Cutting a course: examining the effects of historical thinning treatments on directing forest response to bark beetle outbreaks

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Abstract

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Bark beetle outbreaks are major natural disturbances in temperate forests across the northern hemisphere, contributing to extensive tree mortality and driving forest change. Recent widespread and severe outbreaks—and projected climate-driven changes to disturbance activity—have raised concerns about forest resilience and the interaction of future outbreaks with other disturbances (e.g., fire). Thinning (i.e., density reduction) treatments may promote resilience to bark beetles by fostering resistance or bolstering forest capacity to respond post outbreak, but opportunities to test treatment efficacy and longevity have been rare. Further, forest managers must consider the effects of thinning on additional objectives such as tradeoffs between fire hazard mitigation and carbon storage. Here, I used a replicated study of old-growth lodgepole pine stands thinned in 1940 and affected by a recent (early 2000s) severe mountain pine beetle outbreak to examine the effects of thinning on (1) components of resilience to outbreak, and (2) post-outbreak fire hazard and carbon storage. I measured stand structural attributes in the field ~8 years post-outbreak and compared resistance to beetle attack (tree- and stand-scale survival), successional trajectories, fuel profiles, and aboveground carbon biomass between uncut (control) and thinned treatment units. Thinning six decades prior to mountain pine beetle outbreak had limited effects on resistance, but additional effects of thinning on stand trajectories, surface and canopy fuel profiles, and aboveground carbon storage persisted following severe outbreak. This study broadens the temporal extent of our understanding of thinning effects on directing forest response to bark beetle outbreaks, with important implications for developing effective management decisions in the face of global change.

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INTRODUCTION

Natural disturbances are important drivers of forest dynamics worldwide (Turner 2010). Through relatively discrete events, disturbances shape forest patterns, processes, and trajectories across time and space by altering resource availability or the physical environment (Pickett and White 1985, Turner 2010). However, alteration of disturbance regimes by global climate change (Seidl et al. 2017) threatens ecosystem services (Seidl et al. 2016), biodiversity (Thom and Seidl 2016), and creates uncertainty about future ecosystem dynamics. In temperate forests, native bark beetles (Coleoptera: Curculionidae: Scolytinae) and wildfire are prominent disturbance agents projected to increase under warmer and drier climate conditions (Sommerfeld et al. 2018). Over the past three decades, bark beetle outbreaks and fires have affected tens of millions of hectares of forests in the Northern Hemisphere (Westerling 2016, Kautz et al. 2017), resulting in widespread tree mortality and subsequent alteration of forest structure, composition, and function (Bentz et al. 2009, McLauchlan et al. 2020). These disturbances and their potential interactions raise concerns about future forest resilience (i.e., ability to recover structure and function following disturbance; Walker et al. 2004) and maintenance of ecosystem services (Buma 2015, Johnstone et al. 2016, Stevens-Rumann et al. 2018, McWethy et al. 2019). Therefore, understanding, anticipating, and responding to the effects of increasing disturbance activity on forest dynamics remain major challenges for forest managers (Millar and Stephenson 2015).

Understanding the influence of forest management strategies on consequences of bark beetle outbreaks remains a key research priority (Morris et al. 2017). Thinning (i.e., density reduction) is a common management strategy for reducing bark beetle outbreak severity (Fettig and Hilszczanski 2015). Thinning may increase ecological resilience to outbreak by reducing the availability of susceptible host trees (Fettig et al. 2007) and altering post-outbreak successional trajectories through stimulation of advance regeneration (DeRose and Long 2014). Thinning may also reduce post-outbreak fire hazard by lowering abundance of canopy and coarse surface fuels, though not without tradeoffs for other management objectives such as carbon storage (Donato et al. 2013). Yet, the longevity of treatment effects is not well tested, particularly with respect to the typical beetle outbreak return interval (20–130 years; Jarvis and Kulakowski 2015). Previous studies exploring the effects of thinning on post-outbreak forest dynamics have focused on treatments applied post-outbreak (e.g., salvage logging; Collins et al. 2012, Donato et al. 2013), or shortly prior to outbreak (e.g., 5–25 years; Temperli et al. 2014, Hood et al. 2016). However, understanding the effects of pre-outbreak treatments, especially when applied decades prior to outbreak, on forest response remains an important knowledge gap.

This thesis addresses these knowledge gaps by examining past (1940s) silvicultural treatments affected by a subsequent (2000s) mountain pine beetle (*Dendroctonus ponderosae*) outbreak on subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) stands in the southern Rocky Mountains (Colorado, USA). Using detailed field measurements collected in permanent experimental plots, I empirically test the effects of historical stand-thinning treatments on directing forest response to mountain pine beetle outbreak. In Chapter 1, I reconstruct pre-outbreak stand structure to examine the influence of historical treatments on two components of resilience to outbreak: resistance and successional trajectories of live tree legacies. In Chapter 2, I develop comprehensive fuel profiles for each stand to examine the effects of historical treatments on post-outbreak fire hazard and aboveground carbon storage. This work helps fill critical research gaps concerning the relationship between disturbance and land use, and interactions among disturbances (Turner 2010).

REFERENCES

Bentz, B., J. Logan, J. MacMahon, C. D. Allen, M. Ayres, E. Berg, A. Carroll, M. Hansen, J. Hicke, L. Joyce, W. Macfarlane, S. Munson, J. Negron, T. Paine, J. Powell, K. Raffa, J. Regniere, M. Reid, W. Romme, S. J. Seybold, D. Six, D. Tomback, J. Vandygriff, T. Veblen, M. White, J. Witcosky, and D. Wood. 2009. Bark beetle outbreaks in western North America: Causes and consequences. University of Utah Press, Salt Lake City, UT.

Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15.

Collins, B. J., C. C. Rhoades, M. A. Battaglia, and R. M. Hubbard. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. Forest Ecology and Management 284: 260–268.

Donato, D. C., M. Simard, W. H. Romme, B. J. Harvey, and M. G. Turner. 2013. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. Forest Ecology and Management 303:160–174.

Fettig, C. J., K. D. Klepzip, R. F. Billings, A. S. Munson, T. E. Nebeker, J. F. Negron, and J. T. Nowak. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238:24–53.

Fettig, C. J., and J. Hilszczański. 2015. Chapter 14 – Management strategies for bark beetles in conifer forests. Pages 555–584 in F. E. Vega and R. W. Hofstetter, editors. Bark Beetles. Academic Press.

Hood, S. M., S. Baker, and A. Sala. 2016. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. Ecological Applications 26:1984–2000.

Jarvis, D. S., and D. Kulakowski. Long-term history and synchrony of mountain pine beetle outbreaks in lodgepole pine forests. Journal of Biogeography 42:1029–1039.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Kautz, M., A. J. H. Meddens, R. J. Hall, and A. Arneth. 2017. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Global Ecology and Biogeography 26:533–552.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, J. M. Varner, T. T. Veblen, S. A. Adalsteinsson, J. K. Balch, P. Baker, E. Batllori, E. Bigio, P. Brando, M. Cattau, M. L. Chipman, J. Coen, R. Crandall, L. Daniels, N. Enright, W. S. Gross, B. J. Harvey, J. A. Hatten, S. Hermann, R. E. Hewitt, L. N. Kobziar, J. B. Landesmann, M. M. Loranty, S. Y. Maezumi, L. Mearns, M. Moritz, J. A. Myers, J. G. Pausas, A. F. A. Pellegrini, W. J. Platt, J. Roozeboom, H. Safford, F. Santos, R. M. Scheller, R. L. Sherriff, K. G. Smith, M. D. Smith, and A. C. Watts. 2020. Fire as a fundamental ecological process: Research advances and frontiers. Journal of Ecology 108:2047–2069.

McWethy, D. B., T. Schoennagel, P. E. Higuera, M. Krawchuk, B. J. Harvey, E. C. Metcalf, C. Schultz, C. Miller, A. L. Metcalf, B. Buma, A. Virapongse, J. C. Kulig, R. C. Stedman, Z. Ratajczak, C. R. Nelson, and C. Kolden. 2019. Rethinking resilience to wildfire. Nature Sustainability 2:797–804.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Morris, J. L., S. Cottrell, C. J. Fettig, W. D. Hansen, R. L. Sherriff, V. A. Carter, J. L. Clear, J. Clement, R. J. DeRose, J. A. Hick, P. E. Higuera, K. M. Mattor, A. W. R. Seddon, H. T. Seppa, J. D. Stednick, and S. J. Seybod. 2017. Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. Journal of Applied Ecology 54:750–760.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, NY.

Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology 53:120–129.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Sommerfeld, A., C. Senf, B. Buma, A. W. D'Amato, T. Després, I. Díaz-Hormazábal, S. Fraver, L. E. Frelich, Á. G. Gutiérrez, S. J. Hart, B. J. Harvey, H. S. He, T. Hlásny, A. Holz, T. Kitzberger, D. Kulakowski, D. Lindenmayer, A. S. Mori, J. Müller, J. Paritsis, G. L. W. Perry, S. L. Stephens, M. Svoboda, M. G. Turner, T. T. Veblen, and R. Seidl. 2018.

Patterns and drivers of recent disturbances across the temperate forest biome. Nature Communications 9:4355.

Temperli, C., T. T. Veblen, S. J. Hart, D. Kulakowski, and A. J. Tepley. 2015. Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. Ecosphere 6:art231.

Thom, D., and R. Seidl. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews 91:760–781.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Walker, B., C. S. Holling, S. R. Carpenter, and A. P. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9:5.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B: Biological Sciences 371:1–10.

Chapter 1. DOES THE LEGACY OF HISTORICAL THINNING TREATMENTS FOSTER RESILIENCE TO BARK BEETLE OUTBREAKS IN SUBALPINE FORESTS?

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ABSTRACT

As the climate warms, promoting ecological resilience to increasing disturbance activity is a key management priority. Across the Northern Hemisphere, tree mortality from widespread and severe bark beetle outbreaks raises concerns about 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 forest 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- 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 susceptible trees and basal area that survived the outbreak did not differ from the control in historical thinning treatments, except for treatments that removed nearly all susceptible trees, where survival probability approximately doubled. Although resistance to MPB outbreak was largely unaffected by historical thinning, the legacy of treatments shifted dominance from large- to small-diameter lodgepole pine by the time of the outbreak, resulting in historically thinned stands with ~2x 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 in the heaviest historical thinning treatments, where sapling dominance of shade-tolerant, unsusceptible conifers was lower than control stands. After six decades, thinning treatments have minimal effect on resistance to bark beetle outbreaks, but leave persistent legacies in shaping post-outbreak 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 changes in disturbance regimes may increase the likelihood that forests will undergo changes in ecosystem state—including transition to non-forest—by altering regeneration success (e.g., Harvey et al. 2016, Stevens-Rumann et al. 2018, Turner et al. 2019, Coop et al. 2020) or environmental conditions that shape succession (e.g., 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 ecological 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, lowering stand density by removing low-vigor trees reduces resource competition, thus increasing defensive capacity (e.g., Fettig et al. 2007) or reproductive capacity (e.g., Flathers et al. 2016) of remaining trees. At the stand scale, alteration of structure (i.e., density, basal area, spatial arrangement), 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 towards 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 early 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, most 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. 2012a), water and nutrient cycling (Pugh and Gordon 2013, Mikkelson et al. 2013), wood products (Weed et al. 2013), and wildlife habitat (Saab et al. 2014). Further, spatial heterogeneity in stand structural conditions created by outbreaks may persist for decades, affecting future beetle infestations (e.g., Kashian et al. 2011, Hart et al. 2015). Severe bark beetle outbreaks are natural disturbances that have been documented throughout recent centuries (e.g., 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). Thus, consequences of recent outbreaks on forest structure and function and their likely changes in the future represent 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, Griffin et al. 2013, Donato et al. 2013b), during outbreak (e.g., Cole et al. 1983, McGregor et al. 1987), or with short periods (i.e., 5–25 years) between treatment implementation and outbreaks (e.g., 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 provide 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 years (Cole and Amman 1980, Taylor et al. 2006, Bentz et al. 2009, Axelson et al. 2009, Alfaro et al. 2010, Jarvis and Kulakowski 2015). Simulation studies can forecast predictions of thinning effects on forest dynamics into the future (e.g., Ager et al. 2007, Collins et al. 2011, 2012, Donato et al. 2013b, 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 test the effects of historical stand-thinning treatments on two components of forest resilience to bark beetles: resistance to outbreak and post-outbreak successional trajectories. Using a long-term replicated experimental study of old-growth lodgepole pine stands thinned in the mid-20th century that were subsequently affected by a severe MPB outbreak in the early 21st century (~60 years 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?

We expected historical thinning to increase resistance to MPB at tree and stand spatial scales compared to uncut stands (Q1). At the individual tree scale, resistance to beetle attack is affected by 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, suitable host abundance, and spatial heterogeneity; 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 spatial scales, we expected TSI would enhance effects of thinning on resistance due to removal of additional susceptible trees and further reductions in resource competition among remaining trees.

We also expected historical thinning to modify post-outbreak stand successional trajectories (Q2). Bark beetle outbreaks alter structural legacies by reducing live—and increasing dead—host tree basal area and density (Klutsch et al. 2011, Diskin et al. 2011) and shifting size and age distributions of host trees towards 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 to uncut 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 towards late-seral communities (Diskin et al. 2011, Kayes and Tinker 2012). Therefore, we expected uncut stands would have greater proportions that are 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 towards 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 meters (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 seedlings/saplings 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-year mean from 1981–2010) temperatures ranging from -7 degrees Celsius (°C) in January to 14°C in July, and an annual mean of 3°C (PRISM Climate Group 2012). Annual mean precipitation is 550 millimeters (mm), with two-thirds 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-year-old forest (Moir et al. Unpublished) where harvest-cutting units were established in 1938. Full details of the experiment are described by Wilm and Dunford (1948) but are summarized here (Table 1.1). Four replicates of five different thinning treatments were conducted on 2-ha (approx. 142 m by 142 m) treatment units arranged in a block design (20 total units; Appendix A: Fig. A.1). 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 centimeters (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 timber 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.

Table 1.1. Residual stand structure across treatment unit replicates following both thinning and subsequent timber stand improvement (TSI) treatments in 1940.

Treatment	Reserve volume† (m^3 ha^{-1})	Stem density‡ (stems ha^{-1})		Basal area‡ (m^2 ha^{-1})		Thinning method	Description
		Mean	(%)	Mean	(%)		
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[1]	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

[1] More stems in the heavy thinning treatment and nearly equal basal area compared to the moderate thinning plots is due to a greater number of trees below merchantable size (dbh < 24 cm) occurring on the heavy thinning plots.

In 2003 (63 years 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 years post-treatment and ~8 years post-outbreak) we measured post-outbreak stand structure within 0.25 ha (50 x 50 m) plots located in each thinning and TSI treatment combination (Appendix A: Fig. A.1). For treatment units thinned ~60 years 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 since 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 minimum buffer between plot and treatment unit boundaries (not including the additional 19 m isolation strip). The total number (n = 28) of replicate plots across each of the treatment categories was 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 A: Table A.1 for details). Plots ranged in elevation from 2,799 to 2,999 m and were positioned on northerly aspects with slopes ranging from 5.6 to 25.9 degrees.

Using established sampling design protocols (Simard et al. 2011, Donato et al. 2013a), 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. 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 x 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 x 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 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., some bark and small branches missing, no needles; 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 to 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 B). We used these growth rate models to assign pre-outbreak dbh for all overstory and midstory trees based on their 2018 dbh measurement. Trees that were 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 same 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 B). 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 time of 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 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 the 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.

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).

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 increased resistance (i.e., higher survival proportion of lodgepole pine density or basal area), and a negative coefficient would indicate reduced resistance (i.e., lower survival proportion of lodgepole pine density or basal area).

Q2: Testing the effects of historical thinning intensity on post-outbreak stand successional trajectories.

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

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 live pre- (2004) and post- (2018) outbreak mean 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- and post-outbreak by treatment, using smoothed kernel density estimation for display. Changes in diameter distributions as a function of thinning and/or outbreak were assessed among treatments (thinning treatments vs. control for both pre- and post-outbreak periods) and within treatments (post- 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 the direction (right [larger] vs. left [smaller] shift), magnitude (extent), or location (position on horizontal axis) of the difference—information of ecological relevance. 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]). The sign and magnitude of *M* indicate the direction (negative, left-shifted; positive, right-shifted) and distance of shift in the test distribution compared to 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).

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 trees (referred to as spruce-fir) to represent the late-seral species component. We then compared the spruce-fir proportion of the total live post-outbreak (2018) 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, and major treatment and TSI thinning terms were treated as nested fixed effects. Relative to the control, a positive coefficient would indicate shift towards late-seral structure (i.e., higher spruce-fir proportion of density or basal area), and a negative coefficient would indicate shift towards early-seral structure (i.e., lower spruce-fir proportion of density or basal area).

For all statistical tests, significance was assessed according to the 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 the packages *lme4* (Bates et al. 2015) and *glmmTMB* (Brooks et al. 2017) for fitting regression models, and *jtools* (Long 2020) for visualizing model predictions.

RESULTS

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 C: Table C.1).

Historical treatment effects on resistance

Overall, we found little to no evidence of a legacy effect of historical thinning increasing resistance 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 (Fig. 1.1A). Regardless of the 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 (Fig. 1.1B). Across treatments, the mean predicted survival probability was less than 50% for trees larger than 18 cm dbh, less than 10% for trees larger than 26 cm dbh, and less than 1% for trees larger than 35 cm dbh (Fig. 1.1A).

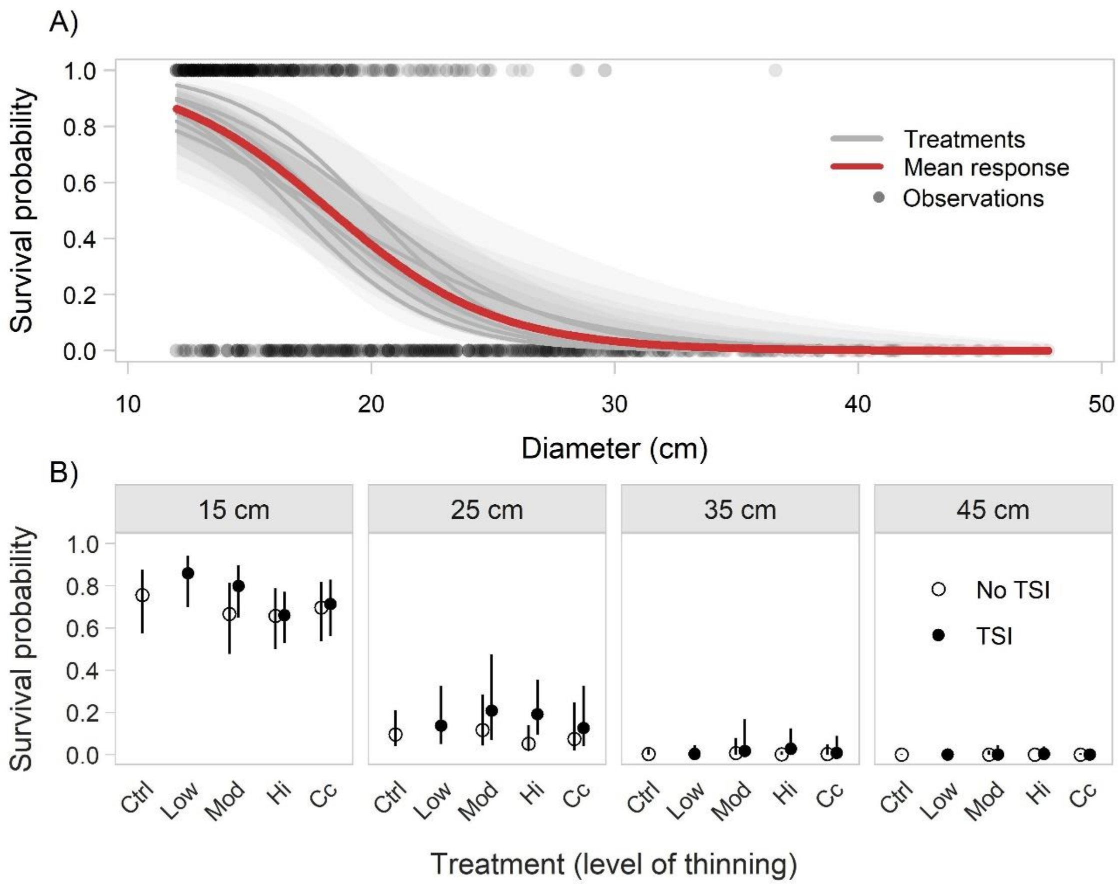

Figure 1.1. Modeled effects of tree diameter and thinning intensity on tree-scale survival probability for susceptible lodgepole pine trees (pre-outbreak dbh ≥ 12 cm). (A) Predicted overall effect of diameter on survival probability. Semi-transparent points represent individual observations of tree survival (1) or mortality (0). Gray lines represent 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 represent predicted probabilities with 95% confidence intervals. Closed circles represent thinning plus timber stand improvement (TSI), and open circles represent thinning treatments without TSI. See Appendix C: Table C.2 for model output.

At the stand scale, except for 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. 1.2). 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. 1.2). 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) ($P = 0.06$; Fig. 1.2).

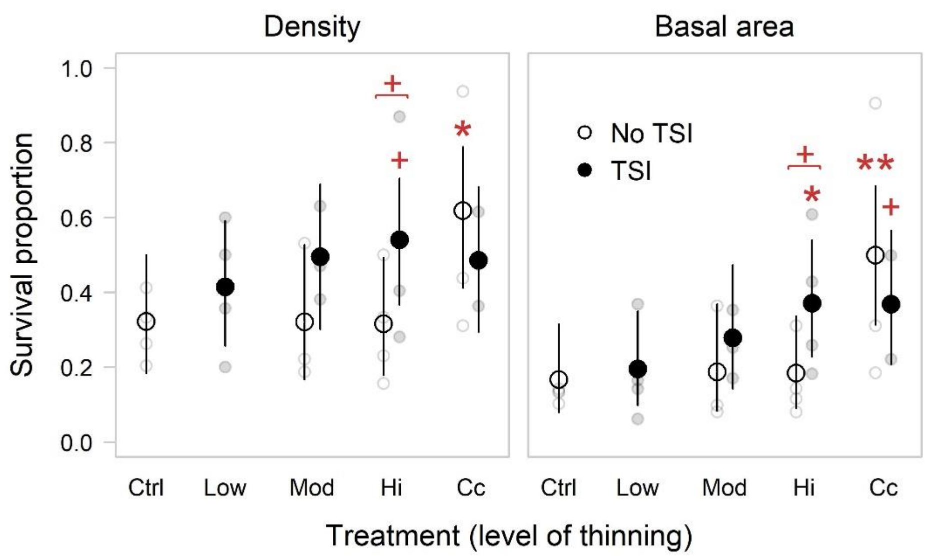

Figure 1.2. Predicted effects of thinning on stand-scale survival proportion of stem density (left) and basal area (right) for susceptible lodgepole pine (pre-outbreak dbh ≥ 12 cm). Treatments increase in intensity from left to right (Ctrl = control; Low = light; Mod = moderate; Hi = heavy; Cc = clearcut). Gray points are observed survival proportion for each plot replicate. Black circles are predicted mean proportions with 95% confidence intervals. Closed circles represent thinning plus timber stand improvement (TSI), and open circles represent 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 treatments with and without TSI. See Appendix C: Table C.3 for model output.

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 until the beginning of the MPB outbreak ~60 years later, 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 live pre-outbreak (2004) midstory ($5 \leq$ dbh < 12 cm) and sapling stem densities (dbh < 5 cm) than the control for all species combined, driven by lodgepole pine (Fig. 1.3A, Table 1.2). Live pre-outbreak overstory (dbh $\geq$ 12 cm) and seedling (height < 1.4 m) densities were similar between historically thinned and uncut stands (Table 1.2). Live pre-outbreak basal area was also similar between treatments for all species combined (Fig. 1.4A) and individually (Fig. 1.4C), though the relative sizes of contributing trees differed among thinned and uncut stands. Live pre-outbreak QMD was ~33% lower in historically thinned stands than the control for all species combined (Fig. 1.4E). Trends in live pre-outbreak 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. 1.4G). Aspen was absent or sparsely represented in all treatments, with the exception of clearcut stands in which it was still a minor component compared to the conifer species (Table 1.2). Pre-outbreak total live tree diameter distributions in historically thinned stands were left-shifted (i.e., fewer large and more small trees) compared to the control ($P <$ 0.001; Fig. 1.3A). Shifts were dominated by lodgepole pine and differed from the control with similar magnitudes across levels of historical thinning (Fig. 1.3A; Appendix D: Table D.2).

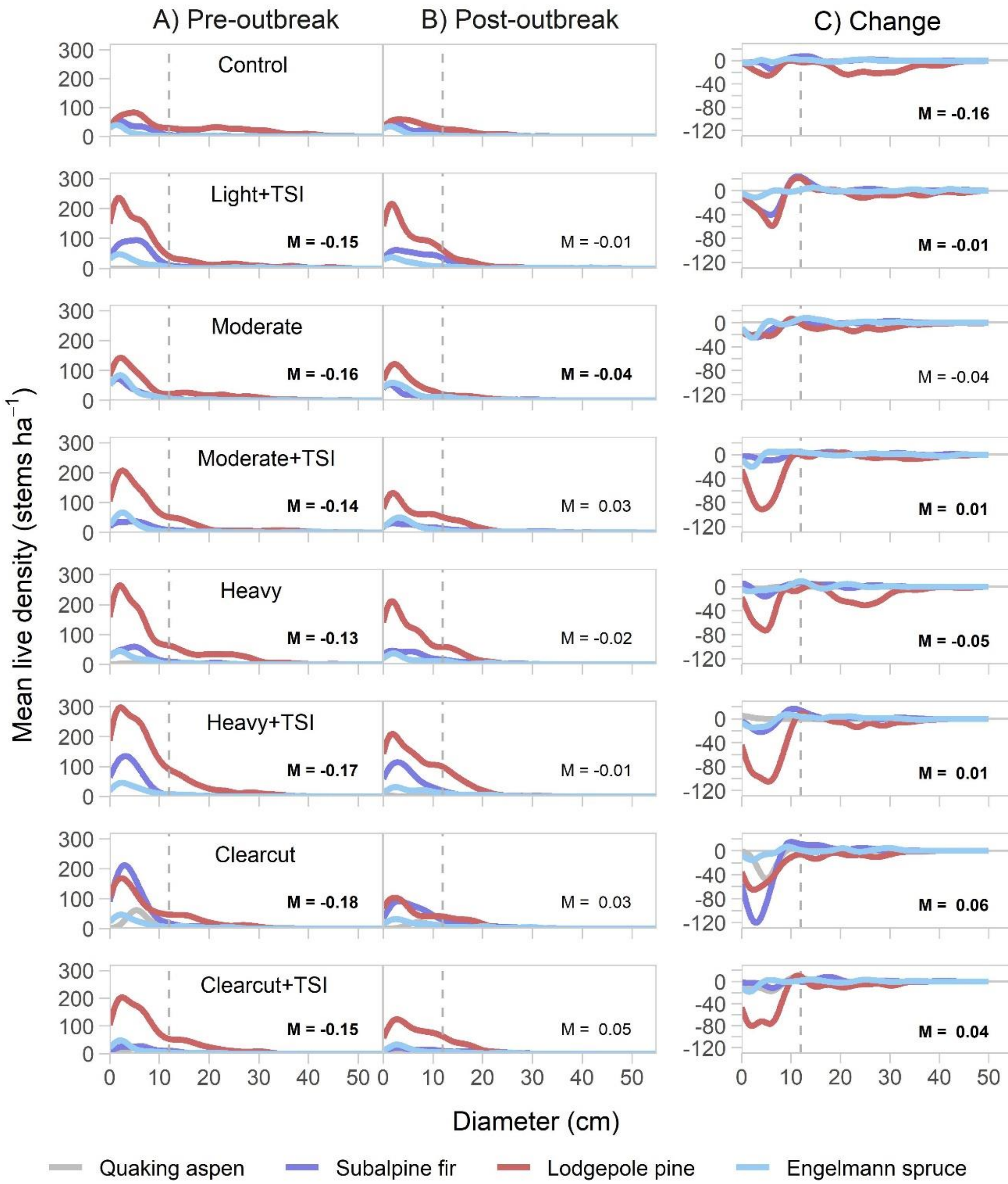

Figure 1.3. Stand-scale mean diameter distributions of live trees (height ≥ 1.4 m) (A) pre- (2004) and (B) post- (2018) MPB outbreak, and (C) subsequent change in distributions for each thinning treatment intensity. Lines represent kernel-smoothed stem density for each species averaged across plot replicates (*n* = 4 for control, light, and each heavy treatment; *n* = 3 for each moderate and clearcut treatment). Dashed vertical lines represent 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- vs. pre-outbreak; C). Bold values indicate significant ($P < 0.1$) departures according to K-S tests. See Table 1.2 for summary statistics and Appendix D: Table D.2 for species-specific quantitative analysis.

