thinned stands led to convergence in post-outbreak live tree stand structure. One exception was the heaviest historical thinning treatments (59–77% basal area removed), for which sapling dominance of shade-tolerant, unsusceptible conifers was lower than control stands. After six decades, thinning treatments have had minimal effect on resistance to bark beetle outbreaks, but leave persistent legacies in shaping post-outbreak successional trajectories.

Key words: biotic disturbance; Dendroctonus ponderosae; *disturbance interactions; forest management; Fraser Experimental Forest, Colorado, USA; lodgepole pine; mountain pine beetle;* Pinus contorta; *resistance; Rocky Mountains; successional trajectories.*

Introduction

In temperate and boreal forests worldwide, disturbances (e.g., insect outbreaks, fires, and windstorms) are integral to shaping ecosystem structure, composition, and function (Turner 2010). However, climate-driven increases in disturbance activity threaten ecosystem

services (Turner 2010, Seidl et al. 2016) and raise concerns about forest function and persistence (Johnstone et al. 2016, Seidl et al. 2017). Increases in the extent, frequency, duration, and intensity of disturbances have been observed or predicted for drought (Allen et al. 2010, Millar and Stephenson 2015), fire (Jolly et al. 2015, Westerling 2016), bark beetle outbreaks (Raffa et al. 2008, Bentz et al. 2010), and pathogen activity (Weed et al. 2013). Such shifts in disturbance regimes may increase the likelihood of forests undergoing changes in ecosystem state—including transition to non-

forest—by altering regeneration success (Harvey et al. 2016, Stevens-Rumann et al. 2018, Turner et al. 2019, Coop et al. 2020) or environmental conditions that shape succession (McLauchlan et al. 2014, Johnstone et al. 2016). Consequently, managing forests to maintain structure and ecosystem services is a critical challenge.

A key priority of forest management facing a warming climate and increasing disturbance activity is promoting resilience, the capacity of a system to absorb disturbance, reorganize, and retain essentially the same structure and function after perturbation (Walker et al. 2004). One dimension of resilience to disturbance that is a focus of ecosystem management is resistance, the ability of a system to remain unchanged when perturbed (Gunderson 2000). Silvicultural treatments that reduce stand density (e.g., thinning) and remove low-vigor trees can promote resistance by bolstering the capacity of remaining trees to withstand the stress of a subsequent disturbance. At the tree scale, decreasing stand density by removing low-vigor trees reduces resource competition, therefore increasing defensive capacity (Fettig et al. 2007) or reproductive capacity (Flathers et al. 2016) of remaining trees. At the stand scale, alteration of structure (i.e., density, basal area, spatial arrangement) and species composition can decrease stand susceptibility to disturbances such as fire and bark beetle outbreaks by reducing the number of susceptible trees remaining (McIver et al. 2013, DeRose and Long 2014).

A second dimension of fostering resilience to disturbance is increasing the capacity of forests to return to their pre-disturbance structure and function after disturbance-driven changes occur. Silvicultural treatments can alter post-disturbance responses by manipulating structural and compositional legacies (i.e., individuals or biomass from the pre-disturbance ecosystem that persist following a disturbance; Franklin et al. 2000, Johnstone et al. 2016). Such treatments can influence the effects of disturbance on subsequent stand dynamics, including size and age distributions and species dominance (DeRose and Long 2014). For instance, treatments promoting the growth and reproduction of a specific disturbance-resistant species can direct post-disturbance stand successional trajectories toward community dynamics less susceptible to that future disturbance (Hood et al. 2016, Young et al. 2020). However, treatment effects can attenuate or amplify with time following implementation and result in different outcomes depending on the interval between treatment and subsequent stress or disturbance (Reinhardt et al. 2008, DeRose and Long 2014). Therefore, testing the effectiveness and longevity of silvicultural treatments on forest resilience to disturbance is an important knowledge gap.

Across the Northern Hemisphere, profound effects of recent outbreaks of native bark beetles (Coleoptera: Curculionidae: Scolytinae) in temperate forests (Kautz et al. 2017) present a critical management context for promoting forest resilience. Between the late 1990s and mid-2000s, bark beetle outbreaks have caused extensive tree mortality over tens of millions of hectares (ha) of conifer forests in the USA (Meddens et al. 2012), Canada (Kurz et al. 2008), and central Europe (Kautz et al. 2011). In western North America, the majority of tree mortality from these recent outbreaks is associated with mountain pine beetles (MPB; *Dendroctonus ponderosae*) primarily attacking lodgepole pine (*Pinus contorta* var. *latifolia*) (Raffa et al. 2008, Kautz et al. 2017). Bark beetle outbreaks are important drivers of many components of forest function, including forest growth and regeneration following overstory tree mortality (Bentz et al. 2009), carbon sequestration (Hicke et al. 2012*a*), water and nutrient cycling (Mikkelson et al. 2013, Pugh and Gordon 2013), wood products (Weed et al. 2013), and wildlife habitat (Saab et al. 2014). Furthermore, spatial heterogeneity in stand structural conditions created by outbreaks may persist for decades, affecting future beetle infestations (Kashian et al. 2011, Hart et al. 2015). Severe bark beetle outbreaks are natural disturbances that have been documented throughout recent centuries (Baker and Veblen 1990, Jarvis and Kulakowski 2015, Negrón and Huckaby 2020). However, future outbreak dynamics are expected to be released from previous climatological constraints (Bentz et al. 2010) as warmer and drier climate conditions can drive rapid beetle reproduction and growth, decrease cold-induced beetle mortality, and increase tree physiological stress (Bentz et al. 2009). Therefore, exploring the consequences of recent outbreaks on forest structure and function and their likely changes in the future represents a key management priority (Morris et al. 2017).

Alteration of forest structure and composition through thinning treatments is often considered as a management strategy for increasing forest resilience to bark beetle outbreak (Fettig and Hilszczański 2015), but the longevity of treatment effectiveness remains uncertain. Most studies examining the interaction between different thinning strategies and forest response to bark beetle outbreaks have been conducted post-outbreak (e.g., salvage logging; see Collins et al. 2011, Donato et al. 2013*b*, Griffin et al. 2013), during outbreak (Cole et al. 1983, McGregor et al. 1987), or with short periods (i.e., 5–25 yr) between treatment implementation and outbreaks (Mitchell et al. 1983, Whitehead and Russo 2005, Temperli et al. 2014, Hood et al. 2016, Crotteau et al. 2019). Studies of treatments implemented years to decades prior to outbreaks have provided valuable insights into treatment effectiveness but are limited in temporal extent, particularly in the context of the typical return interval of bark beetle outbreaks. For lodgepole pine forests across western North America, MPB outbreak return intervals range from 20 to 130 yr (Cole and Amman 1980, Taylor et al. 2006, Axelson et al. 2009, Bentz et al. 2009, Alfaro et al. 2010, Jarvis and Kulakowski 2015). Simulation studies can project thinning effects on forest dynamics into the future (Ager et al. 2007, Collins et al. 2011, 2012, Donato et al. 2013*b*, Pelz et al. 2015), but empirical tests of the longevity of

thinning treatments on promoting resilience to bark beetle outbreaks remain largely unexplored.

Here, we tested the effects of historical stand-thinning treatments on two components of forest resilience to bark beetles: (1) resistance to outbreak and (2) post-outbreak successional trajectories. Using a long-term replicated experimental study of old-growth lodgepole pine stands that were thinned in the mid-20th century and subsequently affected by a severe MPB outbreak in the early 21st century (~60 yr post-thinning), we asked the following questions:

1) *Do stand-thinning treatments increase resistance to outbreaks, and does resistance differ across spatial scales?*

Specifically, what are the effects of historical thinning intensity (removal of large-diameter trees) and timber stand improvement (TSI; additional removal of low-vigor small-diameter trees) on (a) tree-scale survival probability of susceptible (dbh ≥ 12 cm) lodgepole pine, and (b) stand-scale survival proportion of susceptible lodgepole pine density and basal area?

2) *Do stand-thinning treatments modify post-outbreak stand successional trajectories?*

Specifically, what are the effects of historical thinning intensity and TSI on (a) pre- and post-outbreak live stand structure (density, basal area, quadratic mean diameter [QMD], and diameter distributions), and (b) post-outbreak live late-seral species proportion across size classes?

For Question 1, we expected historical thinning to increase resistance to MPB compared with uncut (i.e., control) stands at both tree and stand spatial scales. At the tree scale, resistance to beetle attack is affected by individual tree diameter, age, and vigor (i.e., defensive ability); larger diameter, older, and less vigorous trees are generally more susceptible to attack due to beetle preference for, and greater reproductive success in, hosts with these qualities (Safranyik and Carrol 2006). Therefore, we expected greater tree-scale resistance in historically thinned stands due to increases in vigor for remaining trees via reduced resource competition. At the stand scale, resistance to outbreak is influenced by stem density, spatial heterogeneity, and suitable host abundance; denser and more homogeneous stands dominated by suitable hosts typically exhibit higher levels of beetle-caused mortality (Fettig et al. 2007, Klutsch et al. 2009, Nelson et al. 2014, Hood et al. 2016). Therefore, we expected greater stand-scale resistance in historically thinned stands due to reduction of susceptible lodgepole pine density and basal area. At both scales, we expected TSI to enhance effects of thinning on resistance due to removal of additional susceptible trees and further reductions in resource competition among remaining trees.