Table 1.2. Stand density and species composition of live trees (height ≥ 0.1 m) pre- (2004) and post- (2018) outbreak.

Species	Live density (stems ha^{-1})																			
	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
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 (Δ)] in mean. Dashes (–) indicate treatments having no observations in both pre- 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 D: Table D.1 for model outputs). Models were not developed for quaking aspen due to lack of sufficient number of observations.

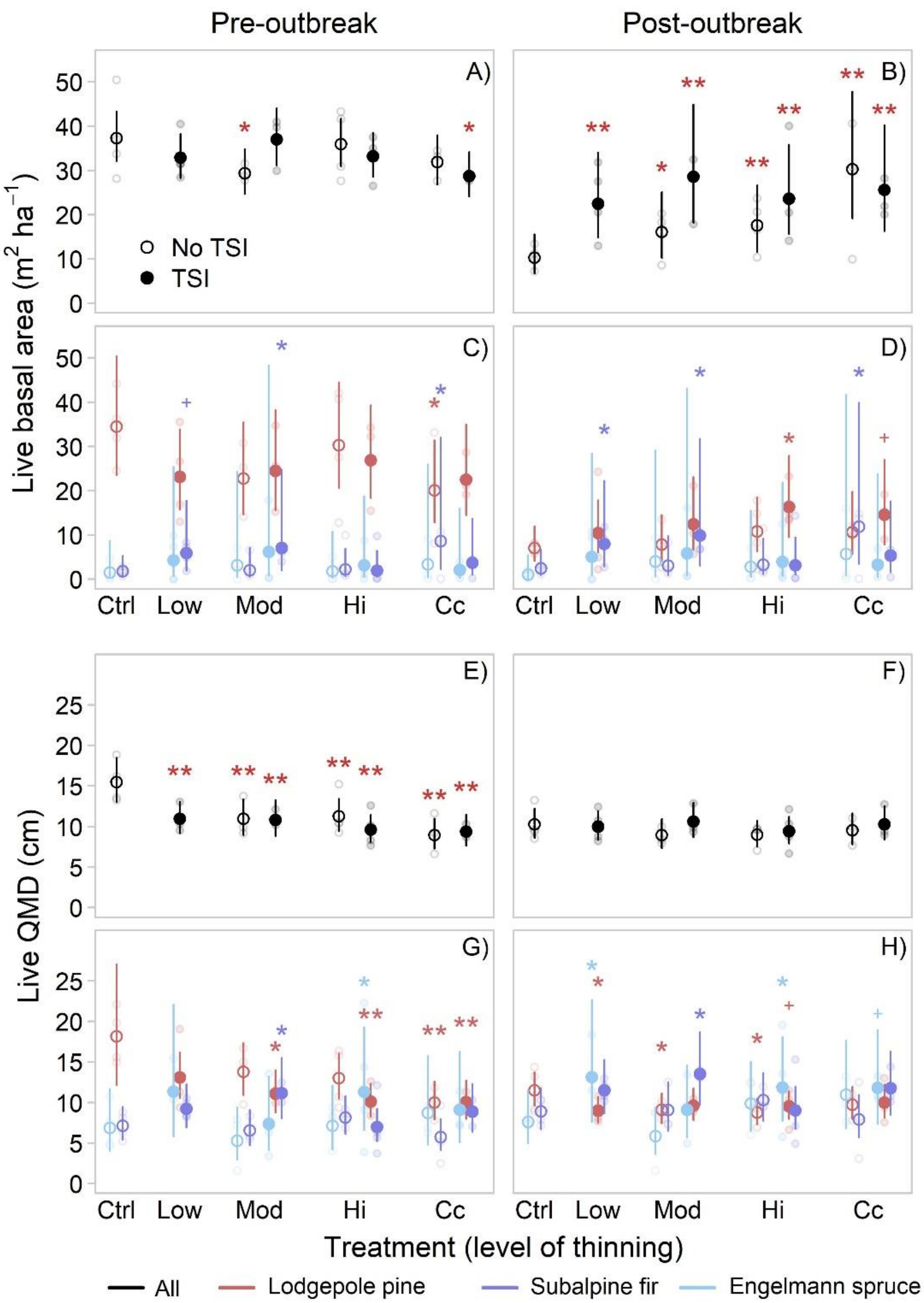

Figure 1.4. Predicted effects of thinning intensity on stand-scale pre- (2004) and post- (2018) outbreak live basal area (A–D) and quadratic mean diameter (QMD, E–H) for all trees combined (A–B, E–F) and by individual species (C–D, G–H). Treatments increase in level of thinning from left to right (Ctrl = control; Low = light; Mod = moderate; Hi = heavy; Cc = clearcut). Semi-transparent points represent observed mean values for each plot replicate. Opaque circles represent predicted means with 95% confidence intervals. Closed circles represent thinning plus timber stand improvement (TSI), and open circles represent thinning treatments without TSI. Asterisks indicate strength of evidence of a difference from the control for parameter coefficients according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). See Appendix D: Table D.3 for model output.

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 live diameter distributions were erased. Historically thinned stands had greater live post-outbreak (2018) overstory, midstory, and sapling stem density than the control for all species combined, driven by lodgepole pine (Fig. 1.3B, Table 1.2). Live post-outbreak seedling stem density was similar between historically thinned and uncut stands across species (Table 1.2). Unlike pre-outbreak stand structure (Fig. 1.4A), post-outbreak live basal area was ~2–3 times greater in historically thinned stands than in the control for all species combined (Fig. 1.4B). These differences were, in part, driven by greater lodgepole pine in heavier historical thinning treatments relative to the control (Fig. 1.4D) and by greater subalpine fir in the lighter historical thinning treatments relative to the control (Fig. 1.4D). In contrast, post-outbreak live tree QMD did not differ between historically thinned stands and the control for all species combined (Fig 1.4F)—the net result of greater QMD for both late-seral conifer species and lower QMD for lodgepole pine across multiple historically thinned treatments compared to the control (Fig. 1.4H). Additionally, post-outbreak total live tree diameter distributions in historically thinned stands were generally similar to the control (Fig. 1.3B). Species-specific post-outbreak live tree distributions were similar to the control for most historically thinned stands (Appendix D: Table D.2).

Live stand structure changed from pre- 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 1.2). The greatest magnitude of change in total live density occurred in saplings for historically thinned stands and in overstory trees for the control (Table 1.2). Change in overstory trees differed in direction between lodgepole pine (negative) and late-seral conifers (positive), while change in live density of saplings (negative) and seedlings (positive) was consistent across all species (Table 1.2).

Post-outbreak total live tree diameter distributions differed ($P < 0.001$) from pre-outbreak distributions for all stands except moderate thinning (Fig. 1.3C). Compared to the control, historically thinned stands showed lower magnitudes of change in total tree diameter distributions, and most (excluding light+TSI and heavy) differed in direction of change (right shift compared to left shift) from the control (Appendix D: Table D.2). That is, post-outbreak total live tree diameter distributions in historically thinned stands had fewer small and more large trees than before the outbreak (as a product of tree growth), while post-outbreak distributions in control stands had more small and fewer large trees than before the outbreak (as a product of mortality). Shifts were dominated by lodgepole pine; all stands, exclusive of clearcut+TSI, had left shifts in diameter distributions of live lodgepole pine trees, though the magnitude of change was lower in historically thinned stands compared to the control (Fig. 1.3C). All stands were characterized by a reduction in live susceptible diameter (dbh ≥ 12 cm, gray dashed line) lodgepole pine post-outbreak compared to pre-outbreak (Fig. 1.3C). 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. 1.3C). 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 D: Table D.2). Aspen diameter distributions displayed right shifts for both clearcut and clearcut+TSI treatments (Appendix D: Table D.2).

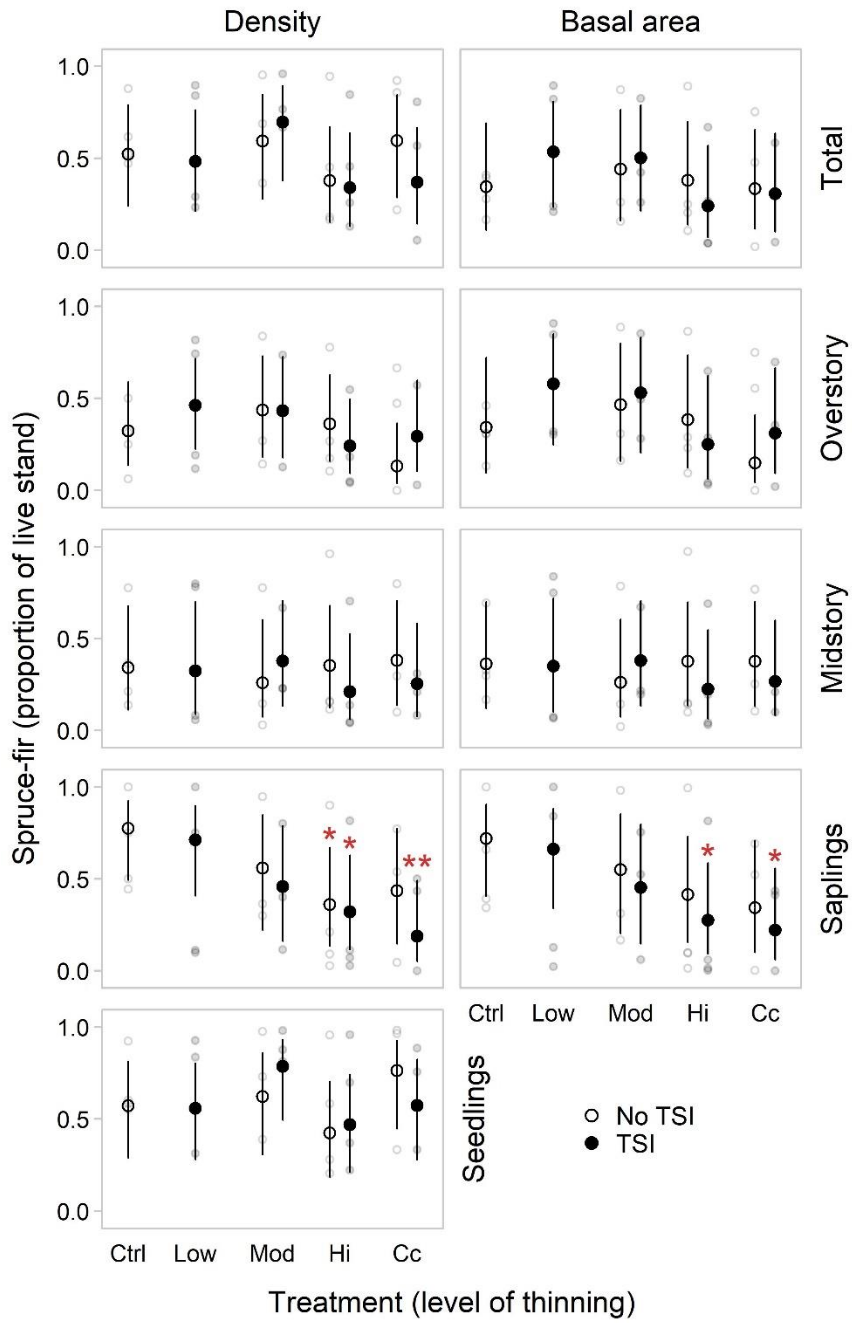

Figure 1.5. Predicted effects of thinning on stand-scale spruce-fir (S-F) proportion of post-outbreak (2018) live stem density (left) and basal area (right) combined for total, overstory (dbh ≥ 12 cm), midstory (5 ≤ dbh < 12 cm), sapling (dbh < 5 cm, height ≥ 1.4 m), and seedling (height 0.1–1.39 m) trees. Treatments increase in intensity from left to right (Ctrl = control; Low = light; Mod = moderate; Hi = heavy; Cc = clearcut). Semi-transparent points represent observed proportion for each plot replicate. Opaque circles represent predicted S-F proportions with 95% confidence intervals. Closed circles represent thinning plus timber stand improvement (TSI), and open circles represent thinning treatments without TSI. Asterisks indicate strength of evidence of a difference from the control for parameter coefficients according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). See Appendix D: Table D.4 for model output.

We found little evidence that historical thinning had an 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, except for in the treatments with the highest thinning intensities (heavy, heavy+TSI, and clearcut+TSI), where the relative dominance of spruce-fir was ~50% lower than the control (Fig. 1.5). For density and basal area, we found no evidence of an effect of TSI (Fig. 1.5).

DISCUSSION

Understanding the legacy of past management actions on promoting 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 exceedingly rare, but they offer critical insight into the longevity of management treatments. By exploring the effects of thinning treatments on forest resilience to bark beetle outbreak over a temporal scale comparable to 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 that occurred ~60 years 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

We found no evidence in support of our expectation that thinning ~60 years prior to outbreak would affect tree-scale resistance of susceptible lodgepole pine to MPB. If a tree was of susceptible size at the time of outbreak, its probability of survival was very low, regardless of the stand-scale thinning treatment applied in the stand where the tree was located (Fig. 1.1). 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 for greater MPB brood production, reduced larval intraspecific competition, and faster beetle development (Amman and Cole 1983). 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 to 25 cm dbh), 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). Although we saw greater variability in survival probability within and among treatments for trees of intermediate sizes (Fig. 1.1B), we detected no significant differences among treatments. That is, in the context of thinning, potential effects of increased vigor leading to greater tree-level resistance to MPB outbreak had eroded following >60 years of stand development.

We found limited evidence of an effect of thinning ~60 years prior to outbreak on stand-scale resistance of susceptible lodgepole pine density and basal area to MPB. This effect was detected only in the heavy+TSI, clearcut, and clearcut+TSI treatments, which were a near-total or total overstory removal with additional removal of advanced regeneration (via TSI). These heaviest treatments removed nearly all the susceptible individuals ~60 years prior to outbreak and, as a result, were the only stands in which the mean diameter of pre-outbreak susceptible lodgepole pine trees was smaller than 20 cm and no trees exceeded 40 cm diameter (Appendix C: Table C.1). The lack of evidence for a difference between the control and historically thinned stands at lower thinning intensities (i.e., those with a portion of overstory trees left uncut) suggests that the efficacy of lower-intensity thinning treatments can fade quickly as stands regrow, and there may be a threshold of thinning intensity that affects MPB outbreak resistance (e.g., Mata et al. 2003, Williams et al. 2018, Negrón 2019). For example, intense thinning (total overstory removal, similar to the clearcut treatments) 1 to 25 years prior to 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), whereas less intense thinning (partial overstory removal, similar to the light, moderate, and heavy treatments) has been effective when conducted during (McGregor et al. 1987) or 8 to 10 years prior to (Whitehead and Russo 2005) outbreak. Partial overstory removal may be ineffective at increasing resistance over longer time periods 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). As a result, stands may require thinning at intervals resembling the lower range of the MPB outbreak return interval (~25 years; Mata et al. 2003) to keep susceptible basal area below the resistance threshold, suggesting that only the heaviest thinning treatments may have positive effects on resistance over a temporal scale matching the mean outbreak return interval. However, thinning at treatment intervals of ~30 years may result in increased susceptibility to outbreak compared to uncut stands due to the maintenance of stand composition that can be dominated by greater homogeneity in live host tree basal area and density (Ager et al. 2007).

In addition to thinning intensity and timing that were the focus of our study, the spatial scale and arrangement of treatments can be important for building stand resistance to MPB outbreak. Thinning can be useful at reducing 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 the thinned stands are surrounded by unmanaged susceptible stands (Schmid and Mata 2005, Johnson et al. 2014). Further, inter-tree spacing may be an important consideration in conjunction with aggregate residual density when reducing stand susceptibility to attack (Whitehead and Russo 2005). At broader watershed and regional scales, increasing spatial heterogeneity in size and age classes and host species abundance may impede outbreak spread (Chapman et al. 2012, Nelson et al. 2014, DeRose and Long 2014). However, such broad scale management operations are costly and likely unfeasible across the spatial extent of severe bark beetle outbreaks (DeRose and Long 2014).

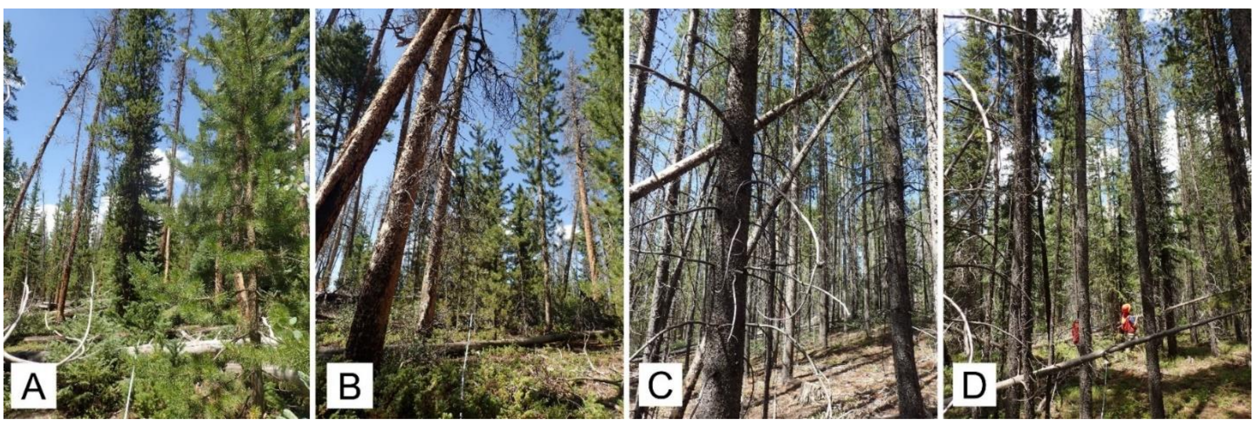

Figure 1.6. Representative photos of stand structure in uncut and thinned treatments post (2018) mountain pine beetle (*Dendroctonus ponderosae*) outbreak (2004) in subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests of the Fraser Experimental Forest, Colorado, USA. Treatments were conducted in 1940 (~60 years prior to outbreak) and ranged from uncut control (A), to clearcut (D; removal of all trees with dbh ≥ 24 cm). On one half of each thinned unit, timber stand improvement (TSI) thinning was conducted in addition to the major thinning treatment. Differences in structure as a result of 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. Photo credits: J. E. Morris.

In some cases, the effect of TSI (additional removal of small diameter trees after the main thinning treatment ~60 years prior to outbreak) was as strong as the overall thinning treatment, which focused on overstory trees. For example, the heavy thinning treatment without TSI (where 83% of the merchantable timber was removed but understory trees were left remaining in the 1940s; Fig. 1.6B) closely resembled the control treatment (Fig. 1.6A) in pre-outbreak (2004) stand structure and resistance to MPB outbreak (Fig. 1.2). Conversely, the heavy thinning treatment with TSI (same overstory treatment but understory trees were also removed; Fig. 1.6C) closely resembled the clearcut treatment (Fig. 1.6D) in pre-outbreak stand structure and resistance to MPB outbreak (Fig. 1.2). The removal of some 9 to 24 cm dbh trees ~60 years prior to outbreak, which were likely lodgepole pine based on stand development at the time of treatment, resulted in a reduction of susceptible lodgepole pine trees for the recent outbreak. Similar to TSI, thinning from below (i.e., removal of lower canopy trees) may also enhance effects of microclimate, tree vigor, and inter-tree spacing on reducing susceptibility of stands (Whitehead and Russo 2005, Coops et al. 2008, Fettig and Hilszczański 2015). While initially perceived as a minor treatment in the 1940s, implementing TSI may have important implications for amplifying or extending the longevity of treatment effects six decades later.

Increasing forest resistance to outbreak at the stand scale through intense thinning treatments may buy time in the short term, but eventually stands will again become susceptible to bark beetle outbreak (DeRose and Long 2014). Although the clearcut and heavy+TSI treatments in this study were resistant to the recent (2000s) MPB outbreak, they are likely to be susceptible to future (e.g., 2 to 3 decades later) outbreaks sooner than uncut stands (Collins et al. 2011) due to the creation of stand conditions characterized by relatively homogeneous composition favoring host species (e.g., greater basal area and density of live lodgepole pine trees) (Ager et al. 2007, Chapman et al. 2012). Consequently, maintaining long-term resistance requires repeated heavy treatment implementation (Mata et al. 2003, Ager et al. 2007). However, this treatment strategy would likely carry unintended consequences for other management objectives. For instance, tree mortality from bark beetle outbreaks can negatively impact services such as 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 enrich soils (Griffin et al. 2013). Further, frequent thinning of subalpine forests at this intensity would in many cases represent a fundamental departure from the natural range of variability in stand structure (Peet 2000) and should therefore be considered in the context of other resilience-based management goals and/or prioritized to areas around high-value resources such as in the wildland urban interface (Fettig and Hilszczański 2015).

Historical stand-thinning treatments altered post-outbreak successional trajectories

Strong legacies of the 1940s treatments persisted for 60 years until the start of the outbreak in the early 2000s. Overall, the strongest effects of historical thinning on pre-outbreak stand structure were seen for lodgepole pine. This can be ascribed to the age of the stand (~250 years) at the time of thinning, at which stage merchantable-sized lodgepole pine was dominant and therefore the species most removed. 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 differences in live diameter distributions between historically thinned and control stands were erased, though mechanisms of change varied (Fig. 1.3, Appendix D: Table D.2). These results are consistent with previous findings of decreased heterogeneity (i.e., convergence) in tree diameter and basal area among stands post-outbreak (Nelson et al. 2014). Lodgepole pine distributions were shifted left (i.e., fewer large trees) while late-seral, non-MPB host species distributions were shifted 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-tree diameter distributions changed following the outbreak for all stands, though the direction and dominant driver of change varied between historically thinned and control stands (Fig. 1.3C, Appendix D: Table D.2). 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 right (i.e., more large trees, mainly spruce and fir). This is likely from the dominance of MPB-induced mortality of large diameter trees in uncut and lower-intensity historically thinned stands, compared to the dominance of density-dependent mortality of small diameter trees in historically heavily thinned stands.

Historical thinning dampened the effects of the MPB outbreak on 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 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. Although this may represent a measure of resistance of the total live stand to the outbreak, these findings were mostly contributions of the non-susceptible tree population and thus differ from our analysis of stand-scale resistance. Relative to pre-outbreak, all stands post-outbreak had lower live overstory, midstory, and sapling density (Table 1.2), greater live seedling density (Table 1.2), and lower live basal area (Fig. 1.4), following dynamics typical of MPB outbreaks in similar forests (Nelson et al. 2014, Perovich and Sibold 2016). However, compared to uncut stands, the magnitude of total change in these attributes of stand structure was less in historically thinned stands. Most historically thinned stands had greater post-outbreak live overstory, midstory, and sapling stem density (Table 1.2) and greater live basal area (Fig. 1.4) than uncut stands for all species individually and totaled, aligning with previous studies describing similar trends due to lower MPB-induced tree mortality in thinned stands (Hood et al. 2016). Increases in aspen density in both clearcut treatments following the MPB outbreak (Table 1.2) support the finding elsewhere that multiple severe disturbances favor regeneration of species with resprouting capabilities (Bigler et al. 2005, Kulakowski et al. 2013, Pelz and Smith 2013, Hansen et al. 2016).

We found limited evidence to support our hypothesis that uncut stands would have accelerated successional trajectories compared to historically thinned stands. Generally, MPB outbreaks shift forest structure towards greater diversity in species composition in mixed-species stands (Perovich and Sibold 2016, Pappas et al. 2020). This was demonstrated by decreases in overstory density and basal area of lodgepole pine, increases in understory density of all tree species, and an increase in basal area of subalpine fir in the control stands (Table 1.2). Contrary to our expectations, thinning ~60 years prior to outbreak had little effect on relative dominance of late-seral species in 2018, with only the heaviest thinning treatments exhibiting lower spruce-fir proportions of live stem density and basal area compared to the control (Fig. 1.5). One likely explanation is that only the heaviest historical thinning treatments created initial conditions (i.e., larger canopy gaps, more light) favoring regeneration of lodgepole pine over spruce or fir (Lotan and Perry 1983). Further, within the heaviest treatments, we only found evidence of lower spruce-fir proportions of live stem density and basal area 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 years) compared to the temporal scale on which successional dynamics operate (decades to centuries). Simulations based on post-outbreak regeneration suggest stand basal area and density return to pre-outbreak levels in uncut and thinned stands within 80 to 105 years, respectively; lodgepole pine remains the dominant overstory species in thinned stands for 100 to 150 years post-outbreak, while subalpine fir becomes dominant in uncut stands (Collins et al. 2011). Thus, initial regeneration of understory lodgepole pine trees following thinning in 1940 may only have had enough time to be evident in sapling size class trees, whereas successional dynamics stimulated by the MPB outbreak are still developing. As the post-outbreak stands continue to grow and regenerate over time, differences in spruce-fir proportions among thinned and uncut stands in other size classes may emerge.

Directions for future research

Our study provides insights into the effects of historical thinning on community ecology and successional dynamics of live trees following MPB outbreak, and points to several areas for future research. Our reconstruction of pre-outbreak structure relied on growth rates derived from repeat diameter measurements of overstory and midstory trees (dbh $\geq$ 5 cm) in uncut control units. Although site-specific, these rates do not account for the differential effects of density on growth. Further, because only trees with dbh $\geq$ 5 cm were monitored in the control units, modeling the growth rates of saplings (dbh $<$ 5 cm) introduces some additional uncertainty. Consequently, growth rates in the thinned stands likely differed from the control following the MPB outbreak. Dendrochronological analysis of growth releases following both historical treatment and recent outbreak would likely provide more accurate growth rates, though we do not expect that further refining our estimates of growth rates would cause our results to qualitatively change.

Because developing strategies for maintaining resilience is both goal- and disturbance-specific (DeRose and Long 2014), the effects and longevity of thinning treatments on forest resilience to MPB outbreak may have additional implications for other disturbances. Our study looked at trajectories ~8 years post-outbreak, but there is opportunity to evaluate effects further into the future. Lasting differences in species composition between thinned and uncut stands may emerge over a greater time following outbreak and may influence susceptibility to future bark beetle outbreaks. For example, while heavily thinned stands in our study may be more susceptible to future MPB outbreak sooner than uncut stands, greater potential in uncut stands for spruce and fir to replace lodgepole pine as the dominant species (Collins et al. 2011) may impact susceptibility to other bark beetle outbreaks (e.g., spruce beetle, *Dendroctonus rufipennis*; western balsam bark beetle, *Dryocoetes confusus*). Additionally, changes in species dominance may influence the ability of stands to adapt to climate change (Perovich and Sibold 2016). Using a simulation modeling approach to examine post-outbreak successional dynamics over a longer time following the outbreak would extend insight into differences that may emerge between thinned and uncut stands over longer time scales.

While our study focused on live stand structure, important effects of thinning on the post-outbreak dead tree component remain to be explored. Beetle-killed trees become material legacies important for wildlife habitat (Saab et al. 2014), biogeochemical cycling (Mikkelson et al. 2013), and tree regeneration (Collins et al. 2011). Further, MPB outbreaks alter fuel profiles (i.e., abundance and spatial arrangement of biomass) in ways that could interact with fire behavior (Jenkins et al. 2008, Simard et al. 2011, Hicke et al. 2012b, Collins et al. 2012), fire effects (Harvey et al. 2014a, 2014b), and wildland firefighting operations (Jenkins et al. 2012). Thinning may interact with outbreak to influence post-outbreak fire hazard, but density reduction for this purpose may also present tradeoffs with other post-outbreak ecosystem services such as woody carbon storage, merchantable timber, and recreation and tourism (Flint et al. 2009).

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 years 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 diameter distributions between thinned and uncut treatments were erased by the MPB outbreak. However, lasting effects of historical thinning on post-outbreak trajectories manifest in other ways, including shifting successional trajectories toward understory sapling dominance of 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 driving post-outbreak successional trajectories.