For Question 2, we expected historical thinning to modify post-outbreak stand successional trajectories. Bark beetle outbreaks alter structural legacies by reducing live—and increasing dead—host tree basal area and density (Diskin et al. 2011, Klutsch et al. 2011) and shifting size and age distributions of host trees toward smaller and younger classes (Kashian et al. 2011). Therefore, we expected historically thinned stands to have greater overall post-outbreak live density, basal area, and QMD compared with uncut (i.e., control) stands due to lower MPB-induced tree mortality in thinned stands. Outbreaks also alter compositional legacies by shifting dominance to non-host tree species and accelerating successional trajectories toward late-seral communities (Diskin et al. 2011, Kayes and Tinker 2012). Therefore, we expected that uncut stands would have greater proportions of late-seral and shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), representing an accelerated successional trajectory, based on greater assumed MPB-induced pine mortality and subsequent release of non-host species. Conversely, we expected historically thinned stands to have slowed or reversed successional trajectories toward dominance of early-seral lodgepole pine. We expected TSI to enhance the expected effects of thinning on post-outbreak structure and composition due to the removal of additional trees and facilitation of conditions favoring lodgepole pine growth and regeneration (e.g., larger canopy gaps, reduced resource competition).

Methods

Study area

The study was conducted at the Fraser Experimental Forest, located on the Arapaho-Roosevelt National Forest (Colorado, USA) in the southern Rocky Mountains (39°53′N, 105°53′W). Established in 1937, the experimental forest comprises 9,300 ha of subalpine forest between 2,700 and 3,900 m elevation in a headwaters watershed of the Colorado River system (Alexander et al. 1985). Overstory vegetation within the area of the study plots established following stand-replacing fire in 1685 (Bradford et al. 2008) and is characterized by lodgepole pine seral to subalpine fir and Engelmann spruce among scattered aspen (*Populus tremuloides*). Understory vegetation is sparse, consisting of conifer regeneration and shrubs including buffaloberry (*Shepherdia canadensis*) and whortleberry (*Vaccinium* spp.). Soils are shallow and rocky, derived from gneiss and schist (Huckaby and Moir 1998). The climate is temperate, characterized by monthly (30-yr mean from 1981 to 2010) temperatures ranging from −7°C in January to 14°C in July, and an annual mean of 3°C (PRISM Climate Group 2012). Annual mean precipitation is 550 mm, with two-thirds of precipitation falling as snow from October to May (PRISM Climate Group 2012).

The study stands are broadly representative of lodgepole pine/subalpine fir/Engelmann spruce subalpine mixed-species forest communities in the North American Rocky Mountains (Huckaby and Moir 1998).

Study design

Study stands are in >300-yr-old forest (Alexander 1954) where harvest-cutting units were established in 1938. Full details of the experiment have been described by Wilm and Dunford (1948), but are summarized here (Table 1). Four replicates of five different thinning treatments were conducted on 2-ha (~142 × 142 m) treatment units arranged in a block design (20 total units; Appendix S1: Fig. S1). Each plot is surrounded by a 19 m wide isolation strip (i.e., buffer of comparable initial conditions that receive identical treatment to mitigate edge effects from adjacent treatments; Curtis and Marshall 2005). Prior to thinning in 1940, all units were characterized by similar stand structure and species composition: overstory trees with diameter at breast height (dbh; measured 1.40 m above ground) ≥9 cm ranged in density from 741 to 988 stems/ha and basal area from 33.6 to 38.2 m^2/ha. Mean volume of merchantable timber (i.e., stems with dbh ≥ 24 cm) was 70.0 m^3/ha, ranging from 44.3 to 99.1 m^3/ha. Thinning treatments were defined by volume of merchantable timber reserved (i.e., not removed): uncut *control*, 70.0 m^3/ha (i.e., all merchantable volume reserved); *light* thinning, 35.0 m^3/ha; *moderate* thinning, 23.3 m^3/ha; *heavy* thinning, 11.7 m^3/ha; and *clearcut*, 0 m^3/ha (i.e., no merchantable volume reserved). Immediately following the main treatments, TSI treatments were conducted on a random half of each thinned treatment unit where dense groups of young saplings and "undesirable" trees (e.g., malformed, diseased, low-vigor individuals) between 9 and 24 cm dbh were removed to monitor effects on growth rate and stand structure within the major treatments. Mean TSI tree removal was 138 trees/ha, ranging from 72 to 287 trees/ha. All trees were felled and cut by hand, and merchantable logs were removed with horses. Resulting slash was scattered over half of each treatment unit and swamper-burned on the other half.

In 2003 (63 yr post-treatment), increasing MPB activity was observed in the experimental forest (Tishmack et al. 2005), causing extensive mortality of lodgepole pine by 2006 (Hubbard et al. 2013) and continuing until a sharp decline in new infestations in 2010 (Walter and Platt 2013). By 2011, MPB activity in the region had subsided (Vorster et al. 2017), killing 90% of large diameter (dbh > 30 cm) and 10% of small diameter (dbh < 15 cm) lodgepole pine trees over the course of the outbreak (Rhoades et al. 2013). Across the experimental forest, mortality within stands was proportional to the abundance of lodgepole pine, lower in young stands than mature stands, and more closely tied to topographic factors favorable to lodgepole pine (i.e., southerly aspects, lower elevations) than stand age (Vorster et al. 2017).

Field data collection

In July through August 2018 (78 yr post-treatment and ~8 yr post-outbreak) we measured post-outbreak stand structure within 0.25 ha (50 × 50 m) plots located in each thinning and TSI treatment combination (Appendix S1: Fig. S1). For treatment units thinned ~60 yr prior to outbreak, plots were placed at the center of each half of the 2-ha unit (one plot with TSI and the other plot non-TSI). For uncut control units, plots were placed in the center of the 2-ha unit as these units were not split in half in the original study (i.e., no TSI was performed). If necessary, plot locations were shifted slightly to reduce confounding factors when conditions in the center were not representative of the larger treatment area (e.g., presence of old road, stream, or uncharacteristic topographic feature), maintaining a ≥5 m buffer between plot and treatment unit boundaries (not including the additional 19 m isolation strip). The total number of replicate plots ($n = 28$) was distributed across treatment categories as follows: control ($n = 4$), light+TSI ($n = 4$), moderate ($n = 3$), moderate+TSI ($n = 3$), heavy ($n = 4$), heavy+TSI ($n = 4$), clearcut ($n = 3$), and clearcut+TSI ($n = 3$) (see Appendix S1: Table S1 for details). Plots ranged in elevation from 2,799 to 2,999 m and were positioned on northerly aspects with slopes of 5.6°–25.9°.

We measured stand structure (post-outbreak and reconstructed pre-outbreak structure) within each plot to assess MPB-induced tree mortality and post-outbreak successional trajectories using established sampling design protocols (Simard et al. 2011, Donato et al. 2013a). For overstory (dbh ≥ 12 cm) and midstory (5 ≤ dbh < 12 cm) trees, we recorded species, dbh, and signs of MPB attack (i.e., galleries, pitch tubes) for all individuals (live or dead) rooted within three parallel 4 × 50 m belt transects oriented north–south at the west, center, and east portion of each plot. For dead trees, we also recorded status (standing or down) and decay class (1–5, adapted from Lutes et al. [2006] for snags and coarse woody debris). For saplings (dbh < 5 cm, height ≥ 1.40 m) and seedlings (height 0.10–1.39 m), we measured species, dbh (saplings only), height, and status (live or dead) along three 2 × 25 m belt transects oriented parallel (north–south) in the northwest and southeast portions and perpendicular (east–west) in the southwest portion of each plot. All measures were scaled up to per-ha values.

Reconstructing pre-outbreak stand structure

Pre-outbreak (2004) stand structure was reconstructed using decay status of measured trees, diameter growth rates derived from repeat diameter measurements within

TABLE 1. Residual stand structure across treatment unit replicates following both thinning and subsequent timber stand improvement (TSI) treatments in 1940.

Treatment	Reserve volume† (m³/ha)	Stem density‡ (stems/ha) Mean (%)	Basal area‡ (m²/ha) Mean (%)	Thinning method	Description
Control	70.0	944 (100)	35.7 (100)	Uncut	No treatment
Light	35.0	558 (59)	21.0 (59)	Initial step shelterwood cutting	Best trees left remaining, necessarily included many low-vigor trees
Moderate	23.3	413 (44)	14.9 (42)	Heavy selection	Remaining trees selected to ensure adequate restocking and control number of seedlings
Heavy§	11.7	502 (53)	14.7 (41)	Scattered seed-tree cutting	Most vigorous trees left remaining following consideration of spacing, form, and defect; no special attention to seed productive capacity
Clearcut	0.0	341 (36)	8.3 (23)	Full overstory removal	No trees with dbh ≥ 24 cm left remaining, regardless of species and vigor

Notes: Values are means and percent of uncut stands. Described by Wilm and Dunford (1948) and adapted from Alexander (1954).
† Includes trees with dbh ≥ 24 cm.
‡ Includes trees with dbh ≥ 9 cm.
§ More stems in the heavy thinning treatment and nearly equal basal area compared with the moderate thinning plots is due to a greater number of trees below merchantable size (dbh < 24 cm) occurring on the heavy thinning plots.

the control units (Buonanduci et al. 2020), and published height growth rates for seedling height growth (Shepperd 1993, Romme et al. 2005, Pelz et al. 2018).

Overstory (dbh ≥ 12 cm) and midstory trees (5 ≤ dbh < 12 cm) were considered live pre-outbreak if they were live post-outbreak (2018) or dead post-outbreak (snags or downed) with decay class ≤2 (i.e., loss of needles, small branches, and bark; Lutes et al. 2006). Dead trees with heavier signs of decay (decay class >2) were considered to have died prior to the outbreak due to slow wood decomposition rates (e.g., multiple decades to centuries) in high elevation lodgepole pine forests (Harvey 1986). To estimate and assign pre-outbreak dbh of live trees, we used growth rates (annual dbh increment) derived from repeat measurements of tagged trees (dbh range 5.5–69.7 cm) within the 2-ha control units in 2004 and 2018 (Buonanduci et al. 2020) to develop species-specific models describing growth as a function of dbh (Appendix S1: Table S2). We used these growth rate models to assign pre-outbreak dbh for all overstory and midstory trees based on their 2018 dbh measurement. Trees dead in 2018 but considered live in 2004 (based on decay class) were assigned a pre-outbreak dbh equal to their 2018 measurement.