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REFERENCES

Ager, A. A., A. McMahan, J. L. Hayes, and E. L. Smith. 2007. Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. Landscape and Urban Planning 80:301–311.

Alexander, R. R. 1954. Mortality following partial cutting in virgin lodgepole pine. Station Paper No. 16, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Alexander, R. R., C. A. Troendle, M. R. Kaufmann, W. D. Shepperd, G. L. Crouch, and R. K. Watkins. 1985. The Fraser Experimental Forest, Colorado: Research program and published research 1937-1985. General Technical Report RM-118, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Alfaro, R. I., E. Campbell, and B. C. Hawkes. 2010. Historical frequency, intensity and extent of mountain pine beetle disturbance in British Columbia. Pacific Forestry Centre, Victoria, B.C.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. (Ted) Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests part II: population dynamics. Pages 1–59. General Technical Report INT-145, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257:1874–1882.

Baker, W. L., and T. T. Veblen. 1990. Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado, U.S.A. Arctic and Alpine Research 22:65–80.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613.

Bentz, B., J. Logan, J. MacMahon, C. D. Allen, M. Ayres, E. Berg, A. Carroll, M. Hansen, J. Hicke, L. Joyce, W. Macfarlane, S. Munson, J. Negron, T. Paine, J. Powell, K. Raffa, J. Regniere, M. Reid, W. Romme, S. J. Seybold, D. Six, D. Tomback, J. Vandygriff, T. Veblen, M. White, J. Witcosky, and D. Wood. 2009. Bark beetle outbreaks in western North America: Causes and consequences. University of Utah Press, Salt Lake City, UT.

Bigler, C., D. Kulakowski, and T. T. Veblen. 2005. Multiple Disturbance Interactions and Drought Influence Fire Severity in Rocky Mountain Subalpine Forests. Ecology 86:3018–3029.

Björklund, N., and B. S. Lindgren. 2009. Diameter of lodgepole pine and mortality caused by the mountain pine beetle: factors that influence their relationship and applicability for susceptibility rating. Canadian Journal of Forest Research 39:908–916.

Bradford, J. B., R. A. Birdsey, L. A. Joyce, and M. G. Ryan. 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. Global Change Biology 14:2882–2897.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Buonanduci, M. S., J. E. Morris, M. C. Agne, and B. J. Harvey. 2020. Neighborhood context mediates probability of host tree mortality in a severe bark beetle outbreak. Ecosphere 11:e03236.

Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93:2175–2185.

Cole, W. E., and G. D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests, Part 1: Course of an infestation. Pages 1–56. General Technical Report INT-89, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Cole, W. E., D. B. Cahill, and G. D. Lessard. 1983. Harvesting Strategies for Management of Mountain Pine Beetle Infestations in Lodgepole Pine : Preliminary Evaluation, East Long Creek Demonstration Area, Shoshone National Forest, Wyoming. Pages 1–12. Research Note INT-333, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Collins, B. J., C. C. Rhoades, M. A. Battaglia, and R. M. Hubbard. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. Forest Ecology and Management 284:260–268.

Collins, B. J., C. C. Rhoades, R. M. Hubbard, and M. A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecology and Management 261:2168–2175.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, E. Whitman, T. Assal, B. M. Collins, K. T. Davis, S. Dobrowski, D. A. Falk, P. J. Fornwalt, P. Z. Fulé, B. J. Harvey, V. R. Kane, C. E. Littlefield, E. Q. Margolis, M. North, M.-A. Parisien, S. Prichard, and K. C. Rodman. 2020. Wildfire-driven forest conversion in western North American landscapes. BioScience 70:659–673.

Coops, N. C., J. A. Timko, M. A. Wulder, J. C. White, and N. Coops. 2008. Investigating the effectiveness of mountain pine beetle mitigation. International Journal of Pest Management 54:151–165.

Crotteau, J. S., C. R. Keyes, S. M. Hood, and A. J. Larson. 2019. Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak. Ecological Applications 30:1–19.

Curtis, R. O., and D. D. Marshall. 2005. Permanent-plot procedures for silvicultural and yield research. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

DeRose, R. J., and J. N. Long. 2014. Resistance and resilience: a conceptual framework for silviculture. Forest Science 60:1205–1212.

Diskin, M., M. E. Rocca, K. N. Nelson, C. F. Aoki, and W. H. Romme. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain

National Park, Colorado. Canadian Journal of Forest Research 41:782–792.

Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013a. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecological Applications 23:3–20.

Donato, D. C., M. Simard, W. H. Romme, B. J. Harvey, and M. G. Turner. 2013b. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. Forest Ecology and Management 303:160–174.

Fettig, C. J., and J. Hilszczański. 2015. Management Strategies for Bark Beetles in Conifer Forests. Pages 555–584 Bark Beetles. Elsevier.

Fettig, C. J., K. D. Klepzig, R. F. Billings, A. S. Munson, T. E. Nebeker, J. F. Negrón, and J. T. Nowak. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238:24–53.

Flathers, K. N., T. E. Kolb, J. B. Bradford, K. M. Waring, and W. K. Moser. 2016. Long-term thinning alters ponderosa pine reproduction in northern Arizona. Forest Ecology and Management 374:154–165.

Flint, C. G., B. McFarlane, and M. Müller. 2009. Human dimensions of forest disturbance by insects: an international synthesis. Environmental Management 43:1174–1186.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. Conservation in Practice 1:8–17.

Griffin, J. M., M. Simard, and M. G. Turner. 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. Forest Ecology and Management 291:228–239.

Gunderson, L. H. 2000. Ecological resilience — in theory and application. Annual Review of Ecology and Systematics 31:425–439.

Hansen, W. D., W. H. Romme, A. Ba, and M. G. Turner. 2016. Shifting ecological filters mediate postfire expansion of seedling aspen (Populus tremuloides) in Yellowstone. Forest Ecology and Management 362:218–230.

Hart, S. J., T. T. Veblen, N. Mietkiewicz, and D. Kulakowski. 2015. Negative feedbacks on bark beetle outbreaks: widespread and severe spruce beetle infestation restricts subsequent infestation. PLOS ONE 10:1–16.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landscape Ecology 31:2367–2383.

Harvey, R. D., Jr. 1986. Deterioration of mountain pine beetle-killed lodgepole pine in northeast Oregon. R6-86-13, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR.

Hicke, J. A., C. D. Allen, A. R. Desai, M. C. Dietze, R. J. Hall, E. H. Ted Hogg, D. M. Kashian, D. Moore, K. F. Raffa, R. N. Sturrock, and J. Vogelmann. 2012a. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biology 18:7–34.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012b. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hood, S. M., S. Baker, and A. Sala. 2016. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. Ecological Applications 26:1984–2000.

Hubbard, R. M., C. C. Rhoades, K. Elder, and J. Negron. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. Forest Ecology and Management 289:312–317.

Huckaby, L. S., and W. H. Moir. 1998. Forest communities at Fraser Experimental Forest, Colorado. The Southwestern Naturalist 43:204–218.

Jarvis, D. S., and D. Kulakowski. 2015. Long-term history and synchrony of mountain pine beetle outbreaks in lodgepole pine forests. Journal of Biogeography 42:1029–1039.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology and Management 254:16–34.

Jenkins, M. J., W. G. Page, E. G. Hebertson, and M. E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. Forest Ecology and Management 275:23–34.

Johnson, T. N., S. W. Buskirk, G. D. Hayward, and M. G. Raphael. 2014. Tree mortality after synchronized forest insect outbreaks: Effects of tree species, bole diameter, and cutting history. Forest Ecology and Management 319:10–17.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:1–11.

Kashian, D. M., R. M. Jackson, and H. D. Lyons. 2011. Forest structure altered by mountain pine beetle outbreaks affects subsequent attack in a Wyoming lodgepole pine forest, USA. Canadian Journal of Forest Research 41:2403–2412.

Kautz, M., K. Dworschak, A. Gruppe, and R. Schopf. 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. Forest Ecology and Management 262:598–608.

Kautz, M., A. J. H. Meddens, R. J. Hall, and A. Arneth. 2017. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Global Ecology and Biogeography 26:533–552.

Kayes, L. J., and D. B. Tinker. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. Forest Ecology and Management 263:57–66.

Klutsch, J. G., M. A. Battaglia, D. R. West, S. L. Costello, and J. F. Negron. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. Western Journal of Applied Forestry 26:101–109.

Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, and R. Caissie. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. Forest Ecology and Management 258:641–649.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Long, J. A. 2020. Jtools: Analysis and presentation of social scientific data.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. Pages 1–51. Agriculture Handbook No. 606, U.S. Department of Agriculture, Washington, D. C.

Lutes, D. C., R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi.

2006. FIREMON: Fire effects monitoring and inventory system. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Mata, S. A., J. M. Schmid, and W. K. Olsen. 2003. Growth of lodgepole pine stands and its relation to mountain pine beetle susceptibility. Pages 1–19. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

McGregor, M. D., G. D. Amman, R. F. Schmitz, and R. D. Oakes. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Canadian Journal of Forest Research 17:1234–1239.

McIver, J. D., S. L. Stephens, J. K. Agee, J. Barbour, R. E. J. Boerner, C. B. Edminster, K. L. Erickson, K. L. Farris, C. J. Fettig, C. E. Fiedler, S. Haase, S. C. Hart, J. E. Keeley, E. E. Knapp, J. F. Lehmkuhl, J. J. Moghaddas, W. Otrosina, K. W. Outcalt, D. W. Schwilk, C. N. Skinner, T. A. Waldrop, C. P. Weatherspoon, D. A. Yaussy, A. Youngblood, and S. Zack. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). International Journal of Wildland Fire 22:63–82.

McLauchlan, K. K., P. E. Higuera, D. G. Gavin, S. S. Perakis, M. C. Mack, H. Alexander, J. Battles, F. Biondi, B. Buma, D. Colombaroli, S. K. Enders, D. R. Engstrom, F. S. Hu, J. R. Marlon, J. Marshall, M. McGlone, J. L. Morris, L. E. Nave, B. Shuman, E. A. H. Smithwick, D. H. Urrego, D. A. Wardle, C. J. Williams, and J. J. Williams. 2014. Reconstructing disturbances and their biogeochemical consequences over multiple timescales. BioScience 64:105–116.

Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

Menning, K. M., J. J. Battles, and T. L. Benning. 2007. Quantifying change in distributions: a new departure index that detects, measures and describes change in distributions from population structures, size-classes and other ordered data. Oecologia 154:75–84.

Mikkelson, K. M., L. A. Bearup, R. M. Maxwell, J. D. Stednick, J. E. McCray, and J. O. Sharp. 2013. Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. Biogeochemistry 115:1–21.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Mitchell, R. G., R. H. Waring, and G. B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. Forest Science 29:204–211.

Moir, W. H., M. E. Harmon, F. G. Hawksworth, R. E. Brainerd, and J. F. Franklin. Unpublished.

Fifty years of succession in old-growth lodgepole pine and spruce-fir forests in Colorado.

Morris, J. L., S. Cottrell, C. J. Fettig, W. D. Hansen, R. L. Sherriff, V. A. Carter, J. L. Clear, J. Clement, R. J. DeRose, J. A. Hicke, P. E. Higuera, K. M. Mattor, A. W. R. Seddon, H. T. Seppä, J. D. Stednick, and S. J. Seybold. 2017. Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. Journal of Applied Ecology 54:750–760.

Negrón, J. 2019. Biological aspects of mountain pine beetle in lodgepole pine stands of different densities in Colorado, USA. Forests 10:1–18.

Negrón, J. F., K. K. Allen, A. Ambourn, B. Cook, and K. Marchand. 2017. Large-scale thinnings, ponderosa pine, and mountain pine beetle in the Black Hills, USA. Forest Science 63:529–536.

Negrón, J. F., and L. Huckaby. 2020. Reconstructing historical outbreaks of mountain pine beetle in lodgepole pine forests in the Colorado Front Range. Forest Ecology and Management 473:118270.

Nelson, K. N., M. E. Rocca, M. Diskin, C. F. Aoki, and W. H. Romme. 2014. Predictors of bark beetle activity and scale-dependent spatial heterogeneity change during the course of an outbreak in a subalpine forest. Landscape Ecology 29:97–109.

Peet, R. K. 2000. Forests and meadows of the Rocky Mountains. Pages 75–122 North American terrestrial vegetation. 2nd edition. Cambridge University Press, New York, NY.

Pelz, K. A., C. C. Rhoades, R. M. Hubbard, M. A. Battaglia, and F. W. Smith. 2015. Species composition influences management outcomes following mountain pine beetle in lodgepole pine-dominated forests. Forest Ecology and Management 336:11–20.

Pelz, K. A., and F. W. Smith. 2013. How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps. Forest Ecology and Management 299:60–69.

Pelz, K., C. Rhoades, R. Hubbard, and F. Smith. 2018. Severity of overstory mortality influences conifer recruitment and growth in mountain pine beetle-affected forests. Forests 9:536.

Perovich, C., and J. S. Sibold. 2016. Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. Forest Ecology and Management 366:184–192.

PRISM Climate Group. 2012. Oregon State University, http://prism.oregonstate.edu.

Pugh, E., and E. Gordon. 2013. A conceptual model of water yield effects from beetle-induced tree death in snow-dominated lodgepole pine forests. Hydrological Processes 27:2048–2060.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Reinhardt, E. D., R. E. Keane, D. E. Calkin, and J. D. Cohen. 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. Forest Ecology and Management 256:1997–2006.

Rhoades, C. C., J. H. McCutchan, L. A. Cooper, D. Clow, T. M. Detmer, J. S. Briggs, J. D. Stednick, T. T. Veblen, R. M. Ertz, G. E. Likens, and W. M. Lewis. 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proceedings of the National Academy of Sciences 110:1756–1760.

Roe, A. L., and G. D. Amman. 1970. Mountain pine beetle in lodgepole pine forests. Pages 1–23. Research Paper INT-71, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Romme, W. H., M. G. Turner, G. A. Tuskan, and R. A. Reed. 2005. Establishment, persistence, and growth of aspen (Populus tremuloides) seedlings in Yellowstone National Park. Ecology 86:404–418.

Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60:539–559.

Safranyik, L., and A. L. Carrol. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 in L. Safranyik and W. R. Wilson, editors. The Mountain Pine Beetle – A Synthesis of Biology, Management, and Impacts in Lodgepole Pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Schmid, J. M., and S. A. Mata. 1992. Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands. Pages 1–4. Research Note RM-515, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Schmid, J. M., and S. A. Mata. 2005. Mountain pine beetle-caused tree mortality in partially cut plots surrounded by unmanaged stands. Pages 1–11. Research Paper RMRS-RP-54, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology 53:120–129.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Shepperd, W. D. 1993. Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains. Pages 1–8. Research Paper RM-312, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Shore, T. L., and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Page 12. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia.

Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81:3–24.

Smirnov, N. V. 1939. Estimate of deviation between empirical distribution functions in two independent samples. Bulletin Moscow University 2:3–16.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67–94 The mountain pine beetle – a synthesis of biology, management, and impacts in lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Temperli, C., S. Hart, T. Veblen, D. Kulakowski, J. Kelly, and R. Andrus. 2014. Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? Forest Ecology and Management 334:53–63.

Tishmack, J., S. A. Mata, and J. M. Schmid. 2005. Mountain pine beetle emergence from lodgepole pine at different elevations near Fraser, CO. Pages 1–5. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner, M. G., K. H. Braziunas, W. D. Hansen, and B. J. Harvey. 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proceedings of the National Academy of Sciences 116:11319–11328.

Vorster, A. G., P. H. Evangelista, T. J. Stohlgren, S. Kumar, C. C. Rhoades, R. M. Hubbard, A. S. Cheng, and K. Elder. 2017. Severity of a mountain pine beetle outbreak across a range of stand conditions in Fraser Experimental Forest, Colorado, United States. Forest Ecology and Management 389:116–126.

Walker, B., C. S. Holling, S. R. Carpenter, and A. P. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9:5.

Walter, J. A., and R. V. Platt. 2013. Multi-temporal analysis reveals that predictors of mountain pine beetle infestation change during outbreak cycles. Forest Ecology and Management 302:308–318.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83:441–470.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B: Biological Sciences 371:1–10.

Whitehead, R. J., and G. L. Russo. 2005. Beetle-proofed lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle. Pages 1–17. Information Report BC-X-402, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Williams, H., S. Hood, C. Keyes, J. Egan, and J. Negrón. 2018. Subwatershed-level lodgepole pine attributes associated with a mountain pine beetle outbreak. Forests 9:1–17.

Wilm, H. G., and E. G. Dunford. 1948. Effect of timber cutting on water available for stream flow from a lodgepole pine forest. Technical Bulletin No. 968, United States Department of Agriculture.

Winter, M.-B., C. Ammer, R. Baier, D. C. Donato, S. Seibold, and J. Müller. 2015. Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase. Forest Ecology and Management 338:32–45.

Young, D. J. N., M. Meyer, B. Estes, S. Gross, A. Wuenschel, C. Restaino, and H. D. Safford. 2020. Forest recovery following extreme drought in California, USA: natural patterns and effects of pre-drought management. Ecological Applications 30:e02002.

Appendix A. STUDY AND SAMPLING DESIGN

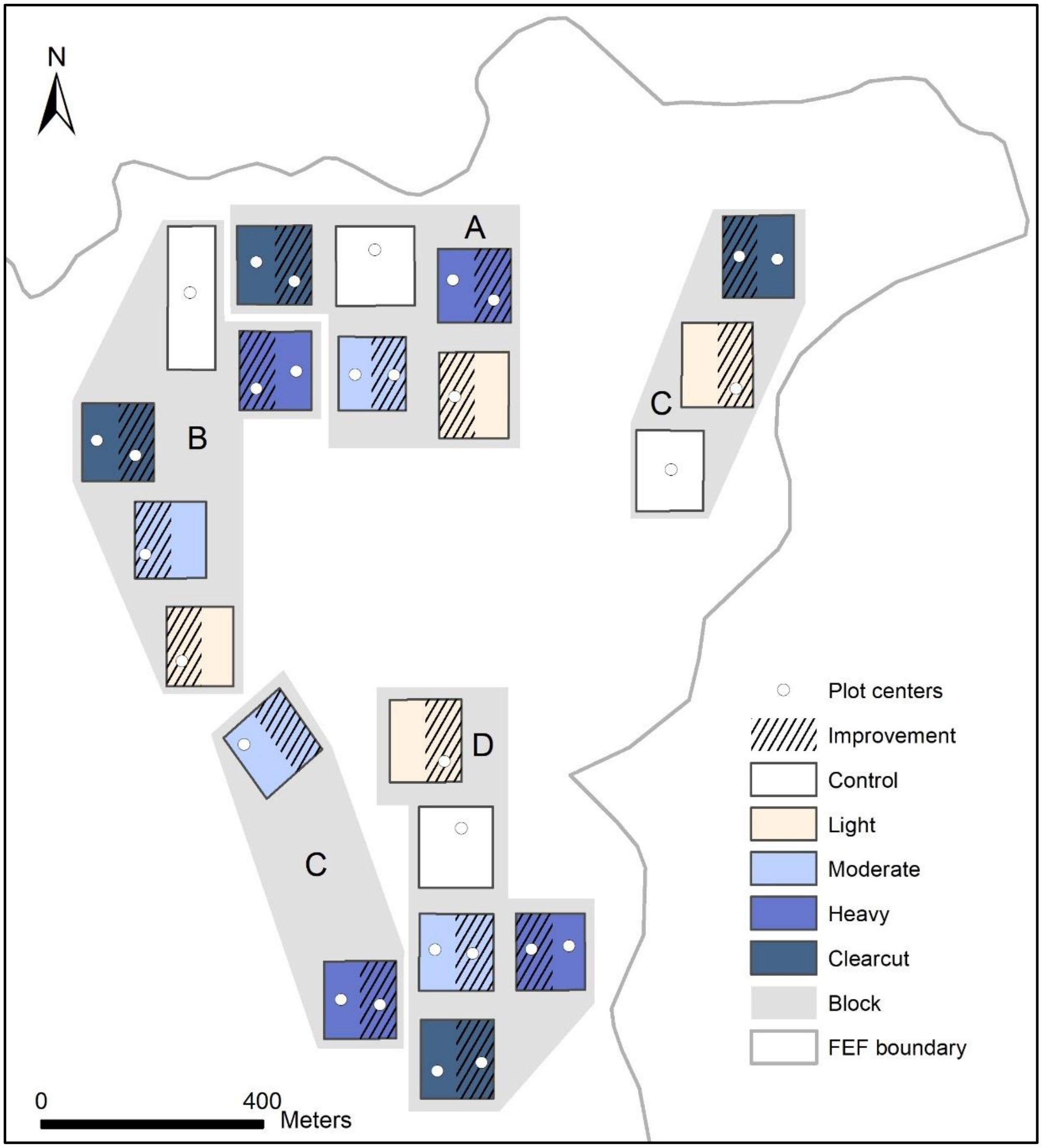

Figure A.1. Schematic of treatment unit layout and sampling design within the Fraser Experimental Forest, Colorado, USA (gray line). Four replicate blocks (A–D) of five different 2-ha thinning units are shown, increasing in volume of trees removed from control (no trees removed) to clearcut (all trees with dbh ≥ 24 cm removed). Hatching designates location of timber stand improvement (TSI) thinning within each major treatment unit. White circles represent the center positions of 0.25 ha plots sampled within the treatment units. Both plots within the clearcut unit in block C were excluded from the study because of more recent fuel break harvests that occurred in the original plot locations (Banning Starr, Fraser Experimental Forest site manager, *personal communication*).

Table A.1. Summary of plots sampled in 2018 by major thinning intensity and minor timber stand improvement (TSI) treatment (total n = 28).

Treatment	TSI	Plot replicates
Control	NA	4
Light[1]	Yes	4
	No	–
Moderate[1]	Yes	3
	No	3
Heavy	Yes	4
	No	4
Clearcut[2]	Yes	3
	No	3

Notes: See Appendix A: Fig. A.1 for plot layout. NA's indicate treatment combinations that did not exist. Dashes (–) indicate treatment combinations not sampled.

[1] Plots not sampled due to lack of suitable placement locations within treatment unit boundaries.

[2] Plots within block C treatment unit excluded because of more recent fuel break harvests that occurred in the original plot locations (Banning Starr, Fraser Experimental Forest site manager, *personal communication*).

Appendix B. RECONSTRUCTING PRE-OUTBREAK STRUCTURE

We estimated pre-outbreak (2004) dbh of live overstory (dbh ≥ 12 cm), midstory (5 ≤ dbh < 12 cm), and sapling (dbh < 5 cm) trees by developing species-specific models of growth as a function of dbh. Using annual dbh increment derived from repeat measures of tagged trees (dbh range 5.5 to 69.7 cm) within the 2-ha control units (Buonanduci et al. 2020), we specified nonlinear models fit to a logistic form for lodgepole pine, subalpine fir, and quaking aspen, and a linear model fit to a quadratic form for Engelmann spruce (Table B.1).

We estimated pre-outbreak height of live seedlings (height 0.10–1.39 m) using published regional measurements. For conifer species (lodgepole pine, subalpine fir, Engelmann spruce), we used annual leader growth estimates of trees <1.4 m tall within Fraser Experimental Forest measured by Pelz et al. (2018) in 2012 (8 years post-outbreak). To account for differences among treatments, we averaged growth rates between reported measurements in moderate (40% total basal area) and high (85% total basal area) overstory mortality areas. These rates are supported by observations of leader growth for lodgepole pine and subalpine fir advance regeneration (i.e., trees established prior to the outbreak) measured by Collins et al. (2011) in uncut stands at Fraser Experimental Forest between 2007–2010 (3 to 6 years post-outbreak). For aspen, since we did not collect information to distinguish clonal stem resprouts (ramets) from genetically distinct seedlings, we averaged height growth observations for ramets (Shepperd 1993) and distinct seedlings (Romme et al. 2005) in the Rocky Mountains 1–14 years post-disturbance. We assumed height growth rates of 5.5 cm/year (77 cm total growth since outbreak) for both lodgepole pine and subalpine fir, 4.5 cm/year (63 cm total) for Engelmann spruce, and 30 cm/year for aspen (420 cm total) (Shepperd 1993, Romme et al. 2005, Pelz et al. 2018).

Table B.1. Diameter growth rate model equations used for determining pre-outbreak (2004) dbh of live trees.

Species	Model form†	*n*	df	RMSE	β_0		β_1		β_2		β_3	
Lodgepole pine	logistic	1,891	1,888	0.12	–		0.17	(0.00)	7.54	(0.23)	1.05	(0.21)
Subalpine fir	logistic	617	614	0.14	–		0.38	(0.01)	9.41	(0.27)	2.34	(0.31)
Engelmann spruce	quadratic	215	212	0.18	-0.06	(0.07)	0.04	(0.01)	0.00	(0.00)	–	
Quaking aspen	logistic	25	22	0.15	–		0.36	(0.06)	8.68	(1.18)	1.72	(1.04)

Notes: Models were developed from repeat diameter measurements of tagged trees (*n* = 2,748) within the 2-ha control units in 2004 and 2018 (Buonanduci et al. 2020). Model terms (β) are presented as coefficient estimates (standard error). *N*, sample size. Df, degrees of freedom. RMSE, root mean square error (i.e., residual standard deviation). Dashes (–) indicate terms not included within the model.

† Models followed the equations $f(x) = \beta_1 / \left(1 + e^{\left(\beta_2 - x / \beta_3\right)}\right)$ and $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$ for logistic and quadratic forms, respectively, where $f(x)$ is the annual dbh growth rate (cm yr^{-1}) and x is dbh (cm).

REFERENCES

Buonanduci, M. S., J. E. Morris, M. C. Agne, and B. J. Harvey. 2020. Neighborhood context mediates probability of host tree mortality in a severe bark beetle outbreak. Ecosphere 11:e03236.

Collins, B. J., C. C. Rhoades, R. M. Hubbard, and M. A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecology and Management 261:2168–2175.

Pelz, K., C. Rhoades, R. Hubbard, and F. Smith. 2018. Severity of overstory mortality influences conifer recruitment and growth in mountain pine beetle-affected forests. Forests 9:536.

Romme, W. H., M. G. Turner, G. A. Tuskan, and R. A. Reed. 2005. Establishment, persistence, and growth of aspen (Populous tremuloides) seedlings in Yellowstone National Park. Ecology 86:404–418.

Shepperd, W. D. 1993. Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains. Pages 1–8. Research Paper RM-312, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Appendix C. RESISTANCE TO OUTBREAK: QUANTITATIVE ANALYSES AND MODEL SUMMARIES

Table C.1. Post-outbreak (2018) structural characteristics of susceptible (pre-outbreak dbh ≥ 12 cm) lodgepole pine host trees for each treatment at individual tree and stand scales.