All (live and dead) saplings (dbh < 5 cm, height ≥ 1.40 m) measured in 2018 were considered live pre-outbreak. All dead saplings were included to account for uncertainty surrounding time of tree death. To determine pre-outbreak dbh of live trees, growth rates were assigned using the models developed for overstory and midstory trees. Saplings dead in 2018 were given a pre-outbreak dbh equal to their 2018 measurement. Seedlings (height 0.10–1.39 m) were considered live pre-outbreak if dead in 2018, or live and at least 0.10 m tall prior to the outbreak. To determine pre-outbreak height

of live seedlings, we accounted for growth between 2004 and 2018 using published height measurements (Appendix S1: Table S2). We subtracted these growth totals from our 2018 measurements to determine which observed live trees would have met our measurement threshold (height ≥ 0.10 m) to be considered live pre-outbreak.

To determine which lodgepole pine trees were susceptible to MPB at the time of the outbreak, we identified 12 cm dbh as the size cutoff below which the trees were not considered susceptible to attack. This cutoff is similar to published thresholds (e.g., 15 cm, Shore and Safranyik 1992; 10 cm, Safranyik and Carrol 2006) and accounted for 96% of observed MPB-killed trees in our study. Overstory trees with pre-outbreak (2004) dbh ≥ 12 cm that were live in 2018, or dead with signs of MPB and decay class ≤2, were considered to be susceptible to MPB. Based on growth rates, this included live trees with post-outbreak (2018) dbh ≥ 14.4 cm. Decay class 3 dead trees (i.e., most bark missing, limb stubs only, sapwood sound) with signs of MPB represented 4% of observed MPB-killed trees but were excluded from the susceptible tree pool for consistency.

Statistical analysis

Q1—Testing effects of historical thinning intensity on resistance at two spatial scales.—To test whether historical thinning affected resistance to MPB, we specified generalized linear mixed effects models predicting survival of susceptible lodgepole pine at each spatial scale (tree and stand). Models were designed to reflect the study design using nested predictors: dbh within TSI within major treatment. Block was included as a random effect for each model to account for potential variations in conditions across treatment blocks.

1. Tree scale.—To test the effects of historical thinning intensity on tree-scale survival probability for susceptible individual lodgepole pine trees (i.e., resistance), we used a logistic regression model. The binary response (killed by MPB, 0 vs. survived, 1) was modeled using a Bernoulli distribution, and major treatment, TSI thinning, and dbh terms were treated as nested fixed effects. Relative to the control, a positive coefficient would indicate increased resistance (i.e., higher probability of survival), and a negative coefficient would indicate reduced resistance (i.e., lower probability of survival).

2. Stand scale.—To test the effects of historical thinning intensity on stand-scale survival proportion of susceptible lodgepole pine density and live basal area (i.e., resistance), we used beta regression models. The proportional response (0, 1) was modeled using a beta distribution, and major treatment and TSI thinning terms were treated as nested fixed effects. Relative to the control, a positive coefficient would indicate a increased resistance (i.e., higher survival proportion of susceptible-sized lodgepole pine density/basal area), and a negative coefficient reduced resistance (i.e., lower survival proportion of susceptible-sized lodgepole pine density/basal area).

Q2—Testing effects of historical thinning intensity on post-outbreak successional trajectories.—To test the effects of historical thinning on post-outbreak stand-scale successional trajectories, we examined live stand structure and the late-seral component across the different treatments.

1. Live stand structure.—To test differences in overall stand structure between historical thinning treatments and the control, we used generalized linear mixed effects models to compare pre-outbreak (2004) and post-outbreak (2018) mean live stem density (overstory, dbh ≥ 12 cm; midstory, 5 ≤ dbh < 12 cm; sapling, dbh < 5 cm; and seedling, height < 1.40 m), basal area, and QMD across treatments. Density was modeled using a negative binomial distribution and basal area and QMD were modeled using gamma distributions. Major treatment and TSI thinning terms were treated as nested fixed effects. To assess differences in size structures among treatments, we estimated diameter distributions for all live trees (height ≥ 1.40 m) pre-outbreak and post-outbreak by treatment, using smoothed kernel density estimation for display. Changes in the shape of diameter distributions as a function of thinning and/or outbreak were assessed among treatments (thinning treatments vs. control for both pre-outbreak and post-outbreak periods) and within treatments (post-outbreak vs. pre-outbreak for each treatment). To statistically compare distributions, we used two complementary approaches: a two-sample Kolmogorov–Smirnov (K-S) test (Smirnov 1939) and a departure index. The K-S test

robustly detects a difference between distributions but does not describe information of ecological relevance, such as the direction (right [larger] vs. left [smaller] shift), magnitude (extent), or location (position on horizontal axis) of the difference. To supplement this, we calculated a departure index, M (Menning et al. 2007):

$$M = \left(\frac{2}{k-1}\right) \sum_{i=1}^{k} \left[\left(\frac{\hat{f}_i}{n_{\hat{f}}} - \frac{f_i}{n_f}\right)(k+1-i)\right]$$

where k is the number of bins (i.e., dbh size classes, 1 cm wide), f_i is the count of trees in bin i, n_f is the total number of trees in the test distribution (i.e., thinning treatments [among-treatment change], post-outbreak [within-treatment change]), and $\hat{f}_i$ and $n_{\hat{f}}$ represent these values for the reference distribution (i.e., control [among], pre-outbreak [within]). Sign and magnitude of M indicate the direction (negative, left-shifted; positive, right-shifted) and distance of shift in the test distribution compared with the reference distribution. Minimum and maximum values of M indicate the range endpoints in the departure index, determined by the symmetry of the reference distribution (−1 to +1 for normal or uniform distributions; absolute range of 2 for all distributions), and provide information on the location of difference. This index is well behaved, standardized, and insensitive to the number of bins in a histogram (Menning et al. 2007).

2. Late-seral component.—To account for the dominance of lodgepole pine on distribution trends, we also examined the influence of historical thinning on structure of the late-seral, shade-tolerant conifer species component within each stand. We combined observations of subalpine fir and Engelmann spruce (referred to as spruce–fir) to represent the late-seral species component. We compared the spruce–fir proportion of the post-outbreak (2018) total live stem density and basal area by size class (all, overstory, midstory, sapling, and seedling) across treatments using mixed effects beta regression models. The proportional response (0, 1) was modeled using a beta distribution with major treatment and TSI thinning terms treated as nested fixed effects. Relative to the control, a positive coefficient would indicate a shift toward late-seral structure (i.e., higher spruce–fir proportion of density or basal area), and a negative coefficient would indicate a shift toward early-seral structure (i.e., lower spruce–fir proportion of density or basal area).

We report individual P-values for all statistical tests, and interpret significance via strength of evidence of a difference based on the following α-levels: strong ($P < 0.01$), moderate ($P < 0.05$), and suggestive evidence ($P < 0.1$). We used this approach to reduce the risk of missing ecologically significant effects due to our modest sample size (i.e., type II error). Analyses were conducted in R (R Core Team 2020) using packages

lme4 (Bates et al. 2015) and *glmmTMB* (Brooks et al. 2017) for model fitting, and *jtools* (Long 2020) for model visualization.

<div align="center">RESULTS</div>

Across all stands, 59% (515 of 874) of stems and 78% of basal area of susceptible lodgepole pine trees were killed by MPB in the recent outbreak. MPB-killed susceptible lodgepole pine trees ranged in diameter from 12.0 to 47.8 cm (mean = 24.3, median = 23.3) and were generally smaller in diameter in historically thinned treatments than the control. Surviving susceptible lodgepole pine trees ranged in diameter from 12.0 to 36.6 cm (mean = 15.9, median = 14.9) and were similar in diameter across treatments (Appendix S1: Table S3).

Historical treatment effects on resistance

Overall, we found little evidence of a legacy effect of historical thinning increasing resistance of susceptible lodgepole pine to the recent MPB outbreak at either scale tested. At the individual tree scale, tree diameter (dbh) was the strongest predictor of survival, having a strong negative effect across all treatments ($P < 0.001$; Fig. 1a). Regardless of historical treatment in the stand within which a tree existed, probability of survival for susceptible lodgepole pine trees declined with increasing dbh and did not differ from the control in any treatment ($P = 0.103$–0.891; Fig. 1b). Across treatments, mean predicted survival probability was <50% for trees larger than 18 cm dbh, <10% for trees larger than 26 cm dbh, and <1% for trees larger than 35 cm dbh (Fig. 1a).

At the stand scale, with the exception of treatments with the highest thinning intensities (heavy+TSI or clearcut treatments), we found no evidence that historical thinning had an effect on resistance to MPB outbreak. Survival proportion for susceptible trees by density was greater than the control (~30%) only within the heavy+TSI (~55%, $P = 0.064$) and clearcut (~60%, $P = 0.022$) thinning treatments (Fig. 2). For basal area, effects were similar: survival proportion was greater than the control (~20%) for the heavy+TSI (~35%, $P = 0.036$), clearcut (~50%, $P = 0.003$), and clearcut +TSI (~35%, $P = 0.051$) thinning treatments (Fig. 2). For both analyses, there was no evidence of an additional effect of TSI within the main treatment. One exception was for the heavy treatment where the survival proportion by both stem density and basal area were 15–25% greater in the heavy treatment with TSI (~55% and ~35%, respectively) than without TSI (~30% and ~20%, respectively) ($P = 0.060$; Fig. 2).