Variable	Total susceptible hosts			Survived hosts			MPB-killed hosts		
	Range	Median	Mean (SE)	Range	Median	Mean (SE)	Range	Median	Mean (SE)
Tree scale									
Diameter (cm)		*n = 874*			*n = 359*			*n* = 515	
Control	12.0–47.8	23.5	24.4 (0.7)	12.0–29.6	15.9	17.0 (0.7)	12.0–47.8	26.5	27.2 (0.8)
Light+TSI	12.4–45.8	21.3	23.1 (0.9)	12.4–24.9	15.1	16.5 (0.6)	15.5–45.8	26.9	28.3 (1.2)
Moderate	12.0–47.3	21.5	21.9 (0.8)	12.0–25.8	15.9	16.7 (0.7)	12.2–47.3	23.2	24.6 (1.0)
Moderate+TSI	12.1–45.0	16.8	20.6 (1.0)	12.1–28.4	14.5	15.4 (0.5)	13.0–45.0	26.5	26.6 (1.5)
Heavy	12.1–45.6	20.9	21.3 (0.6)	12.1–36.6	14.3	15.6 (0.6)	12.3–45.6	23.5	23.8 (0.6)
Heavy+TSI	12.0–39.4	16.8	18.7 (0.5)	12.0–29.6	14.8	15.7 (0.4)	12.0–39.4	20.7	21.7 (0.8)
Clearcut	12.3–36.0	16.8	18.5 (0.6)	12.3–23.8	15.0	15.4 (0.4)	12.6–36.0	20.0	21.2 (0.8)
Clearcut+TSI	12.3–31.8	16.8	18.2 (0.5)	12.3–26.1	14.9	15.7 (0.5)	12.4–31.8	19.3	20.8 (0.7)
Stand scale									
Stem density (stems ha^{-1})									
Control	289–833	527	544 (122)	119–170	153	149 (13)	170–663	374	395 (110)
Light+TSI	170–595	366	374 (98)	51–357	128	166 (68)	85–306	221	208 (46)
Moderate	272–612	544	476 (104)	51–289	136	159 (70)	221–476	255	317 (80)
Moderate+TSI	289–782	357	476 (154)	136–493	136	255 (119)	153–289	221	221 (39)
Heavy	221–867	714	629 (147)	51–306	204	191 (59)	170–731	425	438 (125)
Heavy+TSI	391–799	663	629 (98)	153–425	332	310 (57)	51–476	374	319 (93)
Clearcut	272–765	544	527 (143)	238–255	238	244 (6)	17–527	306	283 (148)
Clearcut+TSI	374–680	663	572 (99)	136–408	323	289 (80)	238–357	255	283 (37)

Basal area (m^2 ha^{-1})												
Control	16.7–39.2	28.4	28.2	(4.7)	2.3–5.2	3.4	3.6	(0.6)	14.5–34.0	25.0	24.6	(4.2)
Light+TSI	10.5–25.3	18.0	17.9	(3.2)	1.0–9.3	2.3	3.7	(1.9)	8.8–17.3	15.4	14.2	(1.9)
Moderate	12.6–27.6	19.8	20.0	(4.3)	1.0–7.2	2.7	3.6	(1.8)	11.6–24.9	12.6	16.4	(4.3)
Moderate+TSI	11.3–24.2	20.6	18.7	(3.8)	2.9–8.5	3.5	5.0	(1.8)	8.4–17.1	15.6	13.7	(2.7)
Heavy	8.8–39.0	25.8	24.8	(6.9)	0.7–5.7	4.6	3.9	(1.1)	8.1–34.5	20.5	20.9	(6.3)
Heavy+TSI	9.4–30.0	18.9	19.3	(4.2)	3.3–8.5	6.7	6.3	(1.2)	3.7–22.2	13.0	13.0	(3.8)
Clearcut	5.1–26.7	14.4	15.4	(6.3)	4.5–4.9	4.6	4.7	(0.1)	0.5–21.8	9.9	10.7	(6.2)
Clearcut+TSI	13.4–20.0	14.8	16.1	(2.0)	3.0–7.4	7.3	5.9	(1.4)	7.4–12.7	10.5	10.2	(1.5)

Notes: Diameter and basal area reflect pre-outbreak tree sizes. SE, standard error. TSI, timber stand improvement.

Table C.2. Results of the mixed effects logistic regression model for tree-scale probability of survival of susceptible lodgepole pine trees (pre-outbreak dbh ≥ 12 cm) as a function of thinning treatment and tree diameter.

Predictor variables	Probability of survival			
	β	SE	*P*	
Treatment effect				
Light+TSI	1.07	1.91	0.574	
Moderate	-1.43	1.73	0.410	
Moderate+TSI	-0.73	1.72	0.672	
Heavy	-0.22	1.61	0.891	
Heavy+TSI	-2.37	1.46	0.103	
Clearcut	-0.33	1.80	0.855	
Clearcut+TSI	-1.01	1.71	0.553	
TSI effect[1]				
Moderate:TSI	0.70	1.74	0.689	
Heavy:TSI	-2.15	1.33	0.105	
Clearcut:TSI	-0.69	1.79	0.701	
Size effect				
Control:dbh	-0.34	0.06	< 0.001	**
Light+TSI:dbh	-0.36	0.08	< 0.001	**
Moderate:dbh	-0.27	0.07	< 0.001	**
Moderate+TSI:dbh	-0.27	0.07	< 0.001	**
Heavy:dbh	-0.35	0.06	< 0.001	**
Heavy+TSI:dbh	-0.21	0.04	< 0.001	**
Clearcut:dbh	-0.34	0.08	< 0.001	**
Clearcut+TSI:dbh	-0.28	0.07	< 0.001	**

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table C.3. Results of the mixed effects beta regression models for stand-scale proportion of surviving susceptible lodgepole pine (pre-outbreak dbh ≥ 12 cm) stem density and basal area as a function of thinning treatment.

Predictor variables	Proportion of survival							
	Density				Basal area			
	β	SE	*P*		β	SE	*P*	
Treatment effect								
Light+TSI	0.40	0.49	0.414		0.19	0.54	0.723	
Moderate	0.00	0.54	0.994		0.14	0.59	0.810	
Moderate+TSI	0.72	0.53	0.170		0.66	0.56	0.241	
Heavy	-0.03	0.50	0.954		0.12	0.55	0.827	
Heavy+TSI	0.91	0.49	0.064	+	1.08	0.51	0.036	*
Clearcut	1.23	0.53	0.022	*	1.61	0.54	0.003	**
Clearcut+TSI	0.69	0.53	0.191		1.07	0.55	0.051	+
TSI effect[1]								
Moderate:TSI	0.73	0.57	0.198		0.52	0.60	0.385	
Heavy:TSI	0.94	0.49	0.057	+	0.96	0.51	0.058	+
Clearcut:TSI	-0.54	0.56	0.334		-0.53	0.53	0.315	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Appendix D. POST-OUTBREAK SUCCESSIONAL TRAJECTORIES: QUANTITATIVE ANALYSES AND MODEL SUMMARIES

Table D.1. Results of the mixed effects regression models for stand-scale live pre- (2004) and post- (2018) outbreak stem density by size class and species[1] as a function of thinning treatment.

Predictor variables	Live density															
	Overstory (dbh ≥ 12 cm)				Midstory (5 ≤ dbh < 12 cm)				Saplings (dbh < 5 cm)				Seedlings (height < 1.4 m)			
	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
							PRE-OUTBREAK									
Total																
Light+TSI	-0.22	0.13	0.099	+	0.83	0.24	0.001	**	0.83	0.35	0.019	*	0.14	0.35	0.693	
Moderate	-0.07	0.14	0.647		0.33	0.26	0.203		0.88	0.38	0.021	*	0.89	0.38	0.019	*
Moderate+TSI	0.03	0.14	0.811		0.85	0.26	0.001	**	0.90	0.38	0.019	*	-0.12	0.38	0.758	
Heavy	0.16	0.13	0.247		0.71	0.24	0.003	**	0.80	0.35	0.024	*	0.02	0.35	0.963	
Heavy+TSI	0.13	0.13	0.339		1.09	0.24	<0.001	**	1.09	0.35	0.002	**	-0.02	0.35	0.962	
Clearcut	0.15	0.14	0.306		1.11	0.26	<0.001	**	1.31	0.38	0.001	**	-0.05	0.38	0.905	
Clearcut+TSI	0.08	0.14	0.573		1.00	0.26	<0.001	**	0.82	0.38	0.033	*	-0.63	0.38	0.101	
Lodgepole pine																
Light+TSI	-0.45	0.27	0.094	+	0.77	0.36	0.029	*	1.16	0.71	0.101		0.55	0.85	0.517	
Moderate	-0.20	0.29	0.500		0.29	0.38	0.453		0.92	0.76	0.228		1.14	0.91	0.212	
Moderate+TSI	-0.17	0.29	0.549		0.96	0.38	0.012	*	1.29	0.76	0.092	+	0.25	0.91	0.786	
Heavy	0.10	0.27	0.699		0.84	0.35	0.017	*	1.26	0.71	0.076	+	0.38	0.85	0.654	
Heavy+TSI	0.07	0.27	0.787		1.26	0.35	<0.001	**	1.42	0.71	0.045	*	0.24	0.85	0.778	
Clearcut	-0.08	0.29	0.781		0.54	0.38	0.158		1.18	0.76	0.122		-0.67	0.91	0.465	
Clearcut+TSI	0.00	0.29	0.987		1.09	0.38	0.004	**	1.27	0.76	0.096	+	-0.57	0.91	0.531	

Subalpine fir															
Light+TSI	0.89	0.92	0.330		1.19	0.74	0.107		0.57	0.88	0.517		-0.16	1.01	0.877
Moderate	0.58	0.99	0.562		-0.35	0.81	0.664		0.53	0.92	0.564		0.68	1.09	0.534
Moderate+TSI	1.09	0.99	0.273		0.56	0.79	0.477		0.08	0.96	0.937		-0.62	1.12	0.578
Heavy	0.58	0.92	0.531		0.06	0.74	0.931		-0.11	0.89	0.899		-0.58	1.13	0.609
Heavy+TSI	0.20	0.92	0.827		0.12	0.79	0.880		0.70	1.01	0.488		-0.39	1.18	0.742
Clearcut	1.09	0.99	0.273		1.65	0.83	0.046	*	1.70	0.96	0.077	+	0.57	1.24	0.643
Clearcut+TSI	0.39	0.99	0.692		0.36	0.81	0.656		-0.55	0.97	0.567		-0.92	1.12	0.413
Engelmann spruce															
Light+TSI	0.77	1.59	0.626		1.28	0.94	0.174		0.44	1.24	0.723		-0.77	1.29	0.550
Moderate	0.89	1.71	0.602		1.18	1.08	0.276		1.16	1.22	0.342		0.56	1.40	0.690
Moderate+TSI	1.06	1.71	0.535		1.44	1.03	0.160		0.91	1.28	0.475		-0.33	1.40	0.812
Heavy	0.51	1.59	0.747		0.81	0.94	0.390		0.15	1.23	0.904		-0.26	1.29	0.839
Heavy+TSI	0.92	1.59	0.563		1.08	1.02	0.287		0.09	1.36	0.947		-0.26	1.29	0.839
Clearcut	1.27	1.71	0.459		1.99	1.21	0.100	+	0.58	1.32	0.659		-0.49	1.40	0.728
Clearcut+TSI	0.69	1.71	0.686		1.06	1.12	0.343		0.62	1.35	0.649		-1.58	1.40	0.257
								POST-OUTBREAK							
Total															
Light+TSI	0.47	0.21	0.025	*	0.90	0.25	<0.001	**	0.77	0.41	0.059	+	-0.13	0.51	0.798
Moderate	0.32	0.23	0.162		0.40	0.27	0.148		0.77	0.44	0.079	+	0.70	0.55	0.205
Moderate+TSI	0.87	0.23	<0.001	**	0.80	0.28	0.003	**	0.64	0.44	0.149		0.68	0.56	0.223
Heavy	0.57	0.21	0.007	**	0.76	0.25	0.003	**	0.70	0.41	0.085	+	-0.22	0.52	0.667
Heavy+TSI	0.81	0.21	<0.001	**	1.09	0.26	<0.001	**	0.93	0.41	0.023	*	-0.61	0.52	0.238

Clearcut	1.01	0.23	<0.001	**	1.05	0.28	<0.001	**	0.77	0.44	0.079	+	0.41	0.60	0.492	
Clearcut+TSI	0.86	0.23	<0.001	**	0.93	0.27	0.001	**	0.46	0.44	0.299		-0.47	0.60	0.434	
Lodgepole pine																
Light+TSI	0.28	0.36	0.428		0.86	0.41	0.036	*	1.25	0.85	0.139		0.03	0.50	0.953	
Moderate	-0.02	0.39	0.957		0.39	0.44	0.377		0.98	0.91	0.283		1.03	0.54	0.055	+
Moderate+TSI	0.67	0.38	0.080	+	0.75	0.44	0.089	+	1.03	0.91	0.257		-0.22	0.54	0.680	
Heavy	0.53	0.36	0.139		0.80	0.41	0.050	*	1.25	0.85	0.138		-0.02	0.50	0.968	
Heavy+TSI	0.90	0.36	0.011	*	1.15	0.41	0.005	**	1.28	0.85	0.129		-0.16	0.50	0.745	
Clearcut	0.55	0.38	0.149		0.32	0.44	0.472		0.95	0.91	0.297		-0.60	0.54	0.264	
Clearcut+TSI	0.78	0.38	0.043	*	0.96	0.44	0.031	*	1.01	0.91	0.270		-1.75	0.54	0.001	**
Subalpine fir																
Light+TSI	0.82	0.80	0.303		1.50	0.75	0.046	*	0.18	1.00	0.855		-0.26	0.74	0.725	
Moderate	0.20	0.90	0.823		-0.42	0.81	0.606		0.22	1.08	0.840		0.57	0.82	0.486	
Moderate+TSI	0.93	0.88	0.293		0.96	0.80	0.231		-0.22	1.08	0.836		0.88	0.80	0.270	
Heavy	0.41	0.86	0.637		0.48	0.72	0.510		-0.07	1.00	0.945		-0.51	0.81	0.527	
Heavy+TSI	0.16	0.89	0.856		0.51	0.75	0.499		0.85	1.00	0.397		-1.10	0.78	0.158	
Clearcut	1.38	0.89	0.119		1.79	0.82	0.029	*	0.84	1.08	0.438		0.52	0.87	0.551	
Clearcut+TSI	0.60	0.88	0.494		0.37	0.81	0.649		-0.63	1.08	0.561		-0.42	0.87	0.632	
Engelmann spruce																
Light+TSI	1.22	1.12	0.277		1.29	0.94	0.171		0.18	1.58	0.908		-0.20	0.75	0.788	
Moderate	1.67	1.21	0.168		0.94	1.17	0.422		0.98	1.71	0.566		0.75	0.81	0.351	
Moderate+TSI	1.45	1.21	0.232		1.85	1.01	0.066	+	0.62	1.71	0.715		0.17	0.81	0.836	
Heavy	1.28	1.12	0.255		0.75	1.00	0.450		0.00	1.58	1.000		-0.61	0.75	0.417	
Heavy+TSI	1.53	1.12	0.175		1.03	1.07	0.335		-0.22	1.58	0.888		-0.38	0.75	0.608	

Clearcut	1.77	1.21	0.145	1.97	1.05	0.062	+	0.18	1.71	0.915	-0.61	0.81	0.452
Clearcut+TSI	1.24	1.21	0.306	1.55	1.03	0.134		0.06	1.71	0.970	-1.30	0.81	0.107

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Density was modeled using a negative binomial distribution. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] Models were not developed for quaking aspen due to lack of sufficient number of observations.

Table D.2. Pre- (2004) and post- (2018) outbreak live tree diameter distributions compared among (Treatment vs. Control) and within (Post vs. Pre) thinning treatments via Menning's Departure Index (*M*; Menning et al. 2007).

Species	Treatment vs. Control (Pre-outbreak)				Treatment vs. Control (Post-outbreak)				Post-outbreak vs. Pre-outbreak (Change)			
	M	Range	*P*		*M*	Range	*P*		*M*	Range	*P*	
Total												
Control		NA				NA			-0.16	-0.42–1.58	<0.001	**
Light+TSI	-0.15	-0.42–1.58	<0.001	**	-0.01	-0.26–1.74	0.190		-0.01	-0.27–1.73	<0.001	**
Moderate	-0.16	-0.42–1.58	<0.001	**	-0.04	-0.26–1.74	0.029	*	-0.04	-0.26–1.74	0.260	
Moderate+TSI	-0.14	-0.42–1.58	<0.001	**	0.03	-0.26–1.74	0.717		0.01	-0.28–1.72	<0.001	**
Heavy	-0.13	-0.42–1.58	<0.001	**	-0.02	-0.26–1.74	0.212		-0.05	-0.29–1.71	0.004	**
Heavy+TSI	-0.17	-0.42–1.58	<0.001	**	-0.01	-0.26–1.74	0.482		0.01	-0.25–1.75	0.001	**
Clearcut	-0.18	-0.42–1.58	<0.001	**	0.03	-0.26–1.74	0.760		0.06	-0.24–1.76	<0.001	**
Clearcut+TSI	-0.15	-0.42–1.58	<0.001	**	0.05	-0.26–1.74	0.298		0.04	-0.27–1.73	<0.001	**
Lodgepole pine												
Control		NA				NA			-0.23	-0.55–1.45	<0.001	**
Light+TSI	-0.27	-0.55–1.45	<0.001	**	-0.09	-0.32–1.68	0.029	*	-0.05	-0.28–1.72	0.053	+
Moderate	-0.22	-0.55–1.45	<0.001	**	-0.09	-0.32–1.68	0.059	+	-0.10	-0.33–1.67	0.019	*
Moderate+TSI	-0.26	-0.55–1.45	<0.001	**	-0.05	-0.32–1.68	0.743		-0.01	-0.28–1.72	0.014	*
Heavy	-0.23	-0.55–1.45	<0.001	**	-0.09	-0.32–1.68	0.082	+	-0.09	-0.31–1.69	<0.001	**
Heavy+TSI	-0.27	-0.55–1.45	<0.001	**	-0.05	-0.32–1.68	0.371		-0.01	-0.27–1.73	0.042	*
Clearcut	-0.26	-0.55–1.45	<0.001	**	-0.04	-0.32–1.68	0.660		-0.02	-0.29–1.71	0.458	
Clearcut+TSI	-0.26	-0.55–1.45	<0.001	**	-0.02	-0.32–1.68	0.751		0.01	-0.28–1.72	0.005	**
Subalpine fir												
Control		NA				NA			0.04	-0.18–1.82	0.009	**
Light+TSI	0.06	-0.18–1.82	0.531		0.09	-0.22–1.78	0.336		0.08	-0.23–1.77	<0.001	**
Moderate	-0.01	-0.18–1.82	0.513		0.01	-0.22–1.78	0.730		0.06	-0.17–1.83	0.482	

Moderate+TSI	0.13	-0.18–1.82	0.240		0.17	-0.22–1.78	0.093	+	0.08	-0.30–1.70	0.040	*
Heavy	0.06	-0.18–1.82	0.564		0.05	-0.22–1.78	0.660		0.03	-0.24–1.76	0.051	+
Heavy+TSI	-0.02	-0.18–1.82	0.015	*	-0.02	-0.22–1.78	0.040	*	0.04	-0.16–1.84	0.002	**
Clearcut	0.00	-0.18–1.82	0.238		0.06	-0.22–1.78	0.494		0.11	-0.17–1.83	<0.001	**
Clearcut+TSI	0.11	-0.18–1.82	0.254		0.15	-0.22–1.78	0.077	+	0.09	-0.28–1.72	0.032	*
Engelmann spruce												
Control		NA				NA			-0.01	-0.17–1.83	0.811	
Light+TSI	0.09	-0.17–1.83	0.297		0.15	-0.16–1.84	0.266		0.05	-0.26–1.74	0.247	
Moderate	0.00	-0.17–1.83	0.715		0.06	-0.16–1.84	0.539		0.05	-0.17–1.83	0.105	
Moderate+TSI	0.09	-0.17–1.83	0.269		0.13	-0.16–1.84	0.175		0.03	-0.25–1.75	0.063	+
Heavy	0.04	-0.17–1.83	0.460		0.11	-0.16–1.84	0.245		0.07	-0.20–1.80	0.028	*
Heavy+TSI	0.08	-0.17–1.83	0.133		0.18	-0.16–1.84	0.046	*	0.09	-0.25–1.75	0.002	**
Clearcut	0.08	-0.17–1.83	0.185		0.20	-0.16–1.84	0.067	+	0.11	-0.25–1.75	0.028	*
Clearcut+TSI	0.04	-0.17–1.83	0.533		0.14	-0.16–1.84	0.247		0.10	-0.20–1.80	0.051	+
Quaking aspen												
Control		NA				NA				–		
Light+TSI		–				–				–		
Moderate		–				–				–		
Moderate+TSI		–				–				–		
Heavy		–				–				–		
Heavy+TSI		–				–				–		
Clearcut		–				–			0.11	-0.23–1.77	<0.001	**
Clearcut+TSI		–				–			0.16	-0.21–1.79	0.001	**

Notes: Sign and magnitude of *M* indicate the direction (negative, left-shifted; positive, right-shifted) and distance of shift in the test distribution (Post, Trt.) compared to the reference distribution (Pre, Control). Minimum and maximum values of *M* indicate the range endpoints of the departure index, determined by the symmetry of the reference distribution (-1 to +1 for normal or uniform distributions). *P*-values indicate results of Kolmogorov-Smirnov (K-S) tests (Smirnov 1939), corresponding with symbols representing strength of evidence of a difference from the reference distribution according to $P < \alpha = 0.01^{**}, 0.05^{*}, 0.1^{+}$. NA's indicate cases in which the Control represented both reference and test distributions. Dashes (–) indicate treatments with no observations in the reference and/or test distributions. TSI, timber stand improvement.

Table D.3. Results of the mixed effects regression models for stand-scale live pre- (2004) and post- (2018) outbreak basal area and QMD by species[1] as a function of thinning treatment.

Predictor variables	Live basal area				Live QMD			
	β	SE	*P*		β	SE	*P*	
				PRE-OUTBREAK				
Total								
Light+TSI	-0.13	0.10	0.204		-0.35	0.11	0.001	**
Moderate	-0.24	0.11	0.025	*	-0.35	0.12	0.003	**
Moderate+TSI	-0.01	0.11	0.943		-0.36	0.12	0.002	**
Heavy	-0.04	0.10	0.699		-0.32	0.11	0.003	**
Heavy+TSI	-0.12	0.10	0.236		-0.48	0.11	<0.001	**
Clearcut	-0.16	0.11	0.146		-0.55	0.12	<0.001	**
Clearcut+TSI	-0.26	0.11	0.016	*	-0.50	0.12	<0.001	**
Lodgepole pine								
Light+TSI	-0.40	0.24	0.102		-0.33	0.20	0.111	
Moderate	-0.41	0.27	0.124		-0.28	0.21	0.182	
Moderate+TSI	-0.34	0.27	0.206		-0.49	0.21	0.017	*
Heavy	-0.13	0.25	0.603		-0.33	0.20	0.104	
Heavy+TSI	-0.25	0.25	0.310		-0.59	0.20	0.003	**
Clearcut	-0.54	0.27	0.047	*	-0.59	0.21	0.004	**
Clearcut+TSI	-0.43	0.27	0.114		-0.59	0.21	0.005	**
Subalpine fir								
Light+TSI	1.21	0.63	0.054	+	0.26	0.19	0.178	
Moderate	0.13	0.72	0.853		-0.08	0.21	0.682	
Moderate+TSI	1.39	0.69	0.042	*	0.45	0.21	0.030	*
Heavy	0.23	0.67	0.734		0.13	0.19	0.499	
Heavy+TSI	0.08	0.69	0.904		-0.03	0.19	0.896	
Clearcut	1.59	0.72	0.029	*	-0.21	0.21	0.298	
Clearcut+TSI	0.74	0.72	0.305		0.22	0.21	0.293	
Engelmann spruce								
Light+TSI	1.07	1.20	0.374		0.50	0.31	0.106	
Moderate	0.74	1.30	0.566		-0.26	0.27	0.329	
Moderate+TSI	1.43	1.30	0.270		0.07	0.27	0.791	
Heavy	0.21	1.20	0.863		0.04	0.25	0.882	
Heavy+TSI	0.76	1.20	0.526		0.50	0.25	0.045	*
Clearcut	0.81	1.30	0.532		0.24	0.27	0.384	
Clearcut+TSI	0.33	1.30	0.799		0.28	0.27	0.303	

				POST-OUTBREAK				
Total								
Light+TSI	0.78	0.19	<0.001	**	-0.03	0.11	0.804	
Moderate	0.45	0.20	0.027	*	-0.14	0.12	0.243	
Moderate+TSI	1.02	0.20	<0.001	**	0.03	0.12	0.770	
Heavy	0.54	0.19	0.004	**	-0.13	0.11	0.213	
Heavy+TSI	0.83	0.19	<0.001	**	-0.09	0.11	0.425	
Clearcut	1.08	0.21	<0.001	**	-0.07	0.12	0.520	
Clearcut+TSI	0.91	0.20	<0.001	**	0.00	0.12	0.993	
Lodgepole pine								
Light+TSI	0.40	0.36	0.276		-0.25	0.11	0.023	*
Moderate	0.11	0.39	0.788		-0.23	0.12	0.048	*
Moderate+TSI	0.57	0.39	0.146		-0.18	0.12	0.129	
Heavy	0.43	0.36	0.235		-0.27	0.11	0.013	*
Heavy+TSI	0.84	0.36	0.020	*	-0.18	0.11	0.089	+
Clearcut	0.42	0.39	0.289		-0.17	0.12	0.162	
Clearcut+TSI	0.73	0.39	0.064	+	-0.14	0.12	0.237	
Subalpine fir								
Light+TSI	1.19	0.59	0.044	*	0.26	0.19	0.177	
Moderate	0.23	0.65	0.725		0.02	0.21	0.937	
Moderate+TSI	1.41	0.65	0.030	*	0.42	0.21	0.043	*
Heavy	0.29	0.61	0.631		0.14	0.19	0.446	
Heavy+TSI	0.26	0.63	0.682		0.01	0.19	0.951	
Clearcut	1.59	0.67	0.018	*	-0.12	0.21	0.563	
Clearcut+TSI	0.79	0.67	0.238		0.28	0.21	0.173	
Engelmann spruce								
Light+TSI	1.65	1.17	0.157		0.55	0.27	0.043	*
Moderate	1.40	1.26	0.264		-0.26	0.24	0.278	
Moderate+TSI	1.80	1.26	0.153		0.18	0.23	0.434	
Heavy	1.04	1.17	0.371		0.26	0.21	0.221	
Heavy+TSI	1.38	1.17	0.235		0.45	0.21	0.038	*
Clearcut	1.77	1.26	0.161		0.37	0.23	0.116	
Clearcut+TSI	1.20	1.26	0.339		0.44	0.23	0.058	+

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Both basal area and QMD were modeled using a gamma distribution with log link. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). QMD, quadratic mean diameter. TSI, timber stand improvement.

[1] Models were not developed for quaking aspen due to lack of sufficient number of observations.

Table D.4. Results of the mixed effects beta regression models for stand-scale proportion of live post-outbreak (2018) spruce-fir (S-F) stem density and basal area by size class as a function of thinning treatment.

Predictor variables	Live S-F density			Live S-F basal area		
	β	SE	*P*	β	SE	*P*
TOTAL						
Treatment effect						
Light+TSI	-0.16	0.72	0.830	0.78	0.73	0.284
Moderate	0.29	0.76	0.703	0.40	0.78	0.604
Moderate+TSI	0.74	0.78	0.343	0.65	0.81	0.423
Heavy	-0.59	0.70	0.402	0.16	0.72	0.828
Heavy+TSI	-0.75	0.71	0.291	-0.51	0.73	0.486
Clearcut	0.30	0.76	0.695	-0.04	0.81	0.957
Clearcut+TSI	-0.62	0.75	0.408	-0.17	0.80	0.831
TSI effect[1]						
Moderate:TSI	0.45	0.81	0.581	0.25	0.83	0.766
Heavy:TSI	-0.16	0.65	0.806	-0.66	0.72	0.359
Clearcut:TSI	-0.92	0.77	0.231	-0.13	0.83	0.878
OVERSTORY (dbh ≥ 12 cm)						
Treatment effect						
Light+TSI	0.59	0.73	0.419	0.97	0.78	0.212
Moderate	0.49	0.79	0.538	0.51	0.83	0.537
Moderate+TSI	0.47	0.79	0.551	0.77	0.84	0.361
Heavy	0.17	0.73	0.817	0.18	0.76	0.812
Heavy+TSI	-0.40	0.74	0.588	-0.45	0.76	0.556
Clearcut	-1.14	0.81	0.159	-1.09	0.90	0.229
Clearcut+TSI	-0.14	0.80	0.864	-0.14	0.84	0.866
TSI effect						
Moderate:TSI	-0.02	0.84	0.985	0.26	0.87	0.766
Heavy:TSI	-0.57	0.74	0.440	-0.63	0.76	0.408
Clearcut:TSI	1.00	0.86	0.245	0.95	0.89	0.289
MIDSTORY (5 < dbh < 12 cm)						
Treatment effect						
Light+TSI	-0.08	0.77	0.921	-0.05	0.77	0.946
Moderate	-0.39	0.78	0.619	-0.47	0.79	0.556
Moderate+TSI	0.16	0.82	0.843	0.08	0.84	0.927

Heavy	0.06	0.71	0.935		0.06	0.72	0.930	
Heavy+TSI	-0.66	0.73	0.364		-0.67	0.74	0.368	
Clearcut	0.17	0.82	0.833		0.06	0.84	0.943	
Clearcut+TSI	-0.42	0.82	0.608		-0.44	0.83	0.596	
TSI effect								
Moderate:TSI	0.55	0.86	0.524		0.54	0.88	0.536	
Heavy:TSI	-0.72	0.71	0.314		-0.73	0.72	0.313	
Clearcut:TSI	-0.59	0.86	0.489		-0.50	0.87	0.563	
SAPLINGS (dbh < 5 cm)								
Treatment effect								
Light+TSI	-0.34	0.83	0.686		-0.26	0.88	0.763	
Moderate	-1.01	0.92	0.275		-0.74	0.97	0.446	
Moderate+TSI	-1.41	0.93	0.131		-1.13	0.98	0.249	
Heavy	-1.81	0.87	0.037	*	-1.28	0.91	0.157	
Heavy+TSI	-1.99	0.87	0.023	*	-1.91	0.91	0.036	*
Clearcut	-1.50	0.93	0.107		-1.59	0.98	0.104	
Clearcut+TSI	-2.71	0.94	0.004	**	-2.19	0.97	0.023	*
TSI effect								
Moderate:TSI	-0.40	1.00	0.689		-0.39	1.05	0.711	
Heavy:TSI	-0.18	0.85	0.835		-0.62	0.89	0.484	
Clearcut:TSI	-1.20	0.97	0.217		-0.60	1.00	0.546	
SEEDLINGS (height < 1.4 m)								
Treatment effect								
Light+TSI	-0.05	0.71	0.938					
Moderate	0.21	0.75	0.781					
Moderate+TSI	1.01	0.77	0.189					
Heavy	-0.60	0.69	0.388					
Heavy+TSI	-0.41	0.69	0.550					
Clearcut	0.88	0.77	0.254					
Clearcut+TSI	0.01	0.74	0.990					
TSI effect								
Moderate:TSI	0.81	0.81	0.320					
Heavy:TSI	0.18	0.62	0.768					
Clearcut:TSI	-0.87	0.78	0.262					

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the statistical difference between stands with and without TSI within the same major treatment.