Historical treatment effects on pre- and post-outbreak successional trajectories

Pre-outbreak.—Overall, we found strong evidence that the legacy of historical thinning treatments persisted for ~60 yr until the beginning of the MPB outbreak, and that these treatments modified post-outbreak stand successional trajectories. Prior to the MPB outbreak, overall live stand structure and diameter distributions differed among historically thinned and uncut stands. Historically thinned stands generally had greater pre-outbreak (2004) live midstory ($5 \leq \text{dbh} < 12$ cm; $P \leq 0.001$) and sapling stem densities (dbh < 5 cm; $P = 0.001$–0.033) than the control for all species combined, primarily driven by lodgepole pine (Fig. 3a, Table 2). Pre-outbreak live overstory (dbh ≥ 12 cm; $P = 0.099$–0.811) and seedling (height < 1.4 m; $P = 0.101$–0.963) densities were similar between most historically thinned and uncut stands (Table 2). Pre-outbreak live basal area was also similar for most treatments for all species combined ($P = 0.016$–0.943; Fig. 4 a) and individually ($P = 0.029$–0.904; Fig. 4c), although the relative sizes of contributing trees differed among thinned and uncut stands. Pre-outbreak live QMD was ~33% lower in historically thinned stands than the control for all species combined ($P = 0.003$; Fig. 4e). Trends in pre-outbreak live QMD were largely driven by a reduction in QMD for lodgepole pine in the heaviest historical thinning treatments while there were no consistent trends for either late-seral species (Fig. 4g). Aspen was absent or sparsely represented in all treatments, with the exception of clearcut stands in which it was still a minor component compared with the conifer species (Table 2). Shapes of pre-outbreak total live tree diameter distributions in historically thinned stands were left-shifted (i.e., fewer large and more small trees) compared with the control ($P < 0.001$; Fig. 3a). Shifts were dominated by lodgepole pine and differed from the control with similar magnitudes across levels of historical thinning (Fig. 3a).

Post-outbreak.—From pre- to post-outbreak, some differences in overall live stand structure between historically thinned stands and control stands either persisted or emerged, while differences in the shape of live diameter distributions were diminished. Most historically thinned stands had greater post-outbreak (2018) live overstory ($P \leq 0.001$–0.162), midstory ($P \leq 0.001$–0.148), and sapling ($P = 0.023$–0.299) stem density than the control for all species combined, driven by lodgepole pine (Fig. 3b, Table 2). Post-outbreak live seedling stem density was similar between historically thinned and uncut stands across species ($P = 0.205$–0.798; Table 2). Unlike pre-outbreak stand structure (Fig. 4a), post-outbreak live basal area was ~2–3 times greater in historically thinned stands than in the control for all species combined ($P \leq 0.001$–0.027; Fig. 4b). These differences were, in part, driven by greater post-outbreak lodgepole pine basal area in heavier historical thinning treatments relative to the control (Fig. 4d) and by greater post-outbreak subalpine fir basal area in the lighter historical thinning treatments relative to the control (Fig. 4d). In contrast, post-outbreak live tree QMD did not differ
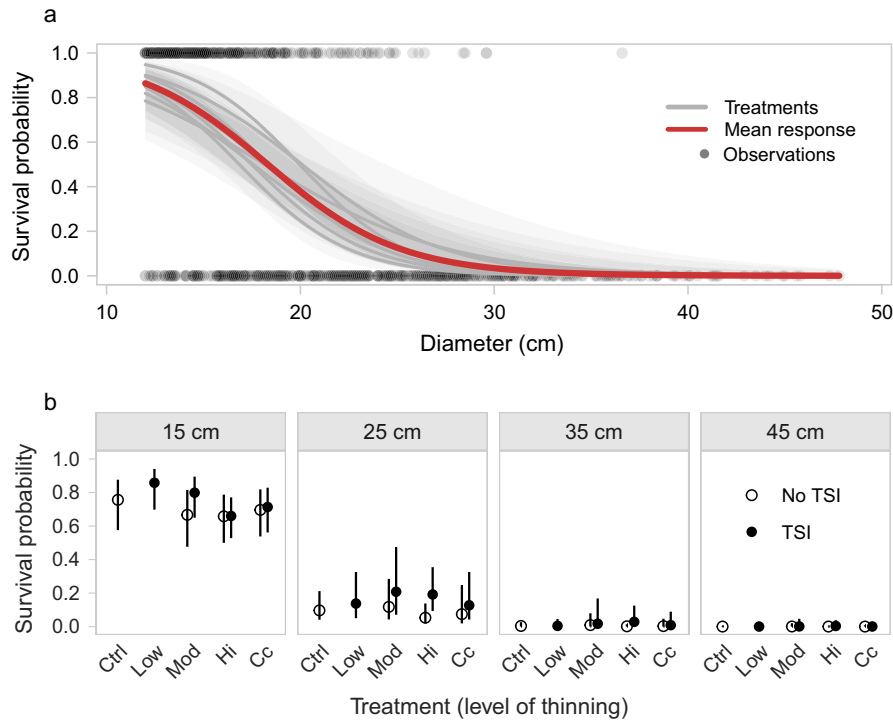
FIG. 1. Modeled effects of tree diameter and thinning intensity on tree-scale survival probability for susceptible lodgepole pine trees (pre-outbreak dbh ≥ 12 cm). (a) Predicted overall effect of diameter on survival probability. Semi-transparent points are individual observations of tree survival (1) or mortality (0). Gray lines are predicted mean response for each individual thinning treatment with shaded 95% confidence intervals. Red line isolates the overall mean effect of diameter across treatment responses. (b) Effects of thinning treatment intensity on survival probability at discrete diameter values (distributed evenly across the observed range). Treatments increase in level of thinning from left to right (Ctrl, control; Low, light; Mod, moderate; Hi, heavy; Cc, clearcut). Circles are predicted probabilities with 95% confidence intervals. Closed circles are thinning plus timber stand improvement (TSI), and open circles are thinning treatments without TSI. See Appendix S1: Table S4 for model output.

between historically thinned stands and the control for all species combined ($P = 0.213$–0.993; Fig. 4f)—the net result of greater QMD for both late-seral conifer species and lower QMD for lodgepole pine across multiple historically thinned treatments compared with the control (Fig. 4h). Whereas total live tree density differed among thinned and uncut stands (Table 2), the shapes of post-outbreak live tree diameter distributions in historically thinned stands (excluding moderate; $P = 0.029$) were similar to the control for all species combined ($P = 0.190$–0.760; Fig. 3b). Species-specific post-outbreak live tree distributions were similar to the control for most historically thinned stands, although leftward shifts in lodgepole pine and rightward shifts in late-seral conifers were evident for some treatments (Appendix S1: Table S7).

Live stand structure changed from pre-outbreak to post-outbreak in all stands. Across all treatments, proportional change in total live density was negative for overstory, midstory, and sapling trees, and positive for seedlings (Table 2). The greatest proportional change in total live density occurred in saplings for historically thinned stands (16–40% decrease) and in overstory trees

for the control (57% decrease; Table 2). Density changes in overstory trees differed in direction between lodgepole pine (negative) and late-seral conifers (positive), while change in saplings (negative) and seedlings (positive) was consistent across all species (Table 2).

Post-outbreak total live tree diameter distributions differed ($P \leq 0.004$) in shape from pre-outbreak distributions for all stands except moderate thinning ($P = 0.260$; Fig. 3c). Compared with the control, historically thinned stands showed lower magnitudes of change in the shapes of total tree diameter distributions, and most (excluding light+TSI and heavy) differed in direction of change from the control (Fig. 3c). Post-outbreak total live tree diameter distributions in historically thinned stands had fewer small and more large trees than before the outbreak (rightward shift due to tree growth), while post-outbreak distributions in control stands had more small and fewer large trees than before the outbreak (leftward shift due to mortality). Shifts were dominated by lodgepole pine; all stands, exclusive of clearcut+TSI, had leftward shifts in diameter distributions of live lodgepole pine trees, although the magnitude of change was lower in historically thinned stands
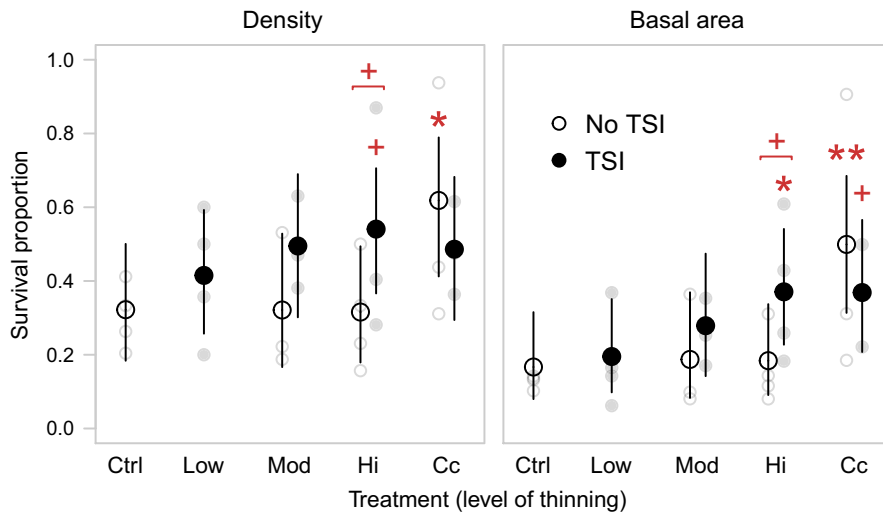
FIG. 2. Predicted effects of thinning intensity on stand-scale survival proportion of stem density (left) and basal area (right) for susceptible lodgepole pine (pre-outbreak dbh ≥ 12 cm). Treatments increase in level of thinning from left to right (Ctrl, control; Low, light; Mod, moderate; Hi, heavy; Cc, clearcut). Gray points are observed survival proportion for each plot replicate. Black circles are predicted mean proportions with 95% confidence intervals. Confidence intervals reflect only the variance of the fixed effects. Closed circles are thinning plus timber stand improvement (TSI), and open circles are thinning treatments without TSI. Asterisks indicate strength of evidence of a difference from the control according to $P < \alpha = 0.01^{**}$ (strong), 0.05^* (moderate), 0.1^+ (suggestive). Brackets correspond to differences between main thinning treatments with and without TSI. See Appendix S1: Table S5 for model output.

compared with the control (Appendix S1: Table S7). All stands were characterized by a reduction in live susceptible diameter (dbh ≥ 12 cm, gray dashed line) lodgepole pine compared with pre-outbreak (Fig. 3c). Change in the diameter distribution of lodgepole pine in the control was dominated by mortality of these susceptible trees, whereas change in the thinned treatments was dominated by mortality of trees in smaller diameter size classes (dbh < 12 cm; Fig. 3c). Diameter distributions of live late-seral conifer species were right-shifted for most stands following the outbreak, with clearcut and clearcut+TSI treatments showing the greatest magnitudes of change (Appendix S1: Table S7). Aspen diameter distributions displayed right shifts for both clearcut treatments (Appendix S1: Table S7).

Historical thinning had little effect on post-outbreak dominance of late-seral species relative to overall composition. Post-outbreak spruce–fir proportion of live stem density and basal area did not differ from the control ($P = 0.159\text{--}0.990$), except in treatments with the highest thinning intensities (heavy, heavy+TSI, clearcut +TSI; $P = 0.004\text{--}0.037$), in which the relative dominance of spruce–fir saplings was ~50% lower (Fig. 5). For density and basal area, we found no evidence of an additional effect of TSI ($P = 0.217\text{--}0.985$; Fig. 5).

DISCUSSION

Understanding the legacy of past management actions on forest resilience to disturbance is important as disturbance activity increases with warming climate. Long-

term experimental studies that allow for testing the effects of past management are rare, but offer critical insight into the longevity of management treatments. By exploring the effects of thinning on forest resilience to bark beetle outbreak over a temporal scale comparable with a typical outbreak return interval, our study addresses key research priorities for managing bark beetle impacts on forest ecosystems (Morris et al. 2017). Our finding that historical thinning treatments had a limited dampening effect on the severity of a MPB beetle outbreak ~60 yr later highlights challenges with promoting long-term resistance to disturbance. However, the effects of historical thinning treatments on directing post-outbreak stand trajectories provide important insights for informing forest management decisions in the face of increasing potential for bark beetle outbreaks.

Historical stand-thinning treatments fostered little to no resistance to MPB outbreak

Counter to our expectations, we found limited support for increased tree-scale resistance following thinning ~60 yr prior to outbreak, highlighting the importance of individual tree size in regulating resistance to MPB. MPB exhibit strong preference for larger trees (Björklund and Lindgren 2009) due to the positive relationship between tree diameter and phloem thickness. Thicker phloem allows greater MPB brood production, reduced larval intraspecific competition, and faster beetle development (Amman and Cole 1983).
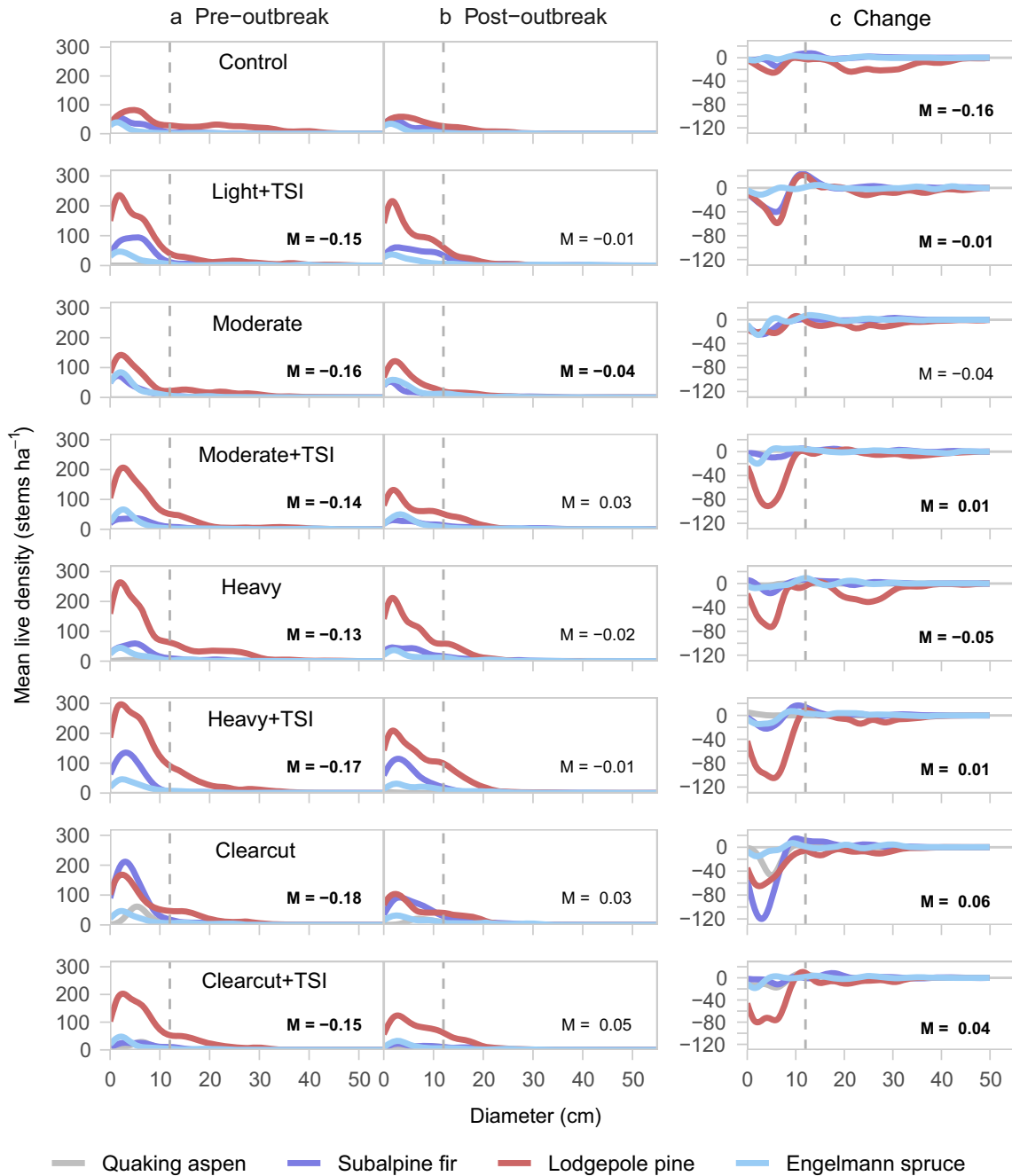
FIG. 3. Stand-scale mean diameter distributions of live trees (height ≥ 1.4 m) (a) pre-outbreak (2004) and (b) post-outbreak (2018), and (c) subsequent change in distributions for each thinning treatment intensity. Lines are kernel-smoothed stem density for each species averaged across plot replicates (*n* = 4 for control, light, and each heavy treatment; *n* = 3 for each moderate and clearcut treatment). Dashed vertical lines are the diameter threshold (dbh ≥ 12 cm) for lodgepole pine tree susceptibility to MPB. Departure index values (*M*) are reported for total density distributions compared among treatments (i.e., thinning vs. control; a, b) and within treatments (i.e., post-outbreak vs. pre-outbreak; c). Bold values indicate significant (*P* < 0.1) departures according to K-S tests. See Table 2 for summary statistics and Appendix S1: Table S7 for species-specific quantitative analyses.

Our modeled probabilities of survival were similar to other studies that documented low (<50%) susceptibility to MPB attack for trees below 20 cm dbh and high (near 100%) susceptibility above 30 cm dbh (Roe and Amman 1970, Negrón 2019, Buonanduci et al. 2020). For trees of intermediate diameter (15–25 cm dbh),

Table 2. Stand density and species composition of live trees (height ≥ 0.1 m) pre-outbreak (2004) and post-outbreak (2018).