REFERENCES

Menning, K. M., J. J. Battles, and T. L. Benning. 2007. Quantifying change in distributions: a new departure index that detects, measures, and describes change in distributions from population structures, size-classes and other ordered data. Oecologia 154:75–84.

Smirnov, N. V. 1939. Estimate of deviation between empirical distribution functions in two independent samples. Bulletin Moscow University 2:3–16.

Chapter 2. FUEL PROFILES AND CARBON STORAGE FOLLOWING BARK BEETLE OUTBREAKS: INSIGHTS FROM A HISTORICAL THINNING EXPERIMENT

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ABSTRACT

Anticipating the consequences of disturbance interactions on ecosystem structure and function remains a critical management priority as disturbance activity increases in response to changing climate conditions. Across the Northern Hemisphere, extensive tree mortality from recent bark beetle outbreaks raises concerns about fire hazard and post-fire forest function. Density reduction (i.e., thinning) treatments may reduce outbreak severity and fire hazard, but not without tradeoffs for other management objectives (e.g., carbon storage). Further, empirical tests of pre-outbreak treatment effects on outbreak and fire interactions remain largely unexplored. We measured forest structure in experimental old-growth subalpine forest stands following a recent (early 2000s) severe mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak to examine the effects of historical (1940s) thinning treatments on gray stage post-outbreak (1) fuel profiles and (2) aboveground carbon storage. Compared to uncut stands, historically thinned stands had ~2x lower surface and ~2–3x greater canopy fuel loads, greater fine-scale spatial heterogeneity of canopy fuels, and ~2x greater live biomass following the MPB outbreak, though total aboveground carbon was similar across all stands. These findings suggest potential for altered post-outbreak fire hazard (e.g., surface and canopy fire potentials, resistance to control) in thinned stands. Additional implications of historical thinning for long-term carbon trajectories and ecosystem services (e.g., wildlife habitat) highlight the legacy of past management on directing forest response to interacting disturbances.

INTRODUCTION

Disturbance activity is increasing in forests across the globe, driven directly and indirectly by climate change (Seidl and others 2017; Sommerfeld and others 2018). As spatial overlap among disturbance mosaics becomes increasingly probable, improving our understanding of disturbance interactions is critical. Feedbacks among multiple disturbances may cause unexpected or nonlinear changes in ecosystem structure and function (Buma 2015), threatening ecosystem services and ecological resilience (Seidl and others 2016). In temperate forests, bark beetle outbreaks (Kautz and others 2017) and wildfires (Jolly and others 2015) are prominent natural disturbances and are projected to increase in response to warmer and drier conditions (Bentz and others 2010; Westerling 2016). Recent (1990s–2000s) outbreaks of native bark beetles (Coleoptera: Curculionidae: Scolytinae) have killed trees across tens of millions of ha of forests in the USA (Meddens and others 2012), Canada (Kurz and others 2008), and central Europe (Kautz and others 2011), while annual area burned, high-severity burn area, and number of large fires have increased over the past three decades (Dennison and others 2014; Westerling 2016; Hanes and others 2018; Parks and Abatzoglou 2020). As fires inevitably intersect with bark beetle outbreaks (Halofsky and others 2020), heightened public attention and management concerns regarding potential fire behavior and effects on forest resources (Jenkins and others 2012) highlight the importance of further understanding this disturbance interaction.

Bark beetle outbreaks and wildfire can interact in complex ways that present challenges for management of forest resources and ecosystem services. Interactions are highly dependent on outbreak stage (Simard and others 2011; Hicke and others 2012b; Jenkins and others 2012; Donato and others 2013a, 2013b; Carlson and others 2017), forest type and dominant fire regime (Baker 2009), and burning conditions (Harvey and others 2014b; Sieg and others 2017). Beetle outbreaks have not been shown to increase fire likelihood (Kulakowski and Jarvis 2011; Meigs and others 2015) or area burned (Kulakowski and Veblen 2007; Hart and others 2015; Hart and Preston 2020). However, tree mortality and alteration of fuel profiles following outbreaks can affect fire hazard (Jenkins and others 2014) and resistance to control (Page and others 2013) when fire does burn through beetle-killed areas. Tree mortality from outbreaks can influence fire hazard (i.e., properties of fuels and other conditions that determine probability of ignition and fire spread; NWCG 2018) by altering surface and crown fire potentials though redistribution of live and dead fuels over time (Simard and others 2011) and changing microclimate conditions (Page and Jenkins 2007). Beetle-killed trees also increase resistance to control (i.e., relative difficulty of constructing and holding a control line as affected by resistance to line construction and fire behavior; NWCG 2018) by elevating firefighter safety hazards, complicating fire suppression operations, and contributing to dangerous post-fire conditions (e.g., increased fall risk from fire-weakened snags) (Page and others 2013).

Outbreak severity and fire severity may also interact to alter post-fire ecosystem function (Talucci and Krawchuk 2019). Forests play a major role in the global carbon (C, hereafter) cycle, with sequestration an increasingly common policy and management objective in forested areas (Smith and others 2019). By killing susceptible host trees, bark beetle outbreaks redistribute C from live to dead pools (Hansen and others 2015), influencing forest C sequestration and emissions as trees decay over time (Kurz and others 2008). Combustion of beetle-killed snags further alters carbon cycles by reducing aboveground biomass and increasing deep charring on trees, influencing total carbon storage, availability, and longevity (Talucci and Krawchuk 2019). Consequently, implications of outbreak-fire interactions on forest resources and ecosystem services are important considerations for forest managers.

Anticipating and mitigating the potential consequences of beetle and fire interactions on forest structure and function represent key management priorities (Morris and others 2017). Silvicultural treatments that alter stand structure and composition (e.g., thinning, salvage logging) may increase resistance to bark beetle outbreaks (e.g., DeRose and Long 2014) and reduce fire hazard (e.g., Crotteau and others 2018a) and resistance to control (e.g., Donato and others 2013b), though treatment efficacy is dependent on intensity and timing. However, silvicultural treatments may also present a tradeoff with total aboveground C storage (Dobor and others 2020) since treatments necessitate removal of large quantities of biomass. Most studies exploring management effects on fire hazard and C storage following beetle outbreak have focused on post-outbreak salvage logging (e.g., Bradford and others 2012; Collins and others 2012; Donato and others 2013b; Griffin and others 2013; Mathys and others 2013; Hood and others 2017) or pre-outbreak thinning over short time frames between treatment and outbreak (e.g., ~4 years; Crotteau and others 2018a). Thus, a key research gap remains concerning examination of pre-outbreak treatment longevity on outbreak and fire interactions. Simulation studies can predict future trajectories of treatment effects on post-outbreak stand conditions (e.g., Ager and others 2007; Collins and others 2012; Donato and others 2013b), but empirical tests of treatment longevity on post-outbreak fire hazard and C dynamics remain largely unexplored.

Here, we conducted a field study to examine the effects of historical stand-thinning treatments on post-outbreak (gray stage, ~8 years post-outbreak) fire hazard and C dynamics. Using a long-term experimental study of old-growth lodgepole pine (*Pinus contorta* var. *latifolia*) stands thinned in the mid-20th century and subsequently affected by a severe mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak in the early 21st century, we asked: (1) *How are fuel profiles after bark beetle outbreak influenced by legacies of historical stand-*

thinning treatments? Specifically, what are the effects of historical thinning intensity on post-outbreak (a) surface fuels, (b) canopy fuels, and (c) fine-scale fuel heterogeneity? (2) *How is aboveground C storage after bark beetle outbreak influenced by legacies of historical stand-thinning treatments?* Specifically, what are the effects of historical thinning intensity on post-outbreak live and dead aboveground C biomass?

Since historical stand-thinning treatments had less MPB-caused tree mortality than uncut stands (Morris and others *in review*), live and dead surface fuels (Q1a) were expected to decrease with greater historical thinning intensity (Jenkins and others 2008). Similarly, live canopy fuels (Q1b) were expected to increase, and dead canopy fuels to decrease, with greater historical thinning intensity (Jenkins and others 2012). Fine-scale fuel heterogeneity (Q1c) was expected to vary with historical thinning intensity, with heavier treatments (i.e., near-total tree removal) having lower heterogeneity than uncut stands, and lighter treatments (i.e., partial tree removal) having greater heterogeneity than uncut stands due promotion of stand complexity by non-stand-replacing disturbances (Donato and others 2013a; Crotteau and others 2018b). Finally, aboveground C storage (Q2) was expected to increase for live biomass and decrease for dead biomass with greater historical thinning intensity (Hansen and others 2015). Total aboveground C was expected to be similar across all stands based on the growth and development of thinned stands for 60 years before the outbreak (D'Amato and others 2011; Donato and others 2013b).

METHODS

Study Area

The Fraser Experimental Forest (39°53' N, 105°53' W), Colorado, USA, is located in subalpine forest on the Arapaho-Roosevelt National Forest and ranges in elevation from 2,700 to 3,900 m

(Alexander and others 1985). Mean annual temperature is 3°C (range -7 to 14°C), and mean annual precipitation is 550 mm (two-thirds snow) (PRISM Climate Group 2012). Prevalent soils include coarse textured Cryochrepts derived from gneiss and schist (Alexander and others 1985; Huckaby and Moir 1998). Forest stands established following stand-replacing fire in 1685 (Bradford and others 2008). Overstory vegetation is dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) seral to subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) among scattered aspen (*Populus tremuloides*). Understory vegetation is sparse, consisting mainly of conifer regeneration, *Shepherdia canadensis*, and *Vaccinium spp.* Study stands are representative of subalpine mixed-species forest communities in the Rocky Mountains (Huckaby and Moir 1998), and dominated by infrequent (135–280 years; Baker 2009) stand-replacing fire events driven primarily by regional-scale climatic variation (Huckaby and Moir 1995; Sibold and others 2006).

Study Design

Experiment details are summarized from Wilm and Dunford (1948) and more recently in Morris and others (*in review*). Twenty 2-ha experimental harvest-cutting units were established in 1938 within >300-year-old stands (Moir and others Unpublished). Units were surrounded by 19 m wide buffers to mitigate edge effects from adjacent treatments and arranged in a block design to capture variability in environmental conditions across the area. Prior to thinning, all units were characterized by similar structure and species composition: mean overstory (diameter at breast height [dbh] ≥ 9 cm) density and basal area ranged from 741–988 stems/ha and 33.6–38.2 m^2/ha, respectively; mean volume of merchantable timber (dbh ≥ 24 cm) was 70.0 m^3/ha (range 44.3–99.1 m^3/ha). In 1940, five different thinning treatments were applied to four replicate units: *clearcut*, 0 m^3/ha merchantable timber reserved (all trees ≥ 24 cm dbh removed); *heavy*, 11.7

m^3/ha reserved; *moderate*, 23.3 m^3/ha reserved; *light*, 35.0 m^3/ha reserved; and *control*, 70.0 m^3/ha reserved (uncut). Additional TSI thinning of low vigor trees (dbh 9–24 cm) was conducted on a random half of each thinned unit; mean removal was 138 trees/ha (range 72–287 trees/ha). All timber was felled by hand and removed with horses. Slash was dispersed over one half and swamper-burned on the other half of each thinned unit. Six decades later, the experimental forest experienced a severe MPB outbreak between 2003–2010 (Vorster and others 2017). Across all experimental units, MPB killed 59% and 78% of susceptible host tree density and basal area, respectively (Morris and others *in review*). See Morris and others (*in review*) for detailed post-outbreak community stand dynamics.

Field Data Collection

We measured post-outbreak stand structure and fuels during summer 2018 (~8 years post-outbreak) within 0.25 ha (50 x 50 m) plots located in the center of each thinning and TSI treatment combination (see Appendix A in Morris and others *in review*). Following exclusion of several plots due to unsuitable or outlying conditions, 28 total plots were sampled across each of the treatment categories: 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). Plots were positioned between 2,799 to 2,999 m elevation on northerly aspects with 5.6 to 25.9° slopes. Sampling design was based on established protocols (Appendix E; Simard and others 2011; Donato and others 2013a). All measures were scaled up to per ha values.

Surface fuel profiles were quantified according to Brown (1974). Dead surface fuels (height < 2 m) were measured along ten 10-m planar intercept transects. Down woody debris (DWD) was categorized according to standard time-lag size classes: 1-h fuels, <0.64 cm diameter; 10-h fuels, 0.64–2.54 cm; 100-h fuels, 2.54–7.62 cm; and 1000-h fuels, >7.62 cm.

Along each transect, 1- and 10-h fuels were tallied for the first 2 m; 100-h fuels were tallied for the first 3 m; and 1000-h fuels were measured for species, decay class (1–5; Lutes and others 2006), and diameter along the entire 10 m. Litter and duff depths were measured at 0.5 and 1.5 m along each transect, and dead fuel depths (distance from highest dead particle to bottom of litter layer) were recorded at three 0.5-m intervals. Percent cover and height of live graminoids, forbs, and low (height < 0.2 m) and tall (height ≥ 0.2 m) woody shrubs were measured in 1-m diameter microplots at the ends of each 10-m transect (20 total microplots). Species and height of live tree seedlings (height 0.1–1.4 m) were recorded within three 2 x 25 m belt transects (50 m^2 each).

Canopy fuel profiles were quantified for all live and dead trees (height ≥ 1.4 m) rooted within three belt transects based on diameter: dbh < 5 cm, 2 x 25 belts (50 m^2 each); dbh ≥ 5 cm, 4 x 50 m belts (200 m^2 each). Species, dbh, total height, and crown base height were measured for all trees; decay class (1–5, adapted from Lutes and others 2006) and presence of broken top were also recorded for dead trees. Canopy cover of live and dead trees was recorded using a spherical densiometer facing each cardinal direction at 12 points evenly distributed across the plot area.

Fuel & Biomass Calculations

Field measures and allometric equations were used to generate fuel profiles for each stand (Appendix F). Surface fuel profiles included biomass of DWD and live understory vegetation. Biomass of DWD was estimated by size class (fine woody debris [FWD]: 1-h, 10-h, 100-h fuels; coarse woody debris [CWD]: 1000-h fuels) using geometric scaling and decay class-specific relative densities (Brown 1974). Biomass of CWD was summarized separately for sound (decay class ≤ 3) and rotten (decay class > 3) fuels. All DWD estimates were slope-corrected. Dry biomass of live understory vegetation was estimated for each functional group (graminoids, forbs, low and tall shrubs) using equations based on percent cover and height of the dominant species (Olson and Martin 1981; Prichard and others 2013). Seedling biomass was estimated using total tree weight equations based on species and height (Brown 1978; Means and others 1994). Total live surface fuel biomass was aggregated into herbaceous (graminoids, forbs) and woody (low and tall shrubs, seedlings) classes.

Canopy fuel profiles included crown fuel biomass, available canopy fuel load (ACFL), canopy bulk density (CBD), canopy base height (CBH), canopy cover, and foliar moisture. Biomass of live and dead crown fuels (foliage, 1-h, 10-h, 100-h branch size classes) was estimated for each tree using species- and region-specific equations based on dbh and/or height (Brown 1978; Standish and others 1985). For dead trees, crown fuel was corrected for branch volume and density loss based on decay class. Volume loss of 1-h fuels was designated as 0% for decay class 1 and 100% for all other classes; loss of 10- and 100-h fuels was designated as 0%, 20%, 50%, 80%, and 100% for decay class 1–5, respectively (Donato and others 2013a). Density loss was designated as 4%, 17%, 28%, 46%, and 67% for decay class 1–5, respectively (Kueppers and others 2004; Bradford and others 2008). For broken-top trees, crown fuel was corrected using a ratio multiplier of remaining crown length to original crown length derived from a regression of crown length ~ dbh for 1,574 unbroken trees ($R^2_{adj} = 0.64$). Available canopy fuel load (ACFL) was calculated as the sum of total foliage, total dead 1-hr fuels, and half live 1-h fuels for all trees (Reinhardt and others 2006; Donato and others 2013a). We distributed ACFL along the crown length of each tree in 0.25 m bins, summing by bins across all trees to generate vertical canopy fuel profiles for each stand (Simard and others 2011; Donato and others 2013a). Canopy bulk density (CBD) was calculated as the maximum running mean across 3-m of the vertical profile (Reinhardt and others 2006). Canopy base height (CBH) was calculated as the lowest height at which CBD exceeded 0.04 kg/m^3 (Sando and Wick 1972; Cruz and others 2004; Donato and others 2013a). Canopy-level foliar moisture was calculated for each stand using an abundance-weighted average of live and dead foliage (Donato and others 2013a). We assumed 100% moisture for live needles and reduced moisture for dead needles: 10% for lodgepole pine (Jolly and others 2012) and 5% for subalpine fir and Engelmann spruce (no estimates available; Donato and others 2013a).

To capture the effects of historical thinning on fine-scale spatial heterogeneity of post-outbreak fuel profiles, we calculated within-stand (i.e., among transects) coefficient of variation (CV) for broad classes of surface and canopy fuels (Fraterrigo and Rusak 2008; Donato and others 2013a). For ACFL, we evaluated heterogeneity in both horizontal and vertical dimensions. Horizontal heterogeneity in ACFL was calculated for separate canopy strata, distributed across the height range of the data: top (height $\geq$ 16 m), middle (8 $\leq$ height < 16 m), and bottom (height < 8 m) strata. Vertical heterogeneity in ACFL was calculated among 1-m bins.

We summed individual surface and canopy fuel components to estimate total, live, and dead aboveground C storage, assuming biomass to be 50% C (Schlesinger 1991).

Statistical Analyses

To test the effects of historical thinning on post-outbreak fire hazard and aboveground C storage, we specified generalized linear mixed effects models predicting fuel and C variables as a function of thinning intensity. Models were specified to reflect the study design with major treatment and TSI thinning terms treated as nested fixed effects. Block was included as a random effect in each model to account for variable conditions across treatment replicates. Response variables (mean, CV) were modeled by gamma (positive continuous response) or beta (proportional continuous response) distributions. Significance for all statistical tests was assessed according to the following α-levels: strong ($P < 0.01$), moderate ($P < 0.05$), and suggestive ($P < 0.1$) evidence of differences. This approach minimizes the risk of overlooking ecologically meaningful effects due to modest sample size (i.e., Type II error). Analyses were conducted in R (R Core Team 2020) using the packages *lme4* (Bates and others 2015) and *glmmTMB* (Brooks and others 2017) for model fitting and *jtools* (Long 2020) for model visualization.

RESULTS

Following the outbreak, historically thinned stands had greater live (and lower dead) basal area and density than uncut stands (Fig. 2.1). Post-outbreak basal area was ~2–3 times greater for live trees (Fig. 2.1A) and half as much for dead trees (Fig. 2.1B) in most thinned stands compared to the control. Dead QMD was ~2 times less in most historically thinned stands compared to the control (Fig. 2.1D), while live QMD was similar across all stands (Fig. 2.1C). Live overstory (dbh ≥ 12 cm) density was ~2–3 greater in most thinned stands than the control (Fig. 2.1E), though dead overstory density was similar across all stands (Fig. 2.1G–F). In contrast, live understory (dbh < 12 cm) density was similar across all stands, with the exception of the moderate intensity treatment (Fig. 2.1H). Density of dead understory trees was ~2–9 times greater in thinned stands than the control for trees with fine fuels attached (Fig. 2.1I) but did not differ from the control for trees with fine fuels fallen (Fig. 2.1J). TSI had little additional effect on post-outbreak structure (Fig. 2.1). See Appendix G for full statistical outputs of all stand structural variables.

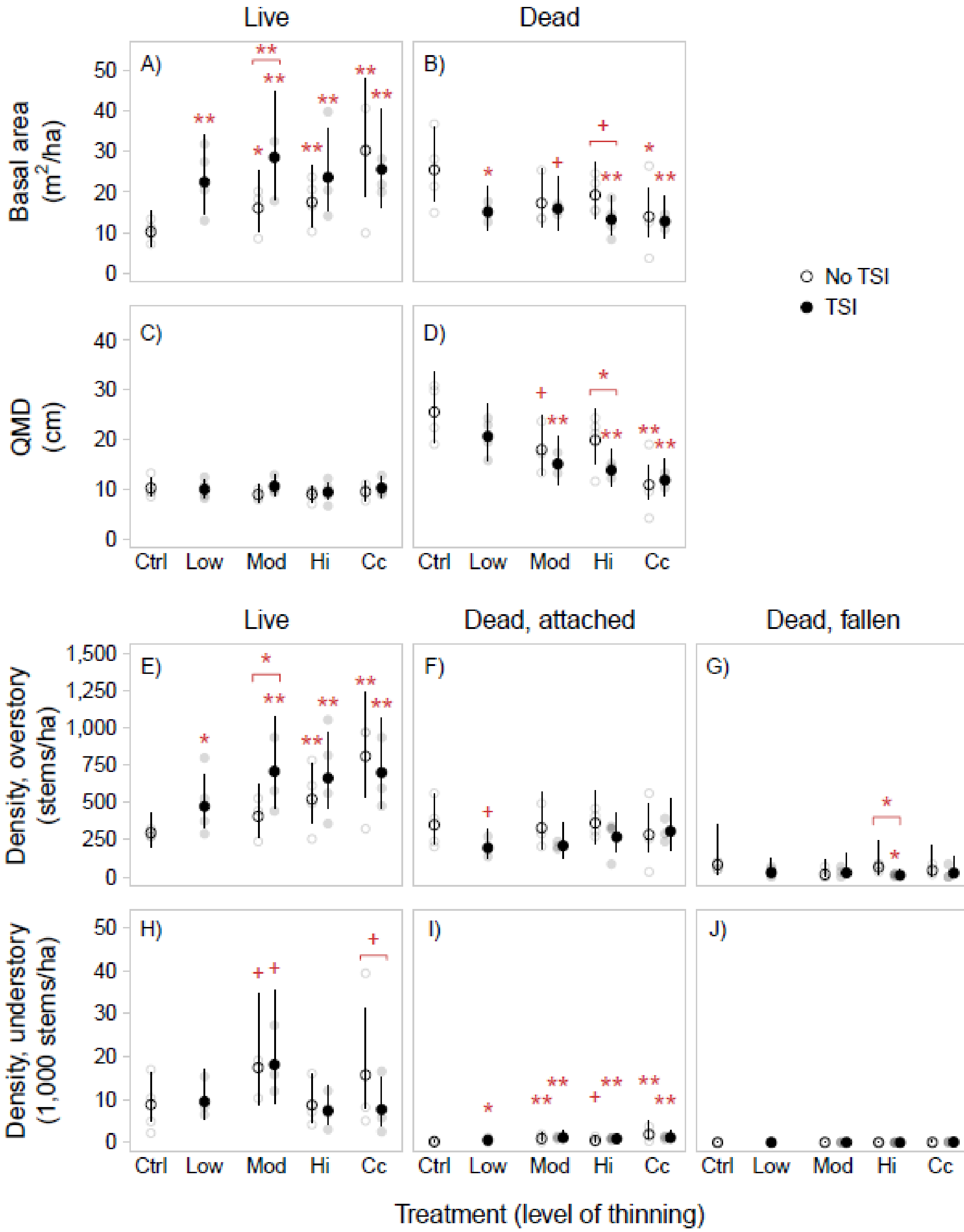

Figure 2.1. Post-outbreak stand structure across historical thinning treatments. Black circles represent predicted means with 95% confidence intervals. Gray points represent observed mean values for each plot replicate. Treatments increase in level of thinning from left to right (Ctrl = control; Low = light; Mod = moderate; Hi = heavy; Cc = clearcut). Closed and open circles represent thinning with and without timber stand improvement (TSI), respectively. Threshold for overstory (**E**–**G**) vs. understory (**H**–**J**) density is 12 cm dbh. Dead trees were classified with fine fuels attached (**F**, **I**) if decay class 1, otherwise fine fuels fallen (**G**, **J**). Asterisks represent difference from the control according to P < 0.01**, 0.05*, 0.1+. Panels **A** and **C** are reproduced from Morris and others (*in review*).

Fuel Profiles

Overall, historically thinned stands had lower post-outbreak surface fuel loads (Fig. 2.2) and greater canopy fuel loads (Figs. 2.3 and 2.4) compared to uncut stands. Thinned stands generally had surface fuel profiles characterized by lower DWD and live biomass (Fig. 2.2); canopy fuel profiles with greater total foliage and branch biomass, ACFL, and cover (Fig. 2.3); and greater fine-scale spatial heterogeneity in most canopy fuel variables (Fig. 2.5) than the control. See Appendix H for full statistical outputs of all fuel profile variables.

Most post-outbreak surface fuel loads were lower in historically thinned stands compared to uncut stands (Fig. 2.2). 10-h fine fuel loads (Fig. 2.2B), 1000-h sound coarse fuel loads (Fig. 2.2D), and live herbaceous (Fig. 2.2I) and woody (Fig. 2.2J) biomass were ~2 times lower in most thinned stands compared to the control. Duff depth was ~2 times greater in most thinned stands than the control (Fig. 2.2G). 100-h fuel load (Fig. 2.2C) and depths of litter (Fig. 2.2F) and dead fuel (Fig. 2.2H) were similar to the control for most thinned stands. 1-h (Fig. 2.2A) and 1000-h rotten (Fig. 2.2E) fuel loads did not differ across treatments. TSI had little additional effect on post-outbreak surface fuel profiles, but further reduced live woody biomass for moderate and heavy treatments (Fig. 2.2J).

Most post-outbreak canopy fuel loads were greater in historically thinned stands compared to uncut stands (Figs. 2.3 and 2.4). Thinned stands had greater total foliage biomass (~2–3x; Fig. 2.3A), 1- and 10-h branch fuels (~0.2–0.5x; Fig. 2.3D, G), ACFL (~2x; Fig. 2.3M), and canopy cover (~1.5x; Fig. 2.3P) than the control. Total trends were driven heavily by live fuels: live foliage biomass (Fig. 2.3B), 1-, 10-, and 100-h branch fuels (Fig. 2.3E, H, K), ACFL (Fig. 2.3N), and canopy cover (Fig. 2.3Q) were ~2–3 times greater in most thinned stands than the control. CBH was ~3 times higher in most thinned treatments than the control (Figs. 2.4B and 2.6). Mean CBD (Figs. 2.4A and 2.6) and foliar moisture (Fig. 2.4C) in thinned stands were similar to the control, but vertical distribution of CBD differed across treatments (Fig. 2.6). CBD was concentrated at greater canopy heights and displayed lower variability among plot replicates in heavily thinned stands compared to the control and lighter thinning intensities (Fig. 2.6). TSI had little additional effect on post-outbreak canopy fuel profiles (Figs. 2.3 and 2.4).