Species	Overstory (dbh ≥ 12 cm)			Midstory (5 ≤ dbh < 12 cm)			Saplings (dbh < 5 cm)			Seedlings (height < 1.4 m)		
	Pre	Post	P(Δ)	Pre	Post	P(Δ)	Pre	Post	P(Δ)	Pre	Post	P(Δ)
Total												
Control	684 (109)	293 (13)	−0.57	540 (94)	425 (82)	−0.21	1,353 (327)	1,145 (323)	−0.15	1,005 (296)	7,420 (3,169)	6.38
Light+TSI	548 (53)	497 (112)	−0.09	1,258 (226)	1,067 (163)	−0.15	3,120 (691)	2,625 (672)	−0.16	1,156 (111)	7,186 (2,075)	5.22
Moderate	640 (34)	402 (86)	−0.37	742 (88)	635 (65)	−0.15	2,709 (638)	2,198 (562)	−0.19	2,457 (813)	13,333 (2,546)	4.43
Moderate+TSI	708 (133)	652 (147)	−0.08	1,230 (219)	924 (64)	−0.25	3,231 (434)	2,286 (256)	−0.29	893 (258)	16,035 (4,737)	16.95
Heavy	799 (72)	536 (111)	−0.33	1,118 (243)	922 (181)	−0.17	2,929 (611)	2,380 (529)	−0.19	1,022 (214)	6,600 (2,514)	5.46
Heavy+TSI	778 (78)	697 (152)	−0.10	1,641 (316)	1,313 (354)	−0.20	4,068 (911)	3,139 (963)	−0.23	988 (300)	4,305 (966)	3.36
Clearcut	793 (74)	754 (215)	−0.05	1,649 (545)	1,218 (468)	−0.26	4,650 (1,493)	2,782 (761)	−0.40	960 (431)	14,740 (11,191)	14.35
Clearcut+TSI	742 (94)	669 (138)	−0.10	1,462 (226)	1,054 (45)	−0.28	3,300 (433)	2,193 (501)	−0.34	536 (215)	6,052 (4,637)	10.29
Lodgepole pine												
Control	621 (122)	208 (21)	−0.66	353 (84)	272 (93)	−0.23	726 (225)	574 (212)	−0.21	436 (130)	1,675 (616)	2.85
Light+TSI	395 (104)	276 (129)	−0.30	765 (322)	642 (284)	−0.16	1,955 (931)	1,697 (881)	−0.13	754 (100)	1,725 (440)	1.29
Moderate	510 (111)	204 (69)	−0.60	470 (108)	402 (117)	−0.14	1,409 (708)	1,206 (642)	−0.14	1,362 (980)	4,712 (2,735)	2.46
Moderate+TSI	521 (156)	408 (206)	−0.22	924 (275)	578 (145)	−0.37	2,275 (723)	1,427 (529)	−0.37	558 (236)	1,340 (584)	1.40
Heavy	689 (136)	353 (118)	−0.49	820 (311)	608 (241)	−0.26	2,131 (826)	1,663 (706)	−0.22	637 (260)	1,642 (509)	1.58
Heavy+TSI	667 (102)	514 (94)	−0.23	1,241 (268)	863 (154)	−0.30	2,783 (577)	1,952 (579)	−0.30	553 (250)	1,424 (662)	1.58
Clearcut	572 (172)	363 (40)	−0.37	606 (115)	374 (35)	−0.38	1,824 (217)	1,156 (280)	−0.37	223 (191)	916 (629)	3.10
Clearcut+TSI	623 (108)	453 (125)	−0.27	1,048 (186)	708 (130)	−0.32	2,377 (541)	1,535 (494)	−0.35	246 (183)	290 (191)	0.18
Subalpine fir												
Control	38 (16)	64 (26)	0.67	157 (70)	128 (67)	−0.19	426 (136)	379 (133)	−0.11	352 (129)	4,958 (2,941)	13.10
Light+TSI	94 (26)	149 (42)	0.59	404 (184)	349 (162)	−0.14	832 (284)	650 (202)	−0.22	302 (124)	4,858 (2,104)	15.11
Moderate	68 (43)	85 (43)	0.25	147 (91)	108 (70)	−0.27	617 (228)	420 (68)	−0.32	715 (285)	7,057 (2,335)	8.88
Moderate+TSI	113 (11)	153 (26)	0.35	204 (34)	204 (52)	0.00	456 (60)	405 (52)	−0.11	179 (81)	13,802 (4,833)	76.25
Heavy	68 (41)	106 (61)	0.56	221 (137)	230 (124)	0.04	490 (299)	464 (290)	−0.05	218 (153)	4,204 (2,776)	18.31
Heavy+TSI	47 (32)	85 (63)	0.82	285 (239)	319 (274)	0.12	960 (865)	905 (815)	−0.06	268 (224)	2,278 (990)	7.50
Clearcut	113 (64)	244 (127)	1.15	623 (381)	521 (348)	−0.16	1,993 (1,513)	1,102 (735)	−0.45	558 (491)	13,177 (11,251)	22.60
Clearcut+TSI	57 (28)	113 (64)	1.00	176 (79)	119 (39)	−0.32	321 (151)	253 (140)	−0.21	134 (77)	5,003 (4,189)	36.33
Engelmann spruce												
Control	26 (16)	21 (8)	−0.17	30 (15)	26 (5)	−0.14	202 (87)	193 (88)	−0.04	218 (74)	737 (179)	2.38
Light+TSI	55 (32)	72 (42)	0.31	89 (60)	77 (52)	−0.14	333 (251)	278 (211)	−0.17	101 (58)	603 (336)	5.00
Moderate	62 (40)	113 (82)	0.82	125 (108)	125 (116)	0.00	684 (467)	571 (371)	−0.16	380 (347)	1,563 (1,332)	3.12
Moderate+TSI	74 (74)	91 (74)	0.23	102 (51)	142 (82)	0.39	500 (272)	454 (245)	−0.09	156 (59)	871 (307)	4.57
Heavy	43 (28)	77 (40)	0.80	77 (40)	85 (53)	0.11	291 (173)	253 (157)	−0.13	168 (89)	402 (177)	1.40
Heavy+TSI	64 (37)	98 (70)	0.53	115 (98)	132 (115)	0.15	325 (280)	266 (227)	−0.18	168 (89)	503 (376)	2.00
Clearcut	91 (82)	125 (108)	0.37	130 (105)	142 (108)	0.09	410 (298)	343 (246)	−0.16	134 (77)	402 (201)	2.00

Live density (stems/ha) applies to the Midstory, Saplings, and Seedlings columns.

(*Continued*)

TABLE 2. Continued

Species	Overstory (dbh ≥ 12 cm)			Midstory (5 ≤ dbh < 12 cm)			Saplings (dbh < 5 cm)			Seedlings (height < 1.4 m)		
	Pre	Post	$P(\Delta)$	Pre	Post	$P(\Delta)$	Pre	Post	$P(\Delta)$	Pre	Post	$P(\Delta)$
Clearcut+TSI	51 (29)	74 (41)	0.44	57 (15)	91 (48)	0.60	342 (251)	269 (195)	−0.21	45 (45)	201 (139)	3.50
Quaking aspen												
Control	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	50 (50)	>0
Light+TSI	4 (4)	0 (0)	−1.00	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	0 (0)	—
Moderate	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	0 (0)	—
Moderate+TSI	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	22 (22)	>0
Heavy	0 (0)	0 (0)	—	0 (0)	0 (0)	—	17 (17)	0 (0)	−1.00	0 (0)	352 (352)	>0
Heavy+TSI	0 (0)	0 (0)	—	0 (0)	0 (0)	—	0 (0)	17 (17)	>0	0 (0)	101 (101)	>0
Clearcut	17 (17)	23 (23)	0.33	289 (289)	181 (181)	−0.37	423 (423)	181 (181)	−0.57	45 (45)	246 (246)	4.50
Clearcut+TSI	11 (11)	28 (28)	1.50	181 (173)	136 (128)	−0.25	260 (251)	136 (128)	−0.48	112 (112)	558 (558)	4.00

Notes: Values are mean (standard error) and proportional change [$P(\Delta)$] in mean. Dashes (—) indicate treatments having no observations in both pre-outbreak and post-outbreak time periods. >0 indicates positive change but no proportion value due to a zero denominator (no observations pre-outbreak). TSI, timber stand improvement. Bold and italicized values indicate suggestive ($P < 0.1$) or greater strength of evidence of a difference from the control according to generalized linear mixed effects models (see Appendix S1: Table S6 for model outputs). Models were not developed for quaking aspen due to lack of sufficient number of observations.

pre-outbreak growth rate and stand structure (density and host species proportion) at the tree neighborhood scale (i.e., 10 m radius from tree) can mediate tree-scale susceptibility to MPB outbreak (Buonanduci et al. 2020). We saw greater variability in survival probability within and among treatments for intermediate diameter trees (Fig. 1b) but found no significant differences among treatments. Therefore, potential thinning effects of increased vigor leading to greater tree-level resistance to MPB outbreak had eroded following >60 yr of stand development.

Limited support for differences in stand-scale resistance of susceptible lodgepole pine (density and basal area) to MPB between uncut and historically thinned stands suggested that the efficacy of thinning treatments can fade over multiple decades as the stands regrow. For example, intense thinning (total overstory removal; e.g., clearcut treatments) 1–25 yr prior to an outbreak has been effective at reducing MPB-caused tree mortality in stands of lodgepole pine (Cole et al. 1983, Vorster et al. 2017) and ponderosa pine (*Pinus ponderosa*) (Schmid and Mata 1992, Hood et al. 2016). In addition, less intense thinning (partial overstory removal; e.g., light, moderate, and heavy treatments) has been effective when conducted during (McGregor et al. 1987) or shortly prior to (8–10 yr; Whitehead and Russo 2005) an outbreak. Over longer time periods, partial overstory removal may be ineffective at increasing resistance due to stimulation of growth releases that allow remaining trees to reach susceptible diameters and come under stress due to competition with each other sooner than more heavily thinned stands (Mitchell et al. 1983). In addition to treatment timing relative to outbreaks, our finding of a stand-scale effect only in treatments that approximated a clearcut suggests a threshold of thinning intensity needed to foster MPB outbreak resistance. Pre-outbreak, the heaviest historical treatments in our study were the only stands below suggested thresholds for MPB outbreak resistance (Mata et al. 2003, Williams et al. 2018, Negrón 2019), with mean diameters of susceptible lodgepole pine trees smaller than 20 cm and no trees exceeding 40 cm diameter (Appendix S1: Table S3).

While perceived as a minor treatment in the 1940s, implementing TSI (removal of small-diameter trees after the main thinning treatment) may have important implications for amplifying or extending the longevity of treatment effects six decades later. In some cases, the effect of TSI was as strong as the overall thinning treatment, which focused on overstory trees. For example, 60 yr after implementation, the heavy thinning treatment without TSI (Fig. 6b) more closely resembled the control treatment (Fig. 6a) in pre-outbreak live stand structure and resistance to MPB outbreak, whereas the heavy thinning treatment with TSI (Fig. 6c) more closely resembled the clearcut treatment (Fig. 6d). The removal of some 9–24 cm dbh trees ~60 yr prior to outbreak, which were likely to be lodgepole pine based on stand
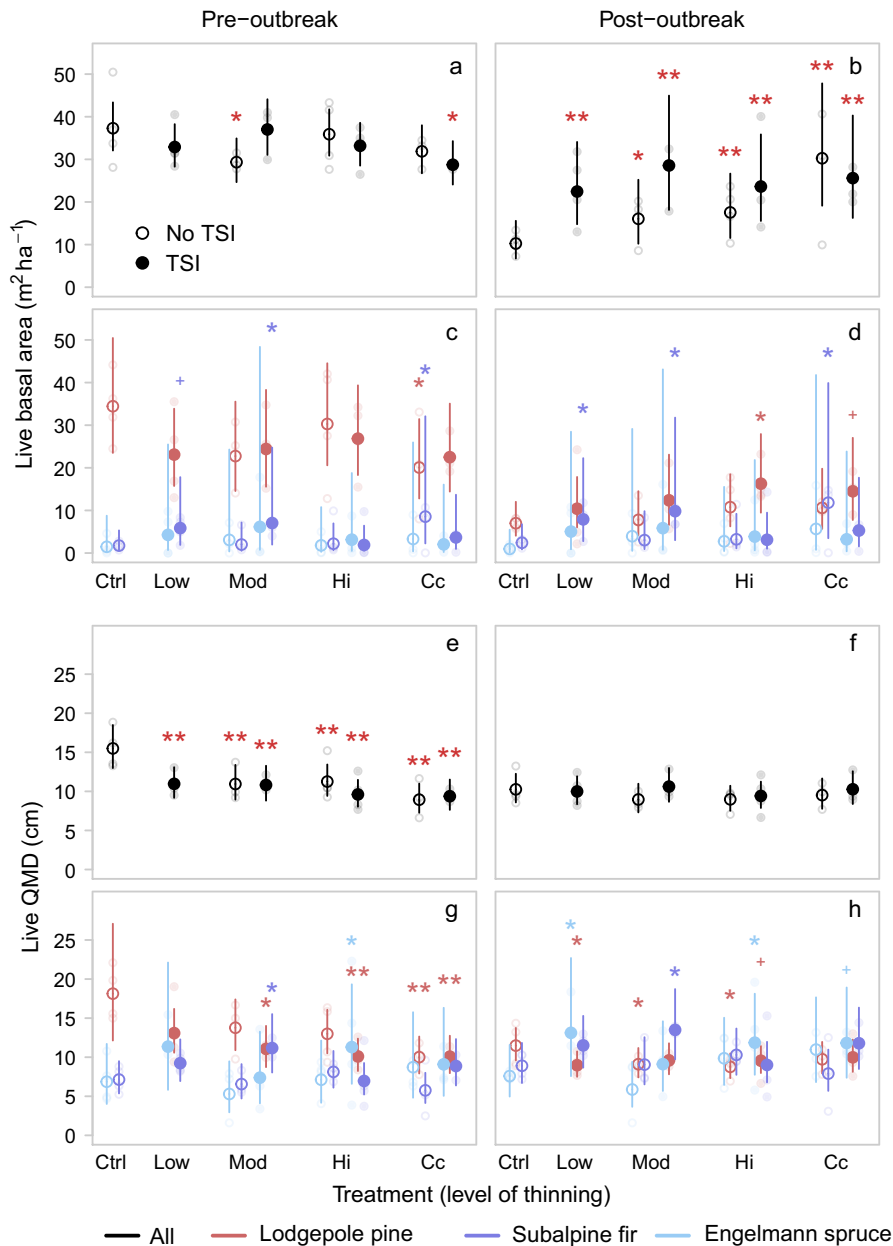
Fig. 4. Predicted effects of thinning intensity on stand-scale pre-outbreak (2004) and post-outbreak (2018) live basal area (a–d) and quadratic mean diameter (QMD, e–h) for all trees combined (a–b, e–f) and by individual species (c–d, g–h). Treatments increase in level of thinning from left to right (Ctrl, control; Low, light; Mod, moderate; Hi, heavy; Cc, clearcut). Semi-transparent points are observed mean values for each plot replicate. Opaque circles are predicted means with 95% confidence intervals. Closed circles are thinning plus timber stand improvement (TSI), and open circles are thinning treatments without TSI. Asterisks indicate strength of evidence of a difference from the control according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). See Appendix S1: Table S8 for model output.

development at time of treatment, resulted in a reduction of susceptible lodgepole pine trees for the recent outbreak. By thinning from below (i.e., removal of lower-canopy trees), TSI may enhance the effects of microclimate, tree vigor, and intertree spacing on reducing susceptibility of stands (Whitehead and Russo 2005, Coops et al. 2008, Fettig and Hilszczański 2015).

Historical stand-thinning treatments altered post-outbreak successional trajectories

Strong legacies of the 1940s treatments persisted for 60 yr until the start of the outbreak in the early 2000s. Overall, the strongest effects of historical thinning on pre-outbreak live stand structure were seen for lodgepole
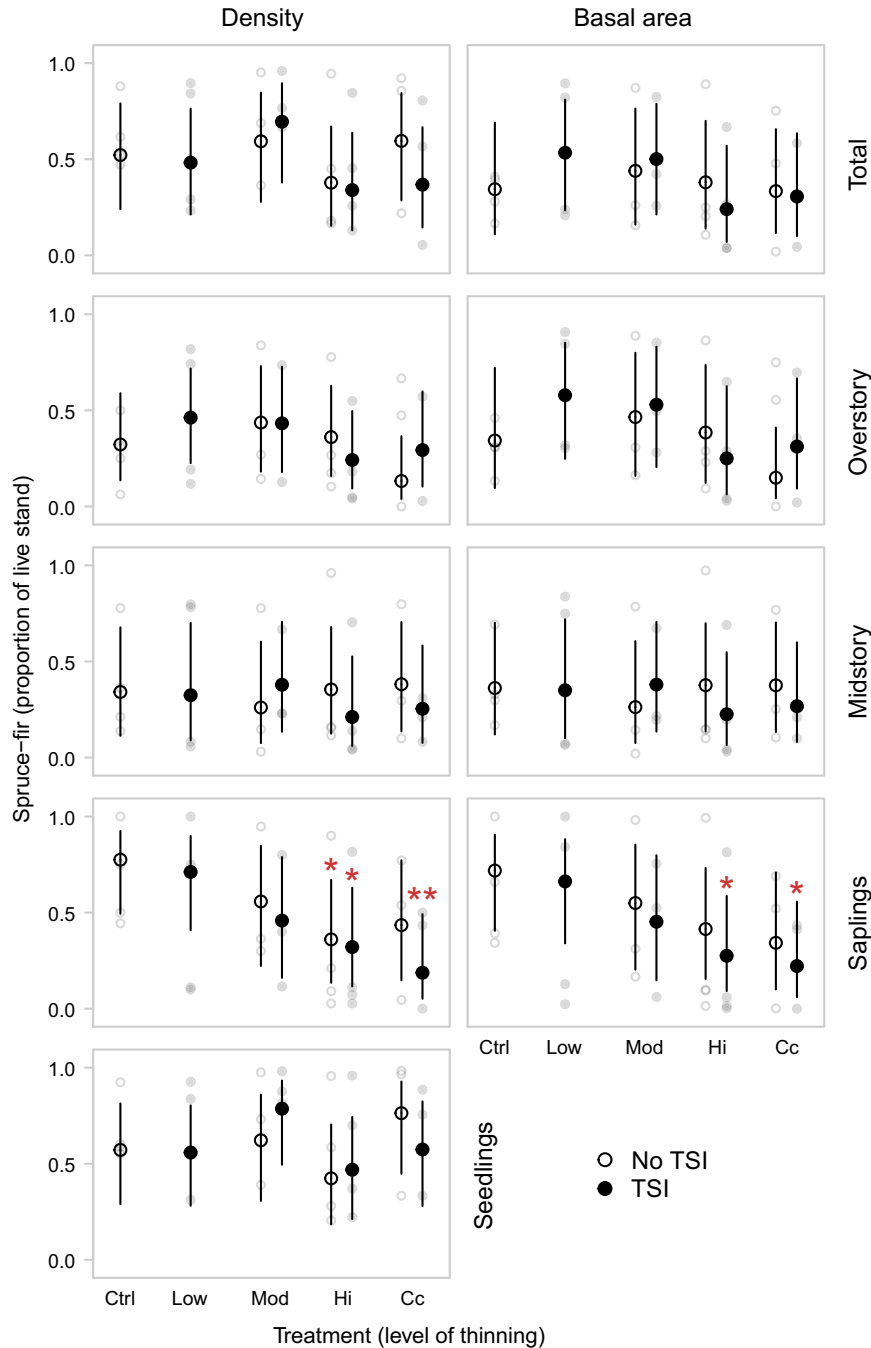
Fig. 5. Predicted effects of thinning intensity on stand-scale spruce–fir (S-F) proportion of post-outbreak (2018) live stem density (left) and basal area (right) combined for total, overstory (dbh ≥ 12 cm), midstory (5 ≤ dbh < 12 cm), sapling (dbh < 5 cm, height ≥ 1.4 m), and seedling (height 0.1–1.39 m) trees. Treatments increase in level of thinning from left to right (Ctrl, control; Low, light; Mod, moderate; Hi, heavy; Cc, clearcut). Semi-transparent points are observed proportion for each plot replicate. Opaque circles are predicted S-F proportions with 95% confidence intervals. Closed circles are thinning plus timber stand improvement (TSI), and open circles are thinning treatments without TSI. Asterisks indicate strength of evidence of a difference from the control according to $P < \alpha = 0.01^{**}$ (strong), 0.05^* (moderate). See Appendix S1: Table S9 for model output.

pine. This can be ascribed to stand age (~250 yr) at the time of thinning, at which stage merchantable-sized lodgepole pine was dominant and therefore the species most commonly removed (Wilm and Dunford 1948).