Post-outbreak fine-scale spatial heterogeneity in fuels within historically thinned stands was greater than uncut stands for most canopy variables, and similar for most surface variables (Fig. 2.5). Within-stand CV in both horizontal and vertical dimensions of ACFL was greater in thinned stands compared to the control (Fig. 2.5). Horizontal heterogeneity in ACFL was ~1.5 times greater in most historically thinned stands than the control for both top (height ≥ 16 m; Fig. 2.5H) and bottom (height < 8 m; Fig. 2.5J) canopy strata. CV in ACFL for middle canopy strata did not differ between most thinned and stands and the control (Fig. 2.5I). Vertical heterogeneity in ACFL was ~1.2 times greater in thinned stands than the control for the heaviest treatment intensities (Fig. 2.5K). Within-stand CV in dead canopy cover was ~2 times greater in thinned stands than the control (Fig. 2.5F). Conversely, within-stand CV in total (Fig. 2.5D) and live (Fig. 2.5E) canopy cover was lower in most thinned stands compared to the control. Within-stand CV in CBH was lower than the control for the most heavily thinned stands (Fig. 2.5G). For surface fuel variables, fine-scale spatial heterogeneity was similar across all stands. Within-stand CV in FWD (Fig. 2.5A), CWD (Fig. 2.5B), and fuel depth (Fig. 2.5C) did not differ across treatments, except for light+TSI which had lower heterogeneity in FWD (Fig. 2.5A) and greater heterogeneity in CWD (Fig. 2.5B) compared to the control. TSI had little additional effect on post-outbreak fine-scale spatial heterogeneity in fuel profiles (Fig. 2.5).

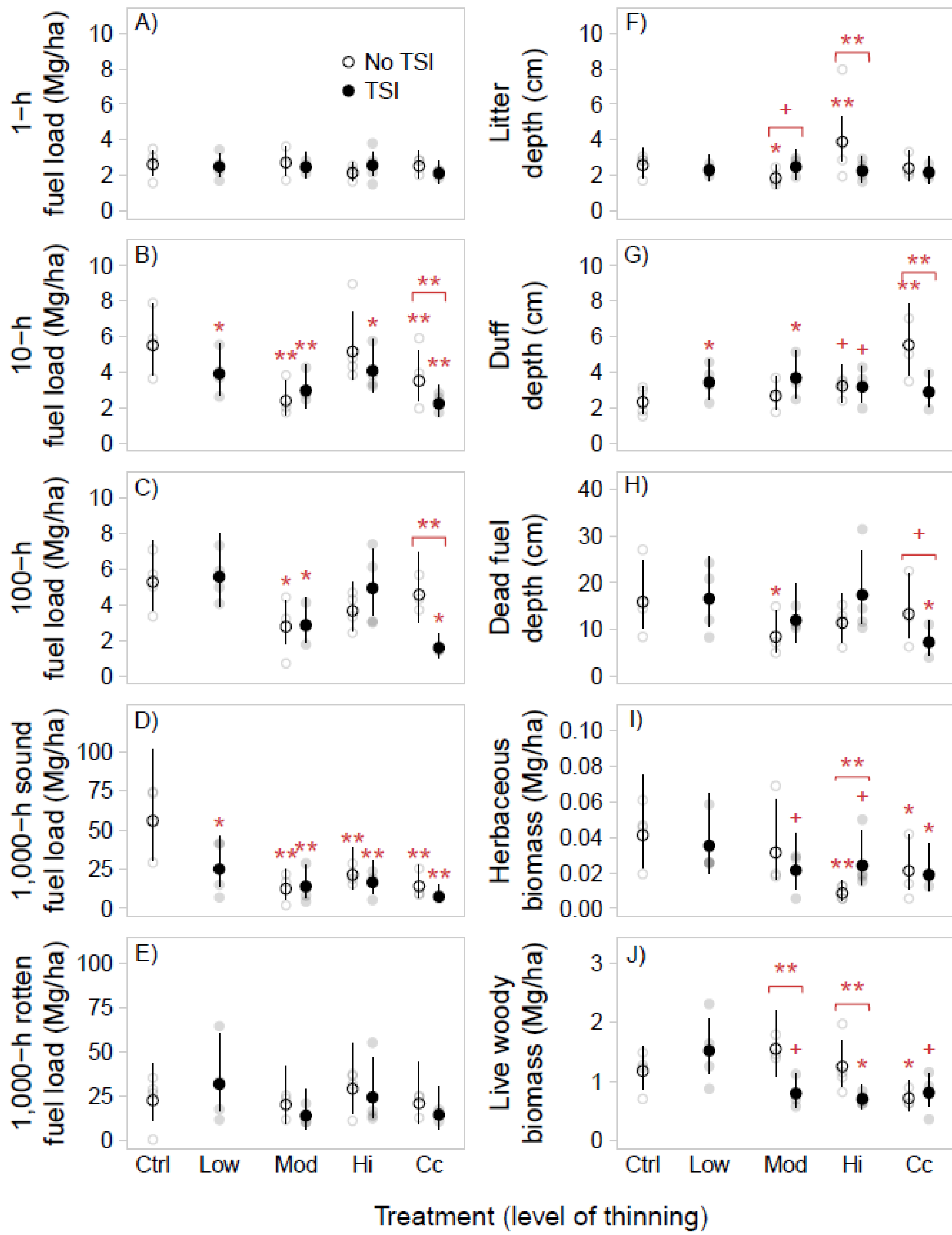

Figure 2.2. Post-outbreak surface fuels across historical thinning treatments. Symbols are described in Fig. 2.1. Asterisks represent difference from the control according to $P < 0.01^{**}$, 0.05^{*}, 0.1^{+}.

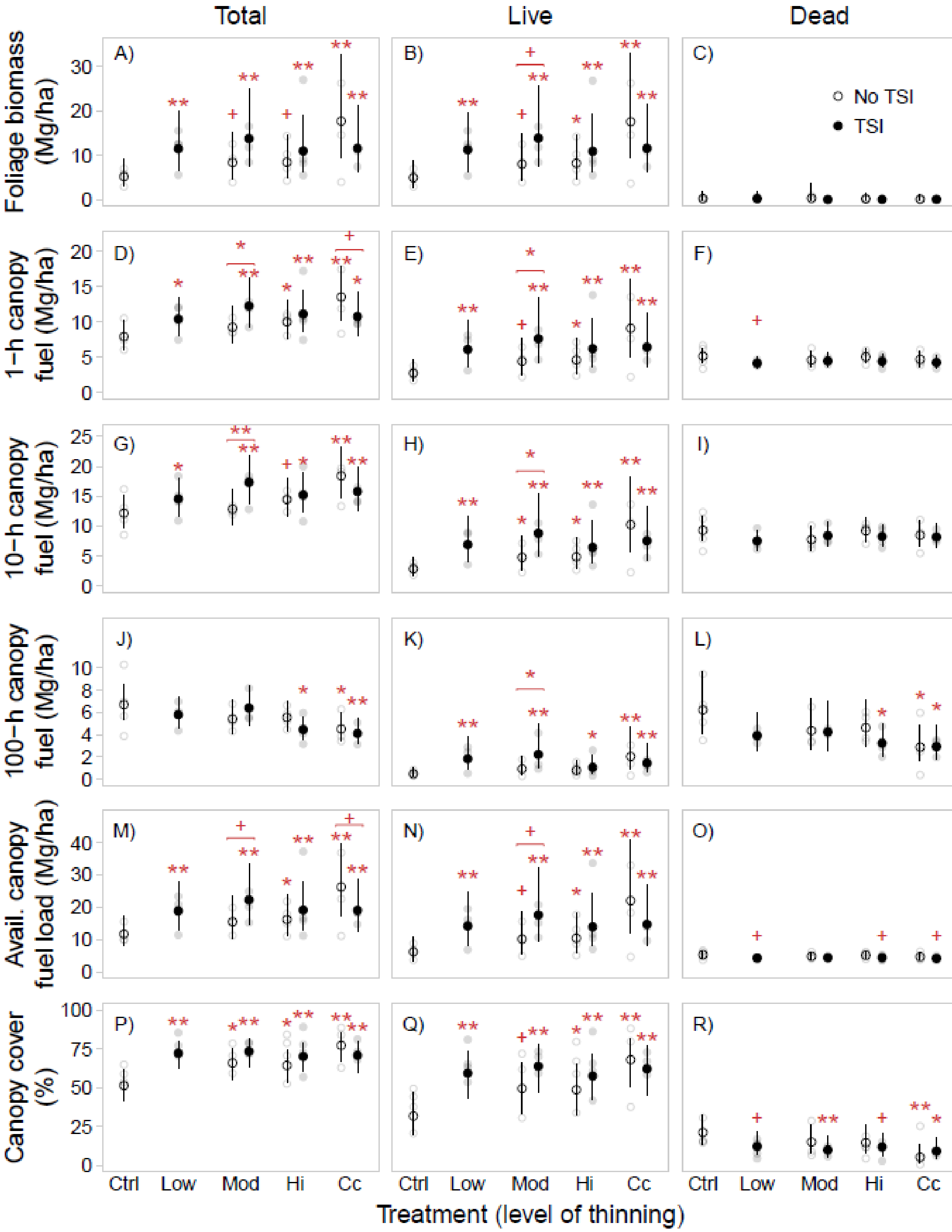

Figure 2.3. Post-outbreak canopy fuels across historical thinning treatments. Symbols are described in Fig. 2.1. Asterisks represent difference from the control according to $P < 0.01^{**}$, 0.05^{*}, 0.1^{+}.

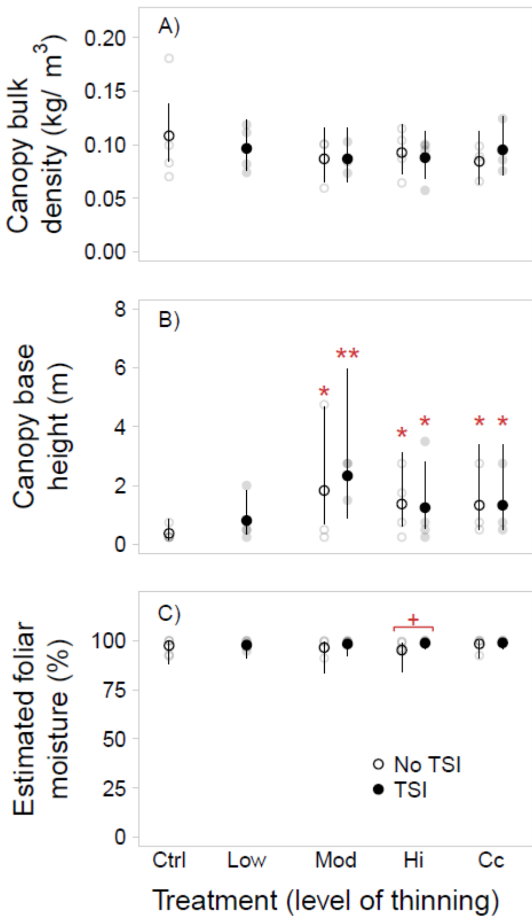

Figure 2.4. Post-outbreak (**A**) canopy base height, (**B**) canopy bulk density, and (**C**) stand-level foliar moisture. Symbols are described in Fig. 2.1. Asterisks represent difference from the control according to $P < 0.01^{**}$, 0.05^{*}, 0.1^{+}.

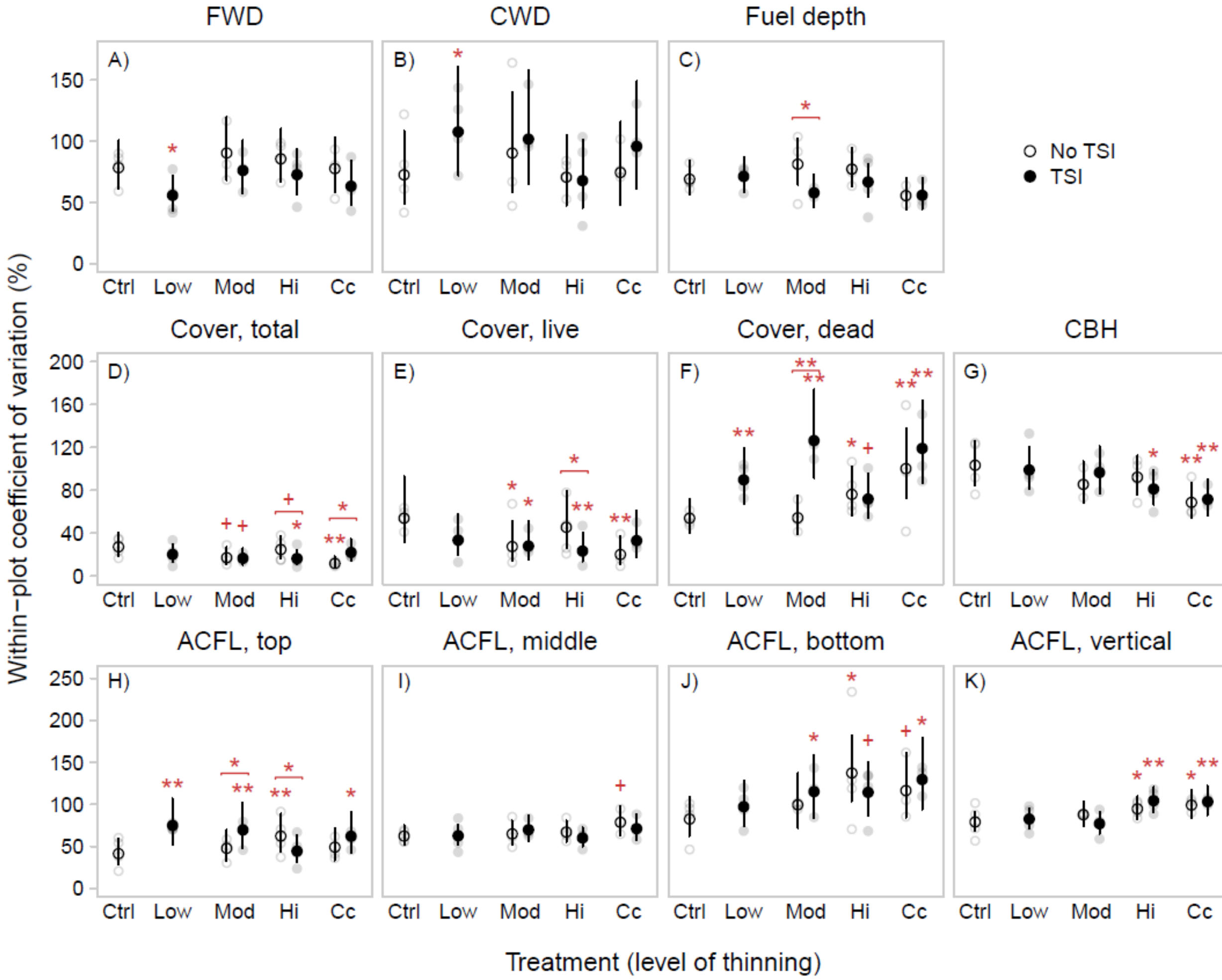

Figure 2.5. Within-stand spatial heterogeneity in fuels across historical thinning treatments. Symbols are described in Fig. 2.1. Heterogeneity in surface fuels is shown for (**A**) fine woody debris (FWD; 1-, 10-, and 100-h particles), (**B**) coarse woody debris (CWD; sound and rotten 1000-h particles), and (**C**) fuel depth (sum of litter and duff). Heterogeneity in canopy fuels is shown for (**D–F**) canopy cover, (**G**) crown base height (CBH; includes live and dead trees), and (**H–J**) horizontal and (**K**) vertical dimensions of available canopy fuel load (ACFL). Horizontal ACFL is shown for (**H**) top (height ≥ 16 m), (**I**) middle (8 ≤ height < 16 m), and (**J**) bottom (height < 8 m) canopy strata. Asterisks represent difference from the control according to $P <$ 0.01**, 0.05*, 0.1^{+}.

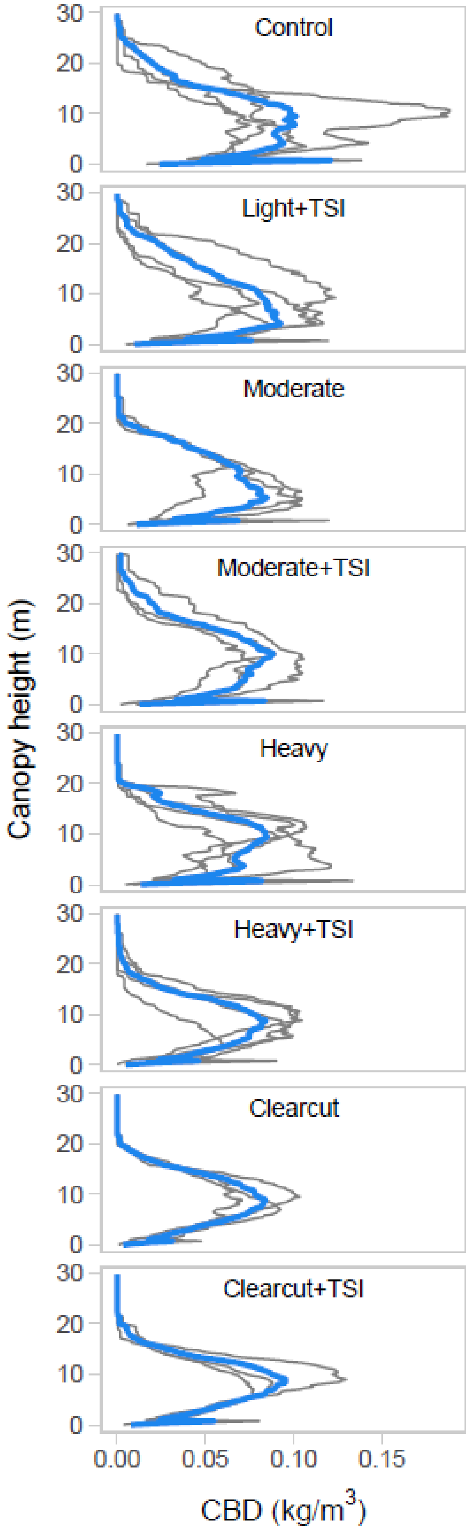

Figure 2.6. Vertical profiles of post-outbreak canopy bulk density (CBD) across historical thinning treatments. Blue lines represent the mean profile among all plot replicates (gray lines).

Aboveground C Storage

Post-outbreak aboveground C storage was greater for live biomass and lower for dead biomass in historically thinned stands compared to uncut stands but was similar for total biomass across all treatments (Fig. 2.7). Aboveground C biomass was ~2 times greater for live (Fig. 2.7B) and ~2 times lower for dead (Fig. 2.7C) pools in thinned stands compared to the control. However, biomass of total aboveground C did not differ among treatments, except for moderate and clearcut+TSI which had ~25% lower total C biomass than the control (Fig. 2.7A). TSI had little additional effect on post-outbreak C storage, further increasing live (moderate) and reducing dead (heavy, clearcut) biomass for some treatments, but not all (Fig. 2.7). See Appendix I for full statistical outputs of C storage variables.

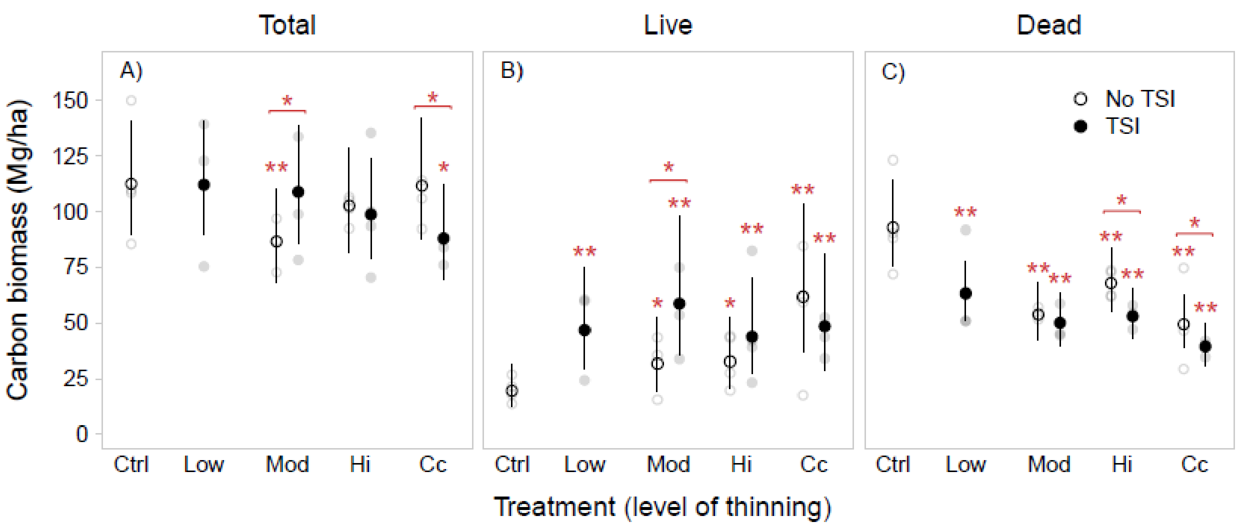

Figure 2.7. Post-outbreak aboveground carbon biomass across historical thinning treatments. Symbols are described in Fig. 2.1. Asterisks represent difference from the control according to $P < 0.01^{**}, 0.05^{*}, 0.1^{+}$.

DISCUSSION

Historical stand-thinning treatments had lasting legacies on fuel profiles and aboveground C storage following the MPB outbreak. Bark beetle outbreaks result in highly altered fuel complexes in which dead woody fuels and live surface fuels dominate (Page and Jenkins 2007). Compared to uncut stands, post-outbreak dynamics in thinned stands were characterized by lower surface and greater canopy fuel loads, greater spatial heterogeneity of fuels, and C stored predominantly in live biomass. These results suggest potential for altered fire hazard and C trajectories post-outbreak in thinned stands and highlight the role of past management on directing ecosystem response to interacting disturbances.

Legacies of Historical Thinning on Post-Outbreak Fuel Profiles

Surface fuels— Our findings suggest that historical stand-thinning treatments have long-lasting effects on mitigating surface fuel loads from MPB outbreaks, at least into the gray stage post-outbreak. This is consistent with our expectations since lower tree mortality from MPB in thinned stands (Morris and others *in review*) results in less dead fuel to break down and accumulate on the surface over time (Jenkins and others 2008). The strongest effects of thinning were for CWD, duff depth, and live biomass. Effects on CWD were limited to sound fuels since rotten fuels were too decayed to have been killed by the MPB outbreak, based on slow decay rates in subalpine forests (Harmon and others 1986). However, differences in rotten CWD between thinned and uncut stands may emerge with greater time since outbreak as downed logs continue to decay. Effects of thinning on fine fuels had likely eroded by the time of measurement since decomposition of fine fuels can occur within years (Harmon and others 1986). Yet, thinning legacies were still evident in the duff layer, with greater duff depths in thinned stands due to decomposition of thinning slash following treatment implementation in 1940 (Keane 2008; Baker 2009). Live surface biomass in thinned stands was lower than uncut stands due to greater live overstory density and thus fewer canopy gaps that are needed for understory species establishment (Jenkins and others 2014). Though, consistent with mature lodgepole pine stands (Baker 2009; Simard and others 2011; Schoennagel and others 2012), live surface fuels comprised a very small proportion of overall biomass across treatments. In comparison, thinning conducted post-outbreak or shortly before outbreak may increase surface fuel loads of FWD and sound CWD (Jenkins and others 2008; Collins and others 2012).

Lower surface fuel loads in historically thinned stands suggest reduced surface fire potential compared to uncut stands (Hicke and others 2012b). Surface fire potential increases with time since outbreak due to the buildup of surface fuel loads as beetle-killed trees decay and fall (Jenkins and others 2008; Hicke and others 2012b). Thus, less DWD and live surface fuel in thinned stands may lower likelihood of surface fire by reducing reaction intensity, fireline intensity, rate of spread, and flame lengths compared to uncut gray stage stands (Baker 2009; Collins and others 2012; Donato and others 2013a). These findings diverge from observed or simulated increases in surface fire potential post-outbreak in salvage logged stands due to increased surface fuel depths (Collins and others 2012) and higher mid-flame wind speeds (Jenkins and others 2014).

Canopy fuels— In contrast to effects on post-outbreak surface fuel loads, our findings suggest that historical stand-thinning treatments promote greater canopy fuel loads into the gray stage post-outbreak. This is consistent with our expectations due to lower tree mortality from MPB in thinned stands (Morris and others *in review*) limiting loss of live canopy fuel (Jenkins and others 2012). The strongest effects of thinning were for total crown fuels (foliage, branches), ACFL, canopy cover, and CBH, with live fuels dominating overall trends. Thinned stands had greater post-outbreak crown fuel, ACFL, and canopy cover than uncut stands due to lower tree mortality from MPB (Morris and others *in review*), thus more trees with live branches and foliage. CBH was also higher in thinned stands due to greater survival and density of lodgepole pine compared to uncut stands (Morris and others *in review*). Whereas subalpine fir and Engelmann spruce often have crowns that extend to the forest floor, self-pruning of lower branches in lodgepole pine trees contributes to taller crown base heights. Thinning effects on dead fuels were limited to 100-h branches, with the heaviest intensity treatments having lower 100-h fuel loads due to smaller MPB-killed trees compared to uncut stands (Morris and others *in review*). In contrast, thinning conducted post-outbreak may decrease ACFL and CBD compared to uncut stands (Jenkins and others 2008).

Alteration of canopy fuels by historical thinning suggests less consistent effects for crown fire potential (Van Wagner 1977). Crown fire potential declines through older post-outbreak stages as dead needles fall and canopy bulk density and aerial fuel continuity are reduced (Page and Jenkins 2007; Jenkins and others 2008; Klutsch and others 2011; Hicke and others 2012b). Taller CBH in historically thinned stands may reduce potential for crown fire initiation compared to uncut stands by decreasing the likelihood of fire transitioning from the surface to the canopy (Baker 2009; Donato and others 2013a). However, once crown fire has been initiated, greater canopy fuel loads in thinned stands may facilitate greater crown fire spread than uncut gray stage stands (Donato and others 2013a). Further, more uniform vertical distributions in CBD and greater live canopy cover in historically thinned stands may increase potential for transition from passive to active crown fire than uncut stands due to greater fuel continuity (Jenkins and others 2008). As with surface fire potential, these findings diverge with reductions in observed or simulated crown fire potential in stands thinned post-outbreak or shortly before outbreak (Baker 2009; Donato and others 2013b; Crotteau and others 2018a).

Fine-scale spatial heterogeneity— Our findings suggest that historical stand-thinning treatments may alter development of fine-scale spatial complexity in post-outbreak canopy fuels, at least into the gray stage. Our expectations that effects would differ by thinning intensity were not supported; responses were fairly consistent across thinning treatments. The strongest effects of thinning on fine-scale spatial heterogeneity were for canopy cover, CBH, and ACFL. In uncut stands, within-stand spatial heterogeneity in fuels increases with time since outbreak as fuels shift from canopy to surface (Donato and others 2013a; Jenkins and others 2014). Heterogeneity in total and live canopy cover was lower in thinned stands due to greater density of live overstory trees than uncut stands. Similarly, heterogeneity in dead canopy cover was greater in thinned stands due to less MPB-induced tree mortality than uncut stands (Morris and others *in review*). Heterogeneity in CBH was lower in the most heavily thinned stands due to stand structure dominated by greater abundance of even-aged live lodgepole pine trees compared to uncut stands (Morris and others *in review*). Horizontal heterogeneity in ACFL was greater in thinned stands for top (height $\geq$ 16 m) and bottom (height < 8 m) canopy strata due to fewer overstory trees and understory tree regeneration in thinned stands. Similarly, vertical heterogeneity in ACFL was greater in thinned stands due to greater abundance of lodgepole pine with more variable crown shapes compared to the uniformly dense crowns of subalpine fir and Engelmann spruce. Thinning had limited effects on surface fuel heterogeneity due to characteristic high spatial and temporal variability in fuels within lodgepole pine forests (Baker 2009), and attenuation of differences between stands by the time of measurement.

Altered fine-scale spatial heterogeneity of canopy fuels in historically thinned stands suggests different crown fire potential compared to uncut stands (Donato and others 2013a). Torching potential gradually increases over time since outbreak as ladder fuels (e.g., understory vegetation, DWD, tree regeneration) accumulate (Hicke and others 2012b). Greater vertical heterogeneity in ACFL in historically thinned stands may reduce torching potential due to reduced fuel continuity compared to uncut stands (Agee and Skinner 2005; Baker 2009; Donato and others 2013a). Reduced spatial heterogeneity in live cover-in historically thinned stands suggest greater potential for transition from passive to active crown fire than uncut stands (Jenkins and others 2008). Though, increased horizontal heterogeneity in ACFL in thinned stands may mediate the positive effects of thinning on crown fire spread by decreasing fuel continuity (Donato and others 2013a).