However, the MPB outbreak acted as a strong filter on diameter distributions and drove post-outbreak convergence in most live tree components of historically thinned and uncut stands. That is, most pre-outbreak

FIG. 6. Representative photographs of stand structure in uncut and thinned treatments post (2018) mountain pine beetle (*Dendroctonus ponderosae*) outbreak (2004) in subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests of the Fraser Experimental Forest, Colorado, USA. Treatments were conducted in 1940 (~60 yr prior to outbreak) and ranged from uncut control (a), to clearcut (d; removal of all trees with dbh ≥ 24 cm). Differences in structure as a result of timber stand improvement (TSI) are illustrated by the heavy treatment without TSI (b) and with TSI (c). Note the differences in abundance and spatial arrangement of live and dead vegetation, gap openings, and species composition among the different thinning treatments. Credit: J.E. Morris.

differences in the shape of live diameter distributions between historically thinned and control stands were diminished, although mechanisms of change varied. Our findings are consistent with shifts toward convergence in tree diameter and basal area among unharvested stands post-outbreak (Nelson et al. 2014), although we show that this can happen in harvested stands as well. Lodgepole pine distributions were shifted to the left (i.e., fewer large trees) while late-seral, non-MPB host species distributions were shifted to the right (i.e., more large trees), corresponding to dynamics controlling MPB behavior: beetle preference for large host trees and growth release of non-host species (Crotteau et al. 2019). Live diameter distributions changed following the outbreak for all stands, although the direction and dominant driver of change varied between historically thinned and control stands. Stands that were uncut or historically thinned at a lower intensity had left shifts in total diameter distributions following the outbreak (i.e., fewer large trees, mainly lodgepole pine), whereas the heavily thinned stands were shifted to the right (i.e., more large trees, mainly spruce and fir). This is likely to be from the dominance of MPB-induced mortality of large-diameter trees in uncut and lower intensity historically thinned stands, compared with the dominance of density-dependent mortality of small-diameter trees in historically heavily thinned stands.

Despite having little effect on stand-scale resistance of the susceptible tree population to MPB, legacies of historical thinning on the non-susceptible tree population strongly affected trajectories of post-outbreak live stand structure. At the stand scale, the greater the number of susceptible individuals removed from the population by the 1940s treatments, the less vulnerable the stand was to outbreak-induced changes in live density, basal area, and QMD. That is, the smaller the trees at the time of

outbreak (i.e., the more heavily the stands were thinned historically), the less change resulted from the outbreak. Relative to pre-outbreak, the lower post-outbreak live overstory, midstory, and sapling density, greater live seedling density, and lower live basal area we found are dynamics typical of MPB outbreaks in similar forests (Nelson et al. 2014, Perovich and Sibold 2016). However, compared with uncut stands, the magnitude of total change in these attributes of stand structure was less in historically thinned stands. These findings supported similar trends of lower MPB-induced tree mortality in thinned ponderosa pine stands when fewer susceptible individuals are present (Hood et al. 2016). Our finding of greater aspen density in clearcut treatments following the MPB outbreak supported the understanding that multiple severe disturbances favor regeneration of species with resprouting capabilities (Kulakowski et al. 2013, Pelz and Smith 2013, Hansen et al. 2016).

Contrary to our expectation, we found limited evidence to support our hypothesis that uncut stands would have accelerated successional trajectories post-outbreak compared with historically thinned stands. In mixed-species stands, MPB outbreaks shift forest structure toward greater diversity in species composition (Perovich and Sibold 2016, Pappas et al. 2020). Our findings in control stands supported this general trend, with decreases in live overstory density and basal area of lodgepole pine, increases in live understory density of all tree species, and an increase in live basal area of subalpine fir. However, as only the heaviest thinning treatments exhibited lower post-outbreak spruce–fir proportions of live stem density and basal area compared with the control, our findings suggest that thinning ~60 yr prior to outbreak had little effect on relative dominance of late-seral species in 2018. One explanation is that only the heaviest historical

thinning treatments created initial conditions (i.e., larger canopy gaps, more light) that favored regeneration of lodgepole pine over spruce or fir (Lotan and Perry 1983). Within the heaviest treatments, we found evidence of lower spruce–fir proportions of live stem density and basal area only within the sapling size class (dbh < 5 cm, established prior to outbreak). This may be due to the timing of our measurement post-outbreak (~8 yr) compared with the temporal scale over which successional dynamics operate (decades to centuries). Simulations based on post-outbreak regeneration suggest live basal area and density return to pre-outbreak levels in uncut and thinned stands within 80–105 yr, respectively; lodgepole pine remains the dominant overstory species in thinned stands for 100–150 yr post-outbreak, while subalpine fir becomes dominant in uncut stands (Collins et al. 2011). Therefore, regeneration of understory lodgepole pine trees following thinning in 1940 may only have had enough time to be evident in the sapling size class, whereas successional dynamics stimulated by the MPB outbreak are still developing. As post-outbreak stands continue to grow and regenerate, differences in live spruce–fir proportions among thinned and uncut stands in other size classes may emerge.

Management implications and directions for future research

Our findings have key implications for management of subalpine forests and point to several areas for future research. Little to no effect of thinning ~60 yr prior to outbreak on resistance of susceptible-sized trees to MPB suggests that maintaining long-term resistance to outbreak requires repeated heavy treatments (Mata et al. 2003, Ager et al. 2007). To keep susceptible basal area below a resistance threshold (~28 m^2/ha; Mata et al. 2003), stands may need thinning at frequencies resembling the lower range of the outbreak return interval (~25 yr; Mata et al. 2003) or at intensities approximating total overstory removal (although see Ager et al. 2007). Spatial scale and arrangement of treatments are also important for building stand resistance to MPB outbreak. Thinning can reduce tree mortality from MPB when conducted in small patches (0.1–7.0 ha; Johnson et al. 2014) and across large areas (10 ha; Negrón et al. 2017), but effectiveness may be reduced if thinned stands are surrounded by dense susceptible stands (Schmid and Mata 2005, Johnson et al. 2014). At watershed and regional scales, increasing spatial heterogeneity in size classes and host species abundance may impede outbreak spread (Chapman et al. 2012, DeRose and Long 2014, Nelson et al. 2014). However, broad-scale management operations are costly and unfeasible across the spatial extent of severe bark beetle outbreaks (DeRose and Long 2014). Incorporating our findings into simulation models could test possible effects of historical treatments across broader areas impacted by MPB, which could

provide insight into the spatial scale necessary for thinning to have a lasting effect on resistance.

Historical treatment legacies on post-outbreak stand structure and species composition—another component of resilience to MPB—suggest that thinning has implications for managing long-term stand successional trajectories. Increasing forest resistance to bark beetle outbreaks at the stand scale through intense thinning treatments may buy time in the short term, but eventually stands will again become susceptible to outbreaks (DeRose and Long 2014). Although clearcut and heavy+TSI treatments in our study were resistant to the recent (2000s) MPB outbreak, they are now characterized by relatively homogeneous composition that favors host species (e.g., greater basal area and density of live lodgepole pine trees) (Ager et al. 2007, Chapman et al. 2012). As such, they are likely to be susceptible to future (e.g., 2–3 decades later) MPB outbreaks sooner than uncut stands (Collins et al. 2011). However, greater potential in uncut stands for spruce and fir to replace lodgepole pine as the dominant species (Collins et al. 2011) may impact future susceptibility to other bark beetle outbreaks (e.g., spruce beetle [*Dendroctonus rufipennis*], western balsam bark beetle [*Dryocoetes confusus*]). Greater dominance by spruce and fir may also reduce the adaptability of stands to climate change due to lower drought tolerance (Perovich and Sibold 2016). Simulating post-outbreak dynamics further into the future could provide insights into thinning legacies that may emerge over longer time scales and allow managers to evaluate treatment efficacy under changing climate conditions.

Managing stands for resilience to MPB is likely to carry unintended consequences for the resilience of other components of stand structure and function. For instance, tree mortality from bark beetle outbreaks can adversely impact recreational safety, property values, and available harvestable timber (Flint et al. 2009), but can also support biodiversity (Winter et al. 2015), provide wildlife habitat via snags and downed wood (Saab et al. 2014), and facilitate biogeochemical cycling (Mikkelson et al. 2013). Therefore by removing potentially susceptible trees, thinning limits the recruitment of large snags and coarse woody debris, which can reduce post-outbreak wildlife habitat and total aboveground carbon storage (Donato et al. 2013b). Partial thinning may also increase stand vulnerability to windthrow (Alexander 1954, 1974). Furthermore, frequent thinning of subalpine forests at high intensity would, in many cases, represent a fundamental departure from the natural range of variability in stand structure, which is driven by relatively infrequent and severe disturbances (Peet 2000). Thinning and outbreaks also alter fuel profiles (i.e., abundance and spatial arrangement of biomass) in ways that interact with fire behavior (Jenkins et al. 2008, Simard et al. 2011, Collins et al. 2012, Hicke et al. 2012b), fire effects (Harvey et al. 2014a, b), and firefighting operations (Jenkins et al. 2012). Therefore, it is important to consider thinning for resilience to MPB

outbreak within the context of potential tradeoffs or synergies with other management goals (Fettig and Hilszczański 2015).

Conclusion

Promoting forest resilience to disturbance is an important priority for ecosystem management, with challenges arising in the context of global change and increasing disturbance activity. Historical silvicultural treatments followed by subsequent disturbance present an opportunity to empirically test hypotheses about fostering resilience of forests to future disturbances (Temperli et al. 2014, Hood et al. 2016, Crotteau et al. 2019) and address key uncertainties surrounding the longevity of treatment effects with respect to the typical disturbance return interval. We found that thinning treatments applied ~60 yr prior to a beetle outbreak were largely ineffective at increasing tree-scale resistance of susceptible-sized lodgepole pine to MPB, and only heavy thinning treatments (e.g., near or total overstory tree removal) promoted stand-scale resistance to MPB. Pre-outbreak differences in the shape of diameter distributions between thinned and uncut treatments were diminished by the MPB outbreak. However, historical thinning had lasting effects on post-outbreak successional trajectories, shifting understory sapling dominance toward early-seral lodgepole pine. Our findings highlight that managing for resistance against disturbances such as bark beetle outbreaks may be challenging, but treatments can have lasting effects on other components of resilience to disturbance.

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Supporting Information

Open Research