While historical thinning may modify fire hazard following bark beetle outbreak, manipulation of fuels in subalpine systems has little impact on actual fire occurrence and severity (Turner and others 1994; Baker 2009). In forests characterized by stand-replacing fire regimes, fuel abundance has limited effect on fire occurrence (Schoennagel and others 2004) and extent (Kulakowski and Veblen 2007; Hart and Preston 2020). Regional-scale climatic variability is the dominant driver of fire occurrence (Mietkiewicz and Kulakowski 2016) and area burned (Hart and Preston 2020), though fire effects and behavior are modulated by local- and meso-scale abiotic and biotic factors (Sibold and others 2006). Effects of bark beetle outbreaks on fire severity depend on burning conditions, outbreak severity, and the interval between outbreak and fire (Harvey and others 2014a). In gray stage stands, decreases in fire severity under moderate burning conditions have been observed for both surface and crown fire metrics (Harvey and others 2014b, 2014a; Agne and others 2016) due to lower abundance of live vegetation susceptible to wildfire (Meigs and others 2016). Accordingly, thinned stands may experience increased fire severity in the gray stage due to less beetle-killed trees and greater live fuels compared to uncut stands. However, given mean probability of burning in subalpine forests with fire rotations of 175–350 years (Baker 2009) would be <1% in a random given year and <50% in a 100-year period, and differences among stands attenuate over time since outbreak as stands regrow, historical treatments may have limited meaningful effects on reducing fire hazard and severity when stands eventually do burn.

Despite limited effects on realistic fire hazard in subalpine systems, historical thinning has important implications for wildlife habitat and operational firefighting activities in beetle-killed forests. Post-outbreak material legacies (e.g., snags, DWD, understory vegetation) provide important wildlife habitat (Saab and others 2014). By promoting greater live tree density and canopy cover, and reducing dead surface and canopy fuels, thinning may have positive effects on post-outbreak habitat for wildlife species that utilize dense, closed canopy stands, but adverse effects on those dependent on canopy openings, herbaceous vegetation, DWD, and snags (Converse and others 2006; Pilliod and others 2006). Additionally, modification of fuel profiles by historical treatments suggests resistance to control may differ between thinned and uncut stands. Resistance to control considers fire behavior, fire suppression, and firefighter safety (Page and others 2013). In the gray stage, beetle-killed snags represent a major hazard for firefighter safety (Jenkins and others 2012). Accumulation of snags and DWD can increase difficulties in fireline construction, access, and establishing escape routes and safety zones (Jenkins and others 2014). Mitigating snag hazards prior to and during suppression operations is critical for promoting safe conditions, but this work is dangerous and time-consuming, particularly post-fire as weakened snags fall (Page and others 2013). While snag overstory density was similar across most treatments, snags in thinned stands were smaller and may present fewer hazards than uncut stands. Additionally, lower amounts of CWD in thinned stands may improve ease of access and construction efforts (Page and others 2013).

Legacies of Historical Thinning on Aboveground C Storage

Historical thinning dampened the effects of the MPB outbreak on aboveground C storage but led to similar total C levels as the control. Through selective tree mortality, bark beetle outbreaks redistribute aboveground C biomass from live to dead pools. Total aboveground biomass remains relatively constant due to the dynamic balance between decomposition of beetle-killed snags and growth of surviving and regenerating trees (Donato and others 2013b; Hansen and others 2015). Consistent with these dynamics, total aboveground C biomass was similar across most treatments. However, thinned stands had twice as much live and half as much dead biomass compared to uncut stands. Residual live vegetation is an important C sink following outbreaks (Bowler and others 2012) that may experience increased productivity due to canopy openings and release from competition (Brown and others 2010). Thus, by reducing outbreak severity (i.e., greater post-outbreak live basal area and density), thinning may accelerate the recovery of post-outbreak live C compared to uncut stands (Hicke and others 2012a). In contrast, post-outbreak salvage logging may reduce aboveground carbon storage and lengthen recovery time compared to unharvested stands (D’Amato and others 2011; Bradford and others 2012; Donato and others 2013b; Mathys and others 2013).

Although thinning may preserve greater amounts of live C following a beetle outbreak compared to uncut stands, initial treatment necessitates immediate removal of substantial amounts of live biomass, potentially resulting in less C stored over time. Typically, in uncut stands, change in C storage following bark beetle outbreak is relatively flat due to the balance between decay and regeneration processes (Donato and others 2013b). Stocks of standing-live C can return to pre-outbreak levels within 25–40 years (Pfeifer and others 2011; Caldwell and others 2013), and productivity rates and total C stocks typically recover within 100 years (Bradford and others 2008; Edburg and others 2011; Hansen and others 2015). While total biomass C in most thinned stands had recovered to uncut levels by the time of measurement, aboveground woody C would have been substantially lower in the thinned treatments during the decades prior to outbreak due to younger stand age (Bradford and others 2008; D'Amato and others 2011) and lower densities of large trees (D'Amato and others 2011). Additionally, return to uncut levels was not always the case for thinned stands; moderate and clearcut+TSI treatments had lower levels of C than the control at time of measurement. Thinning may increase C sequestration in residual trees by stimulating advance regeneration (Bowler and others 2012). Yet, this effect may be offset by competition and density-dependent mortality among understory individuals (Hicke and others 2012a).

Dead biomass is also important to consider when managing for ecosystem C storage. In high-elevation subalpine forests, input and decomposition of dead biomass can contribute over 25% of total ecosystem C storage (Bradford and others 2008). Snags and coarse DWD can take approximately a century (~80–120 years; Brown and others 1998) to decay depending on site conditions (e.g., moisture, temperature; Harmon and others 1986; Keane 2008). These slow decomposition rates allow dead biomass to represent a long-term C store. DWD also represents an important component of soil formation, water cycling (Harmon and others 1986), and wildlife habitat (Fontaine and Kennedy 2012; Saab and others 2014) in forested ecosystems. By reducing amounts of C stored in snags and DWD compared to uncut stands, thinning may result in less stable long-term C balance on site. Though, wood and forest products crafted from merchantable timber removed in thinning operations may present a long-term off-site C store (Eriksson and others 2007). Thus, considering a life cycle analysis of aboveground C storage is important when developing management strategies for addressing global climate change.

Thinning may also have implications for C cycling when outbreak-affected stands do burn (Talucci and others 2020). Beetle-killed trees are more likely than fire-killed trees to develop deep wood charring (i.e., incomplete combustion of dead wood) and have branch structure consumed under both moderate and extreme burning conditions (Harvey and others 2014b; Talucci and Krawchuk 2019). Deep charring of biomass may extend long-term C storage and influence soil nutrient cycling by limiting decomposition and slowing decay (Bird and others 2015). Conversely, branch consumption may limit C cycling by altering DWD accumulation and simplifying snag physical structure (Harmon and others 1986). Thus, by reducing DWD and beetle-killed snags, thinning may lower the potential for long-term C storage in deep char following fire.

CONCLUSION

As disturbance activity increases with warming, drying climate, understanding how disturbances may interact to influence forest structure and function is an important priority for management. Across western North America, spatial overlaps between fire and recent bark beetle outbreaks are receiving heightened public attention and raising concerns about potential altered fire behavior and ecosystem services. Our study capitalized on a unique opportunity to leverage past silvicultural operations affected by subsequent MPB outbreak to empirically test the efficacy and longevity of management actions on influencing post-outbreak fire hazard and aboveground C dynamics. We found that thinning treatments applied ~60 years prior to MPB outbreak reduced surface fuel loads, increased canopy fuel loads, and dampened redistribution of aboveground C from live to dead biomass compared to uncut stands. This work extends our observations of treatment longevity in subalpine forests, highlighting that structural and functional legacies of historical stand-thinning treatments may last half a century and persist following a severe bark beetle outbreak. Our findings of tradeoffs between modification of fuel profiles and aboveground C trajectories following historical thinning support the need to balance multiple objectives for effective forest management (Bradford and D'Amato 2012). Ultimately, this work presents a suite of management options for influencing outbreak-fire interaction effects in forested ecosystems.

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REFERENCES

Agee JK, Skinner CN. 2005. Basic principles of forest fuel reduction treatments. For Ecol Manage 211:83–96.

Ager AA, McMahan A, Hayes JL, Smith EL. 2007. Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. Landsc Urban Plan 80:301–11.

Agne MC, Woolley T, Fitzgerald S. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For Ecol Manage 366:73–86.

Alexander RR, Troendle CA, Kaufmann MR, Shepperd WD, Crouch GL, Watkins RK. 1985. The Fraser Experimental Forest, Colorado: Research program and published research 1937-1985. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station

Baker WL. 2009. Fire Ecology in Rocky Mountain Landscapes. Washington D.C.: Island Press

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF, Seybold SJ. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–13.

Bird MI, Wynn JG, Saiz G, Wurster CM, McBeath A. 2015. The pyrogenic carbon cycle. Annu Rev Earth Planet Sci 43:273–98.

Bowler R, Fredeen AL, Brown M, Andrew Black T. 2012. Residual vegetation importance to net CO2 uptake in pine-dominated stands following mountain pine beetle attack in British Columbia, Canada. For Ecol Manage 269:82–91.

Bradford JB, Birdsey RA, Joyce LA, Ryan MG. 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. Glob Chang Biol 14:2882–97.

Bradford JB, D'Amato AW. 2012. Recognizing trade-offs in multi-objective land management. Front Ecol Environ 10:210–6.

Bradford JB, Fraver S, Milo AM, D'Amato AW, Palik B, Shinneman DJ. 2012. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. For Ecol Manage 267:209–14.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Brown JK. 1974. Handbook for inventorying downed woody material. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station

Brown JK. 1978. Weight and density of crowns of Rocky Mountain conifers. Ogden, UT: Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station

Brown M, Black TA, Nesic Z, Foord VN, Spittlehouse DL, Fredeen AL, Grant NJ, Burton PJ, Trofymow JA. 2010. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. Agric For Meterol 150:254–64.

Brown PM, Shepperd WD, Mata SA, McClain DL. 1998. Longevity of windthrown logs in a subalpine forest of central Colorado. Can J For Res 28:5.

Buma B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:art70.

Caldwell MK, Hawbaker TJ, Briggs JS, Cigan PW, Stitt S. 2013. Simulated impacts of mountain pine beetle and wildfire disturbances on forest vegetation composition and carbon stocks in the Southern Rocky Mountains. Biogeosci Discuss 10:12919–65.

Carlson AR, Sibold JS, Assal TJ, Negrón JF. 2017. Evidence of compounded disturbance effects on vegetation recovery following high-severity wildfire and spruce beetle outbreak. PLoS ONE 12:e0181778.

Collins BJ, Rhoades CC, Battaglia MA, Hubbard RM. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. For Ecol Manage 284:260–8.

Converse SJ, Block WM, White GC. 2006. Small mammal population and habitat responses to forest thinning and prescribed fire. For Ecol Manage 228:263–73.

Crotteau JS, Keyes CR, Hood SM, Affleck DLR, Sala A. 2018a. Fuel dynamics after a bark beetle outbreak impacts experimental fuel treatments. Fire Ecol 14:13.

Crotteau JS, Keyes CR, Hood SM, Larson AJ, Sutherland EK, Wright DK, Egan JM. 2018b. Stand dynamics 11 years after retention harvest in a lodgepole pine forest. For Ecol Manage 427:169–81.

Cruz MG, Alexander ME, Wakimoto RH. 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. For Sci 50:640–58.

D’Amato AW, Bradford JB, Fraver S, Palik BJ. 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. For Ecol Manage 262:803–16.

Dennison PE, Brewer SC, Arnold JD, Moritz MA. 2014. Large wildfire trends in the western United States, 1984–2011. Geophys Res Lett 41:2928–33.

DeRose RJ, Long JN. 2014. Resistance and resilience: a conceptual framework for silviculture. For Sci 60:1205–12.

Dobor L, Hlásny T, Rammer W, Zimová S, Barka I, Seidl R. 2020. Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? J Appl Ecol 57:67–76.

Donato DC, Harvey BJ, Romme WH, Simard M, Turner MG. 2013a. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol Appl 23:3–20.

Donato DC, Simard M, Romme WH, Harvey BJ, Turner MG. 2013b. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. For Ecol Manage 303:160–74.

Edburg SL, Hicke JA, Lawrence DM, Thornton PE. 2011. Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. J Geophys Res: Biogeosci 116:G04033.

Eriksson E, Gillespie AR, Gustavsson L, Langvall O, Olsson M, Sathre R, Stendahl J. 2007. Integrated carbon analysis of forest management practices and wood substitution. Can J For Res 37:671–81.

Fontaine JB, Kennedy PL. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecol Appl 22:1547–61.

Fraterrigo JM, Rusak JA. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecol Lett 11:756–70.

Griffin JM, Simard M, Turner MG. 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. For Ecol Manage 291:228–39.

Halofsky JE, Peterson DL, Harvey BJ. 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecol 16:4.

Hanes C, Wang X, Jain P, Parisien M-A, Little J, Flannigan M. 2018. Fire regime changes in Canada over the last half century. Can J For Res 49.

Hansen EM, Amacher MC, Van Miegroet H, Long JN, Ryan MG. 2015. Carbon dynamics in central US Rockies lodgepole pine type after mountain pine beetle outbreaks. For Sci 61:665–79.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K Jr, Cummins KW. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302.

Hart SJ, Preston DL. 2020. Fire weather drives daily area burned and observations of fire behavior in mountain pine beetle affected landscapes. Environ Res Lett 15:054007.

Hart SJ, Schoennagel T, Veblen TT, Chapman TB. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc Nat Acad Sci USA 112:4375–80.

Harvey BJ, Donato DC, Romme WH, Turner MG. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol Appl 24:1608–25.

Harvey BJ, Donato DC, Turner MG. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc Natl Acad Sci USA 111:15120–5.

Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Ted Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN, Vogelmann J. 2012a. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Glob Chang Biol 18:7–34.

Hicke JA, Johnson MC, Hayes JL, Preisler HK. 2012b. Effects of bark beetle-caused tree mortality on wildfire. For Ecol Manage 271:81–90.

Hood PR, Nelson KN, Rhoades CC, Tinker DB. 2017. The effect of salvage logging on surface fuel loads and fuel moisture in beetle-infested lodgepole pine forests. For Ecol Manage 390:80–8.

Huckaby LS, Moir WH. 1995. Fire history of subalpine forests at Fraser Experimental Forest, Colorado. In: Brown JK, Mutch RW, Spoon CW, Wakimoto RH, editors. Proceedings of the symposium on fire in wilderness and park management. General Technical Report INT-GTR-320. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. pp 205–10.

Huckaby LS, Moir WH. 1998. Forest communities at Fraser Experimental Forest, Colorado. Southwest Nat 43:204–18.

Jenkins MJ, Hebertson E, Page W, Jorgensen CA. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For Ecol Manage 254:16–34.

Jenkins MJ, Page WG, Hebertson EG, Alexander ME. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. For Ecol Manage 275:23–34.

Jenkins MJ, Runyon JB, Fettig CJ, Page WG, Bentz BJ. 2014. Interactions among the mountain pine beetle, fires, and fuels. For Sci 60:489–501.

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nat Commun 6:1–11.

Jolly WM, Parsons RA, Hadlow AM, Cohn GM, McAllister SS, Popp JB, Hubbard RM, Negron JF. 2012. Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. For Ecol Manage 269:52–9.

Kautz M, Dworschak K, Gruppe A, Schopf R. 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For Ecol Manage 262:598–608.

Kautz M, Meddens AJH, Hall RJ, Arneth A. 2017. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Glob Ecol Biogeogr 26:533–52.

Keane RE. 2008. Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. Can J For Res 38:1431–45.

Klutsch JG, Battaglia MA, West DR, Costello SL, Negron JF. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. West J Appl For 26:101–9.

Kueppers LM, Southon J, Baer P, Harte J. 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. Oecologia 141:641–51.

Kulakowski D, Jarvis D. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. For Ecol Manage 262:1686–96.

Kulakowski D, Veblen TT. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88:759–69.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–90.

Long JA. 2020. jtools: Analysis and presentation of social scientific data. https://cran.r-project.org/package=jtools

Lutes DC, Keane RE, Caratti JF, Key CH, Benson NC, Sutherland S, Gangi LJ. 2006. FIREMON: Fire effects monitoring and inventory system. Ft. Collins, CO: U.S.

Department of Agriculture, Forest Service, Rocky Mountain Research Station

Mathys A, Black TA, Nesic Z, Nishio G, Brown M, Spittlehouse DL, Fredeen AL, Bowler R, Jassal RS, Grant NJ, Burton PJ, Trofymow JA, Meyer G. 2013. Carbon balance of a partially harvested mixed conifer forest following mountain pine beetle attack and its comparison to a clear-cut. Biogeosciences 10:5451–63.

Means JE, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW. 1994. Software for computing plant biomass - BIOPAK users guide. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

Meddens AJH, Hicke JA, Ferguson CA. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol Appl 22:1876–91.

Meigs GW, Campbell JL, Zald HSJ, Bailey JD, Shaw DC, Kennedy RE. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6:1–24.

Meigs GW, Zald HSJ, Campbell JL, Keeton WS, Kennedy RE. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environ Res Lett 11:045008.

Mietkiewicz N, Kulakowski D. 2016. Relative importance of climate and mountain pine beetle outbreaks on the occurrence of large wildfires in the western USA. Ecol Appl 26:2525–37.

Moir WH, Harmon ME, Hawksworth FG, Brainerd RE, Franklin JF. Unpublished. Fifty years of succession in old-growth lodgepole pine and spruce-fir forests in Colorado.

Morris JL, Cottrell S, Fettig CJ, Hansen WD, Sherriff RL, Carter VA, Clear JL, Clement J, DeRose RJ, Hicke JA, Higuera PE, Mattor KM, Seddon AWR, Seppä HT, Stednick JD, Seybold SJ. 2017. Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. Marini L, editor. J Appl Ecol 54:750–60.

Morris, JE, Buonanduci MS, Agne MC, Battaglia MA, Harvey BJ. In review. Does the legacy of historical thinning treatments foster resilience to bark beetle outbreaks in subalpine forests? Ecol Appl.

NWCG. 2018. Glossary of Wildland Fire Terminology, PMS 205. National Wildfire Coordinating Group https://www.nwcg.gov/glossary/a-z

Olson CM, Martin RE. 1981. Estimating biomass of shrubs and forbs in Central Washington Douglas-fir stands. Bend, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station

Page WG, Alexander ME, Jenkins MJ. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. For Chron 89:783–94.

Page WG, Jenkins MJ. 2007. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the Intermountain region. For Sci 53:507–18.

Parks SA, Abatzoglou JT. 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985-2017. Geophys Res Lett n/a:e2020GL089858.

Pfeifer EM, Hicke JA, Meddens AJH. 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. Glob Chang Biol 17:339–50.

Pilliod DS, Bull EL, Hayes JL, Wales BC. 2006. Wildlife and invertebrate response to fuel reduction treatments in dry coniferous forests of the western United States: a synthesis. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station

Prichard SJ, Sandberg DV, Ottmar RD, Eberhardt E, Andreu A, Eagle P, Swedin Kjell. 2013. Fuel Characteristic Classification System version 3.0: technical documentation. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

PRISM Climate Group. 2012. Oregon State University, http://prism.oregonstate.edu.

R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing https://www.R-project.org/

Reinhardt E, Scott J, Gray K, Keane R. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Can J For Res 36:2803–14.

Saab VA, Latif QS, Rowland MM, Johnson TN, Chalfoun AD, Buskirk SW, Heyward JE, Dresser MA. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. For Sci 60:539–59.

Sando RW, Wick CH. 1972. A method of evaluating crown fuels in forest stands. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station

Schlesinger WH. 1991. Biogeochemistry: an Analysis of Global Change. 1st ed. San Diego, California: Academic Press

Schoennagel T, Veblen TT, Negron JF, Smith JM. 2012. Effects of Mountain Pine Beetle on Fuels and Expected Fire Behavior in Lodgepole Pine Forests, Colorado, USA. Chen HYH, editor. PLoS ONE 7:e30002.

Schoennagel T, Veblen TT, Romme WH. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 54:661–76.

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. 2016. Searching for resilience:

addressing the impacts of changing disturbance regimes on forest ecosystem services. Angeler D, editor. J Appl Ecol 53:120–9.

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO. 2017. Forest disturbances under climate change. Nat Clim Chang 7:395–402.

Sibold JS, Veblen TT, González ME. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. J Biogeogr 33:631–47.

Sieg CH, Linn RR, Pimont F, Hoffman CM, McMillin JD, Winterkamp J, Baggett LS. 2017. Fires following bark beetles: factors controlling severity and disturbance interactions in ponderosa pine. Fire Ecol 13:1–23.

Simard M, Romme WH, Griffin JM, Turner MG. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol Monogr 81:3–24.

Smith P, Nkem J, Calvin K, Campbell D, Cherubini F, Grassi G, Korotkov V, Hoang AL, Lwasa S, McElwee P, Nkonya E, Saigusa N, Soussana J-F, Taboada MA. 2019. Interlinkages between desertification, land degradation, food security and greenhouse gas fluxes: synergies, trade-offs and integrated response options. In: Shukla PR, Calvo Buendia E, Masson-Delmotte V, Portner H-O, Roberts C, Zhai P, Slade R, Connors S, van Diemen R, Ferrat M, Haughey E, Luz S, Neogi S, Pathak M, Petzold J, Portugal Pereira J, Vyas P, Huntley E, Kissick K, Belkacemi M, Malley J, editors. Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. pp 551–672.

Sommerfeld A, Senf C, Buma B, D’Amato AW, Després T, Díaz-Hormazábal I, Fraver S, Frelich LE, Gutiérrez ÁG, Hart SJ, Harvey BJ, He HS, Hlásny T, Holz A, Kitzberger T, Kulakowski D, Lindenmayer D, Mori AS, Müller J, Paritsis J, Perry GLW, Stephens SL, Svoboda M, Turner MG, Veblen TT, Seidl R. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nat Commun 9:4355.

Standish JT, Manning GH, Demaerschalk JP. 1985. Development of biomass equations for British Columbia tree species. Victoria, B.C.: Canadian Forestry Service, Pacific Forest Research Centre

Talucci AC, Krawchuk MA. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10:e02744.

Talucci AC, Matosziuk LM, Hatten JA, Krawchuk MA. 2020. An added boost in pyrogenic carbon when wildfire burns forest with high pre-fire mortality. Fire Ecol 16:21.

Turner MG, Hargrove WW, Gardner RH, Romme WH. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Veg Sci 5:731–42.

Van Wagner CE. 1977. Conditions for the start and spread of crown fire. Can J For Res 7:23–34.

Vorster AG, Evangelista PH, Stohlgren TJ, Kumar S, Rhoades CC, Hubbard RM, Cheng AS, Elder K. 2017. Severity of a mountain pine beetle outbreak across a range of stand conditions in Fraser Experimental Forest, Colorado, United States. For Ecol Manage 389:116–26.

Westerling AL. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philos Trans R Soc B 371:1–10.

Wilm HG, Dunford EG. 1948. Effect of timber cutting on water available for stream flow from a lodgepole pine forest. United States Department of Agriculture

Appendix E. PLOT SAMPLING DESIGN

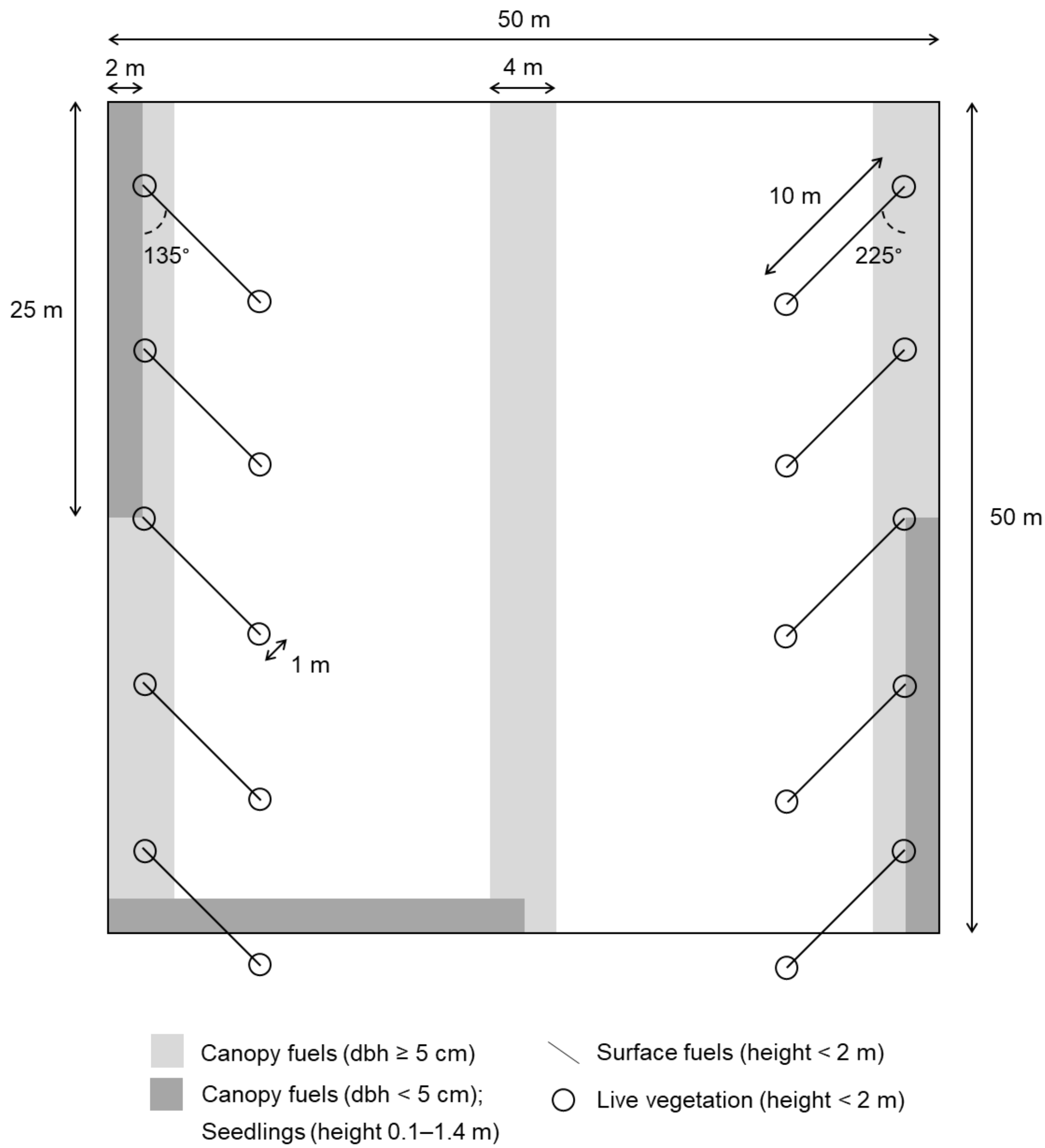

Fig. E.1. Diagram summary of complete plot layout, including all subplot sampling locations.

Appendix F. ALLOMETRIC EQUATIONS

Table F.1. References for allometric equations used in conversion of field measurements.

Biomass component	LODGEPOLE PINE	SUBALPINE FIR	ENGELMANN SPRUCE	QUAKING ASPEN
Crown	Brown 1978			N/A
Foliage				Standish and others 1985
Branches				
Bole	Brown 1978[1]; Pearson and others 1984[2]	Brown 1978[1]; Means and others 1994[2]		Bella and DeFranceschi 1980
Seedling	Brown 1978			Means and others 1994

Biomass component	GRAMINOIDS	FORBS	SHRUBS, TALL[†]	SHRUBS, LOW[‡]
Understory	Olson and Martin 1981		Alaback 1986	Ottmar and others 2002

[1] Trees with dbh ≤ 10 cm
[2] Trees with dbh > 10 cm
[†] Height >= 0.2 m
[‡] Height < 0.2 m

REFERENCES

Alaback PB. 1986. Biomass regression equations for understory plants in Coastal Alaska: effects of species and sampling design on estimates. Northwest Sci 60:90–103.

Bella IE, DeFranceschi JP. 1980. Biomass productivity of young aspen stands in western Canada. Edmonton, A.B.: Canadian Forestry Service, Northern Forest Research Centre

Brown JK. 1978. Weight and density of crowns of Rocky Mountain conifers. Ogden, UT: Intermountain Forest and Range Experiment Station

Means JE, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW. 1994. Software for computing plant biomass - BIOPAK users guide. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

Olson CM, Martin RE. 1981. Estimating biomass of shrubs and forbs in Central Washington Douglas-fir stands. Bend, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station

Ottmar RD, Vihnanek RE, Wright CS. 2002. Stereo photo series for quantifying natural fuels. Volume Va: Oregon white oak, California deciduous oak, and mixed-conifer with shrub types in the western United States. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center

Pearson JA, Fahey TJ, Knight DH. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can J For Res 14:259–65.

Standish JT, Manning GH, Demaerschalk JP. 1985. Development of biomass equations for British Columbia tree species. Victoria, B.C.: Canadian Forestry Service, Pacific Forest Research Centre

Appendix G. POST-OUTBREAK STAND STRUCTURE

Table G.1. Summary of post-outbreak stand structural characteristics by thinning treatment. Values are the mean (standard error) across all trees.

Characteristic	Control (n = 4)	Light+TSI (n = 4)	Moderate (n = 3)	Moderate+TSI (n = 3)	Heavy (n = 4)	Heavy+TSI (n = 4)	Clearcut (n = 3)	Clearcut+TSI (n = 3)
Basal area (m^2/ha)								
Live	10.4 (1.3)	23.2 (4.1)	15.7 (3.6)	26.3 (4.4)	17.8 (2.9)	24.6 (5.5)	27.1 (9.1)	23.4 (2.5)
Dead	25.3 (4.7)	15.2 (1.1)	17.4 (4.0)	16.0 (0.8)	19.4 (2.3)	13.3 (2.2)	14.3 (6.6)	12.9 (1.1)
QMD (cm)								
Live	10.2 (1.0)	10.0 (1.0)	8.8 (0.6)	10.7 (1.1)	9.0 (0.7)	9.5 (1.2)	9.6 (1.0)	10.4 (1.2)
Dead	25.5 (2.9)	20.6 (1.9)	18.1 (3.0)	15.1 (1.2)	19.9 (2.9)	13.9 (0.7)	10.9 (4.3)	11.8 (0.9)
Overstory density (stems/ha)								
Live	293 (13)	497 (112)	402 (86)	652 (147)	536 (111)	697 (152)	754 (215)	669 (138)
Dead, attach	349 (82)	196 (28)	329 (86)	210 (15)	361 (44)	268 (61)	283 (153)	306 (45)
Dead, fall	72 (13)	34 (16)	23 (23)	34 (20)	68 (12)	13 (4)	45 (20)	28 (28)
Understory density (stems/ha)								
Live	8,566 (3,254)	9,810 (1,918)	15,553 (2,691)	18,321 (4,599)	8,979 (2,526)	7,444 (1,852)	17,522 (10,960)	8,245 (4,223)
Dead, attach	181 (117)	546 (224)	922 (533)	1,108 (188)	508 (302)	852 (111)	1,862 (995)	1,113 (199)
Dead, fall	9 (5)	9 (5)	17 (17)	23 (15)	17 (7)	4 (4)	40 (25)	91 (60)

Notes: Basal area and quadratic mean diameter (QMD) include trees with measurable dbh (height ≥ 1.4 m). Overstory includes trees with dbh ≥ 12 cm. Understory includes trees with dbh < 12 cm and height ≥ 0.1 m. Dead, attach includes trees with fine fuels still attached (decay class 1). Dead, fall includes trees with fine fuels fallen (decay class > 1).

Table G.2. Model outputs for post-outbreak basal area and quadratic mean diameter (QMD) as a function of thinning treatment.

Predictor	Live				Dead			
	β	SE	*P*		β	SE	*P*	
BASAL AREA								
Treatment effect								
Light	0.78	0.18	0.000	**	-0.52	0.23	0.023	*
Moderate	0.45	0.20	0.026	*	-0.39	0.25	0.120	
Moderate+TSI	1.02	0.20	0.000	**	-0.47	0.25	0.057	+
Heavy	0.54	0.19	0.004	**	-0.28	0.23	0.225	
Heavy+TSI	0.83	0.19	0.000	**	-0.65	0.23	0.004	**
Clearcut	1.08	0.21	0.000	**	-0.60	0.26	0.018	*
Clearcut+TSI	0.91	0.20	0.000	**	-0.69	0.25	0.006	**
TSI effect								
Moderate:TSI	0.58	0.22	0.009	**	-0.09	0.26	0.744	
Heavy:TSI	0.29	0.19	0.113		-0.37	0.23	0.099	+
Clearcut:TSI	-0.17	0.21	0.437		-0.09	0.26	0.742	
QMD								
Treatment effect								
Light	-0.03	0.11	0.805		-0.21	0.18	0.244	
Moderate	-0.14	0.12	0.243		-0.35	0.20	0.085	+
Moderate+TSI	0.03	0.12	0.770		-0.52	0.20	0.008	**
Heavy	-0.13	0.11	0.213		-0.25	0.19	0.175	
Heavy+TSI	-0.09	0.11	0.427		-0.61	0.18	0.001	**
Clearcut	-0.07	0.12	0.520		-0.85	0.20	0.000	**
Clearcut+TSI	0.00	0.12	0.992		-0.77	0.20	0.000	**
TSI effect								
Moderate:TSI	0.17	0.13	0.182		-0.17	0.22	0.434	
Heavy:TSI	0.05	0.11	0.651		-0.36	0.18	0.049	*
Clearcut:TSI	0.08	0.12	0.538		0.08	0.21	0.698	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table G.3. Model outputs for post-outbreak overstory (dbh ≥ 12 cm) and understory (dbh < 12 cm) density by thinning treatment.

Predictor	Live				Dead, fine fuel attached†				Dead, fine fuel fallen			
	β	SE	*P*		β	SE	*P*		β	SE	*P*	
					OVERSTORY DENSITY							
Treatment effect												
Light	0.08	0.37	0.833		1.11	0.56	0.048	*	0.00	1.41	1.000	
Moderate	0.68	0.40	0.087	+	1.63	0.61	0.007	**	0.69	1.51	0.647	
Moderate+TSI	0.72	0.40	0.071	+	1.81	0.61	0.003	**	0.98	1.51	0.517	
Heavy	-0.01	0.37	0.971		1.03	0.56	0.065	+	0.69	1.40	0.621	
Heavy+TSI	-0.18	0.37	0.623		1.55	0.56	0.006	**	-0.69	1.42	0.625	
Clearcut	0.58	0.41	0.164		2.32	0.61	0.000	**	1.54	1.51	0.308	
Clearcut+TSI	-0.14	0.41	0.736		1.82	0.61	0.003	**	2.37	1.51	0.117	
TSI effect[1]												
Moderate:TSI	0.56	0.24	0.023	*	-0.45	0.37	0.223		0.47	1.01	0.641	
Heavy:TSI	0.24	0.21	0.248		-0.30	0.32	0.347		-1.76	0.88	0.046	*
Clearcut:TSI	-0.15	0.24	0.541		0.08	0.37	0.834		-0.53	1.08	0.620	
					UNDERSTORY DENSITY							
Treatment effect												
Light	0.47	0.21	0.025	*	-0.58	0.32	0.070	+	-1.03	1.02	0.313	
Moderate	0.32	0.23	0.162		-0.06	0.34	0.865		-1.56	1.20	0.195	
Moderate+TSI	0.87	0.23	0.000	**	-0.51	0.34	0.141		-1.09	1.14	0.338	
Heavy	0.57	0.21	0.007	**	0.04	0.32	0.910		-0.22	0.91	0.806	
Heavy+TSI	0.81	0.21	0.000	**	-0.26	0.32	0.408		-1.98	1.01	0.049	*
Clearcut	1.01	0.23	0.000	**	-0.21	0.34	0.548		-0.61	0.95	0.520	
Clearcut+TSI	0.86	0.23	0.000	**	-0.13	0.34	0.706		-1.15	1.08	0.290	
TSI effect												
Moderate:TSI	0.04	0.43	0.924		0.18	0.65	0.776		0.29	1.61	0.858	
Heavy:TSI	-0.17	0.36	0.642		0.52	0.56	0.354		-1.39	1.41	0.327	
Clearcut:TSI	-0.72	0.42	0.089	+	-0.50	0.65	0.437		0.83	1.60	0.606	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

† Decay class 1. Fine fuel fallen, decay class > 1.

Appendix H. Q1 – POST-OUTBREAK FUEL PROFILES

Table H.1. Summary of post-outbreak surface fuels by thinning treatment. Values are the mean (standard error).

Characteristic	Control (*n* = 4)		Light+TSI (*n* = 4)		Moderate (*n* = 3)		Moderate+TSI (*n* = 3)		Heavy (*n* = 4)		Heavy+TSI (*n* = 4)		Clearcut (*n* = 3)		Clearcut+TSI (*n* = 3)	
Fine fuel load (Mg/ha)																
Total	13.7	(1.8)	12.1	(0.4)	8.0	(1.5)	8.6	(1.3)	11.3	(1.3)	11.5	(2.0)	11.1	(2.0)	6.1	(0.6)
1-h	2.7	(0.4)	2.5	(0.4)	2.7	(0.5)	2.5	(0.2)	2.1	(0.2)	2.6	(0.5)	2.6	(0.3)	2.1	(0.1)
10-h	5.7	(0.9)	4.0	(0.6)	2.5	(0.7)	3.2	(0.6)	5.5	(1.2)	4.0	(0.6)	4.0	(1.1)	2.4	(0.3)
100-h	5.3	(0.8)	5.6	(0.7)	2.8	(1.1)	2.9	(0.7)	3.7	(0.5)	4.9	(1.1)	4.6	(0.6)	1.6	(0.1)
Coarse fuel load (Mg/ha)																
Total	80.9	(17.8)	58.0	(16.4)	33.9	(10.0)	27.9	(11.0)	50.6	(3.6)	40.8	(7.0)	35.4	(1.5)	21.9	(1.2)
Sound	58.0	(10.6)	26.2	(8.9)	13.5	(5.9)	13.8	(7.6)	21.3	(2.8)	16.2	(3.9)	14.5	(5.5)	7.4	(0.8)
Rotten	22.9	(7.7)	31.9	(11.8)	20.4	(4.3)	14.1	(3.4)	29.3	(6.1)	24.7	(10.2)	20.8	(4.0)	14.5	(1.9)
Fuel depth (cm)																
Litter	2.6	(0.3)	2.3	(0.1)	1.9	(0.3)	2.6	(0.3)	4.2	(1.3)	2.3	(0.3)	2.5	(0.4)	2.2	(0.2)
Duff	2.4	(0.4)	3.5	(0.5)	2.7	(0.6)	3.7	(0.8)	3.2	(0.3)	3.3	(0.5)	5.2	(1.0)	2.9	(0.6)
Dead fuel	16.4	(3.9)	16.4	(3.7)	9.0	(3.0)	12.1	(1.5)	11.5	(1.9)	17.0	(4.9)	13.8	(4.7)	7.4	(2.1)
Live biomass (Mg/ha)																
Herbaceous	0.04	(0.01)	0.03	(0.01)	0.04	(0.02)	0.02	(0.01)	0.01	(0.00)	0.03	(0.01)	0.02	(0.01)	0.02	(0.00)
Woody	1.18	(0.17)	1.52	(0.31)	1.55	(0.12)	0.80	(0.17)	1.25	(0.25)	0.70	(0.05)	0.72	(0.09)	0.81	(0.24)

Notes: Sound coarse fuels include decay class 1–3; rotten coarse fuels include decay class 4–5. Herbaceous biomass is the sum of graminoids and forbs. Woody biomass is the sum of shrubs and seedlings (height < 1.4 m).

Table H.2. Model outputs for post-outbreak fine surface fuel loads by thinning treatment.

Treatment	1-h fuels			10-h fuels				100-h fuels			
	β	SE	*P*	β	SE	*P*		β	SE	*P*	
Treatment effect											
Light+TSI	-0.05	0.16	0.738	-0.34	0.15	0.020	*	0.05	0.24	0.822	
Moderate	0.04	0.18	0.834	-0.83	0.16	0.000	**	-0.64	0.26	0.013	*
Moderate+TSI	-0.06	0.17	0.726	-0.61	0.16	0.000	**	-0.61	0.26	0.018	*
Heavy	-0.20	0.16	0.208	-0.06	0.15	0.658		-0.37	0.24	0.125	
Heavy+TSI	-0.02	0.16	0.890	-0.30	0.15	0.041	*	-0.07	0.24	0.777	
Clearcut	-0.04	0.17	0.825	-0.45	0.16	0.005	**	-0.15	0.26	0.569	
Clearcut+TSI	-0.22	0.17	0.211	-0.90	0.16	0.000	**	-1.21	0.26	0.000	**
TSI effect[1]											
Moderate:TSI	-0.10	0.19	0.612	0.22	0.17	0.210		0.03	0.28	0.911	
Heavy:TSI	0.18	0.16	0.263	-0.23	0.15	0.110		0.30	0.24	0.215	
Clearcut:TSI	-0.18	0.18	0.334	-0.45	0.17	0.008	**	-1.06	0.28	0.000	**

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.3. Model outputs for post-outbreak coarse surface fuel loads by thinning treatment.

Treatment	1000-h fuels, sound				1000-h fuels, rotten		
	β	SE	*P*		β	SE	*P*
Treatment effect							
Light+TSI	-0.80	0.37	0.030	*	0.34	0.43	0.432
Moderate	-1.50	0.40	0.000	**	-0.11	0.46	0.812
Moderate+TSI	-1.38	0.41	0.001	**	-0.48	0.47	0.308
Heavy	-0.96	0.37	0.010	**	0.25	0.43	0.557
Heavy+TSI	-1.22	0.38	0.001	**	0.07	0.42	0.862
Clearcut	-1.37	0.40	0.001	**	-0.08	0.48	0.870
Clearcut+TSI	-2.01	0.41	0.000	**	-0.44	0.49	0.364
TSI effect[1]							
Moderate:TSI	0.11	0.46	0.806		-0.37	0.49	0.454
Heavy:TSI	-0.26	0.37	0.486		-0.18	0.43	0.677
Clearcut:TSI	-0.64	0.43	0.135		-0.36	0.49	0.456

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Sound fuels include decay class 1–3; rotten fuels include decay class 4–5. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.4. Model outputs for post-outbreak surface fuel depths by thinning treatment.

Treatment	Litter depth				Duff depth				Dead fuel depth			
	β	SE	*P*		β	SE	*P*		β	SE	*P*	
Treatment effect												
Light+TSI	-0.11	0.15	0.464		0.39	0.17	0.021	*	0.04	0.27	0.880	
Moderate	-0.33	0.16	0.044	*	0.14	0.18	0.454		-0.64	0.30	0.031	*
Moderate+TSI	-0.04	0.16	0.826		0.45	0.18	0.012	*	-0.29	0.29	0.329	
Heavy	0.42	0.15	0.006	**	0.32	0.17	0.055	+	-0.33	0.27	0.221	
Heavy+TSI	-0.13	0.15	0.393		0.31	0.17	0.064	+	0.09	0.28	0.751	
Clearcut	-0.07	0.16	0.688		0.86	0.18	0.000	**	-0.18	0.29	0.542	
Clearcut+TSI	-0.17	0.16	0.298		0.22	0.18	0.235		-0.79	0.29	0.007	**
TSI effect[1]												
Moderate:TSI	0.29	0.18	0.097	+	0.32	0.20	0.114		0.35	0.32	0.273	
Heavy:TSI	-0.54	0.15	0.000	**	-0.01	0.17	0.942		0.42	0.27	0.123	
Clearcut:TSI	-0.10	0.17	0.545		-0.65	0.20	0.001	**	-0.61	0.31	0.050	+

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.5. Model outputs for post-outbreak live surface fuel loads by thinning treatment.

Treatment	Herbaceous biomass				Woody biomass			
	β	SE	*P*		β	SE	*P*	
Treatment effect								
Light+TSI	-0.16	0.31	0.612		0.26	0.20	0.205	
Moderate	-0.27	0.34	0.425		0.28	0.22	0.206	
Moderate+TSI	-0.66	0.34	0.051	+	-0.39	0.22	0.076	+
Heavy	-1.58	0.31	0.000	**	0.06	0.20	0.753	
Heavy+TSI	-0.54	0.31	0.085	+	-0.51	0.20	0.011	*
Clearcut	-0.67	0.34	0.048	*	-0.49	0.22	0.023	*
Clearcut+TSI	-0.78	0.34	0.021	*	-0.37	0.22	0.087	+
TSI effect[1]								
Moderate:TSI	-0.11	0.36	0.761		0.12	0.23	0.599	
Heavy:TSI	1.04	0.31	0.001	**	-0.58	0.20	0.004	**
Clearcut:TSI	-0.38	0.38	0.315		-0.66	0.23	0.004	**

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.6. Summary of post-outbreak canopy fuels by thinning treatment. Values are the mean (standard error).

Characteristic	Control (n = 4)		Light+TSI (n = 4)		Moderate (n = 3)		Moderate+TSI (n = 3)		Heavy (n = 4)		Heavy+TSI (n = 4)		Clearcut (n = 3)		Clearcut+TSI (n = 3)	
Foliage biomass (Mg/ha)																
Total	5.3	(0.9)	11.5	(2.1)	8.6	(2.5)	12.2	(2.3)	9.0	(2.2)	12.4	(4.9)	14.9	(6.4)	10.0	(1.3)
Live	5.1	(0.8)	11.3	(2.1)	8.2	(2.5)	12.2	(2.3)	8.8	(2.2)	12.4	(4.9)	14.8	(6.5)	10.0	(1.3)
Dead	0.2	(0.1)	0.2	(0.2)	0.3	(0.3)	0.0	(0.0)	0.2	(0.1)	0.1	(0.0)	0.1	(0.1)	0.1	(0.1)
1-hr fuel (Mg/ha)																
Total	8.0	(0.9)	10.4	(1.1)	9.2	(0.7)	11.3	(1.1)	10.0	(0.7)	11.3	(2.1)	12.6	(2.7)	10.0	(0.2)
Live	2.8	(0.4)	6.2	(1.1)	4.5	(1.2)	6.8	(1.2)	4.9	(1.1)	6.9	(2.4)	7.8	(3.3)	5.7	(0.6)
Dead	5.2	(0.8)	4.2	(0.2)	4.7	(0.8)	4.5	(0.3)	5.1	(0.5)	4.5	(0.4)	4.8	(0.7)	4.3	(0.5)
10-hr fuel (Mg/ha)																
Total	12.2	(1.6)	14.6	(1.5)	12.6	(0.4)	16.3	(1.8)	14.3	(0.7)	15.3	(1.9)	17.4	(2.0)	14.9	(0.8)
Live	2.9	(0.4)	7.1	(1.2)	4.8	(1.4)	7.9	(1.5)	5.1	(1.1)	7.0	(2.3)	8.9	(3.4)	6.7	(1.2)
Dead	9.3	(1.5)	7.5	(0.7)	7.8	(1.2)	8.4	(1.1)	9.2	(0.7)	8.3	(0.8)	8.5	(1.6)	8.2	(0.7)
100-hr fuel (Mg/ha)																
Total	6.7	(1.4)	5.8	(0.5)	5.4	(0.7)	6.4	(0.9)	5.6	(0.5)	4.5	(0.6)	4.5	(0.9)	4.1	(0.6)
Live	0.5	(0.1)	1.9	(0.5)	1.0	(0.4)	2.1	(1.0)	0.9	(0.3)	1.2	(0.5)	1.6	(0.8)	1.2	(0.3)
Dead	6.2	(1.3)	3.9	(0.3)	4.4	(1.1)	4.3	(0.2)	4.7	(0.7)	3.3	(0.6)	2.9	(1.6)	3.0	(0.5)
ACFL (Mg/ha)																
Total	11.9	(1.3)	18.8	(2.6)	15.5	(2.5)	20.2	(2.8)	16.5	(2.3)	20.3	(5.8)	23.6	(7.4)	17.2	(1.2)
Live	6.5	(1.1)	14.4	(2.7)	10.5	(3.1)	15.6	(2.9)	11.2	(2.7)	15.8	(6.0)	18.7	(8.2)	12.8	(1.6)
Dead	5.4	(0.7)	4.4	(0.2)	5.0	(0.6)	4.6	(0.3)	5.3	(0.5)	4.5	(0.4)	4.9	(0.8)	4.4	(0.4)
Canopy cover (%)																
Live	38.0	(6.3)	65.7	(5.7)	54.7	(12.4)	67.4	(4.2)	59.8	(9.7)	63.5	(9.1)	68.4	(15.6)	66.0	(4.2)
Dead	19.1	(3.8)	10.7	(2.9)	14.6	(7.0)	8.9	(1.9)	11.7	(2.9)	10.5	(2.6)	10.0	(7.7)	8.0	(1.0)
Total	57.1	(3.0)	76.4	(3.3)	69.4	(5.6)	76.3	(2.4)	71.5	(6.9)	74.0	(6.7)	78.4	(7.9)	74.0	(3.8)
CBD (kg/m^3)	0.11	(0.02)	0.10	(0.01)	0.09	(0.01)	0.09	(0.01)	0.09	(0.01)	0.09	(0.01)	0.08	(0.01)	0.10	(0.01)
CBH (m)	0.4	(0.1)	0.8	(0.4)	1.8	(1.5)	2.3	(0.4)	1.4	(0.6)	1.3	(0.8)	1.3	(0.7)	1.3	(0.7)
Foliar moisture (%)	96.3	(2.1)	97.8	(1.3)	96.9	(2.9)	99.7	(0.2)	97.5	(1.2)	99.7	(0.2)	97.5	(2.5)	99.5	(0.5)

Notes: ACFL, available canopy fuel load. CBD, canopy bulk density. CBH, canopy base height.

Table H.7. Model outputs for post-outbreak canopy fuels as a function of thinning treatment.

Treatment	Total				Live				Dead			
	β	SE	*P*		β	SE	*P*		β	SE	*P*	
					FOLIAGE BIOMASS							
Treatment effects												
Light+TSI	0.80	0.26	0.002	**	0.82	0.26	0.001	**	0.02	1.42	0.991	
Moderate	0.48	0.28	0.086	+	0.48	0.28	0.084	+	0.38	1.54	0.807	
Moderate+TSI	0.98	0.28	0.000	**	1.03	0.28	0.000	**	-1.70	1.54	0.269	
Heavy	0.49	0.26	0.057	+	0.51	0.26	0.048	*	-0.25	1.42	0.863	
Heavy+TSI	0.75	0.26	0.004	**	0.79	0.26	0.002	**	-1.34	1.42	0.345	
Clearcut	1.23	0.29	0.000	**	1.27	0.29	0.000	**	-0.71	1.54	0.644	
Clearcut+TSI	0.80	0.28	0.004	**	0.85	0.28	0.002	**	-1.23	1.54	0.423	
TSI effects												
Moderate:TSI	0.50	0.31	0.103		0.55	0.30	0.071	+	-2.07	1.64	0.207	
Heavy:TSI	0.26	0.26	0.309		0.28	0.26	0.271		-1.10	1.42	0.440	
Clearcut:TSI	-0.43	0.30	0.153		-0.42	0.30	0.161		-0.52	1.64	0.752	
					1-h CANOPY FUEL							
Treatment effects												
Light+TSI	0.27	0.11	0.012	*	0.80	0.23	0.001	**	-0.21	0.13	0.090	+
Moderate	0.15	0.12	0.196		0.48	0.25	0.060	+	-0.11	0.14	0.430	
Moderate+TSI	0.43	0.12	0.000	**	1.02	0.25	0.000	**	-0.14	0.14	0.307	
Heavy	0.23	0.11	0.032	*	0.52	0.23	0.025	*	-0.02	0.13	0.902	
Heavy+TSI	0.34	0.11	0.002	**	0.81	0.23	0.000	**	-0.15	0.13	0.233	
Clearcut	0.53	0.12	0.000	**	1.20	0.26	0.000	**	-0.09	0.14	0.512	
Clearcut+TSI	0.31	0.12	0.011	*	0.85	0.25	0.001	**	-0.19	0.14	0.160	
TSI effects												
Moderate:TSI	0.28	0.13	0.030	*	0.54	0.28	0.050	*	-0.03	0.15	0.831	
Heavy:TSI	0.10	0.11	0.341		0.30	0.23	0.206		-0.13	0.13	0.284	
Clearcut:TSI	-0.23	0.13	0.071	+	-0.34	0.27	0.203		-0.10	0.14	0.478	
					10-h CANOPY FUEL							
Treatment effects												
Light+TSI	0.18	0.09	0.048	*	0.88	0.22	0.000	**	-0.21	0.14	0.143	
Moderate	0.05	0.10	0.584		0.51	0.25	0.038	*	-0.18	0.16	0.243	
Moderate+TSI	0.35	0.10	0.000	**	1.12	0.25	0.000	**	-0.10	0.16	0.518	
Heavy	0.17	0.09	0.058	+	0.53	0.23	0.019	*	-0.01	0.14	0.945	
Heavy+TSI	0.22	0.09	0.014	*	0.81	0.23	0.000	**	-0.12	0.14	0.413	
Clearcut	0.41	0.10	0.000	**	1.27	0.25	0.000	**	-0.09	0.16	0.559	
Clearcut+TSI	0.26	0.10	0.009	**	0.97	0.25	0.000	**	-0.13	0.16	0.411	
TSI effects												
Moderate:TSI	0.30	0.11	0.005	**	0.62	0.27	0.021	*	0.08	0.17	0.626	
Heavy:TSI	0.05	0.09	0.566		0.28	0.23	0.208		-0.11	0.14	0.454	
Clearcut:TSI	-0.15	0.10	0.142		-0.30	0.26	0.245		-0.04	0.17	0.824	

					100-h CANOPY FUEL							
Treatment effects												
Light+TSI	-0.14	0.16	0.365		1.35	0.37	0.000	**	-0.47	0.29	0.103	
Moderate	-0.21	0.17	0.216		0.65	0.40	0.103		-0.36	0.31	0.252	
Moderate+TSI	-0.05	0.17	0.785		1.54	0.40	0.000	**	-0.38	0.31	0.219	
Heavy	-0.19	0.16	0.238		0.51	0.37	0.167		-0.30	0.29	0.303	
Heavy+TSI	-0.41	0.16	0.011	*	0.79	0.37	0.032	*	-0.66	0.29	0.022	*
Clearcut	-0.39	0.17	0.022	*	1.46	0.42	0.001	**	-0.77	0.32	0.016	*
Clearcut+TSI	-0.49	0.17	0.005	**	1.11	0.41	0.007	**	-0.76	0.31	0.015	*
TSI effects												
Moderate:TSI	0.17	0.18	0.368		0.89	0.45	0.048	*	-0.02	0.33	0.941	
Heavy:TSI	-0.22	0.16	0.169		0.28	0.37	0.440		-0.36	0.28	0.205	
Clearcut:TSI	-0.09	0.18	0.610		-0.35	0.42	0.414		0.02	0.33	0.961	
					AVAILABLE CANOPY FUEL LOAD							
Treatment effects												
Light+TSI	0.47	0.16	0.004	**	0.82	0.25	0.001	**	-0.21	0.11	0.058	+
Moderate	0.28	0.18	0.116		0.48	0.27	0.078	+	-0.09	0.12	0.432	
Moderate+TSI	0.64	0.18	0.000	**	1.03	0.27	0.000	**	-0.18	0.12	0.122	
Heavy	0.32	0.16	0.047	*	0.51	0.25	0.042	*	-0.03	0.11	0.778	
Heavy+TSI	0.49	0.16	0.003	**	0.80	0.25	0.002	**	-0.18	0.11	0.091	+
Clearcut	0.80	0.18	0.000	**	1.25	0.28	0.000	**	-0.12	0.12	0.302	
Clearcut+TSI	0.48	0.18	0.007	**	0.85	0.27	0.002	**	-0.23	0.12	0.053	+
TSI effects												
Moderate:TSI	0.36	0.19	0.063	+	0.55	0.30	0.066	+	-0.09	0.13	0.475	
Heavy:TSI	0.16	0.16	0.313		0.29	0.25	0.257		-0.15	0.11	0.158	
Clearcut:TSI	-0.32	0.19	0.090	+	-0.40	0.29	0.168		-0.11	0.13	0.389	
					CANOPY COVER							
Treatment effects												
Light+TSI	0.90	0.25	0.000	**	1.14	0.36	0.002	**	-0.67	0.36	0.063	+
Moderate	0.60	0.26	0.019	*	0.75	0.38	0.052	+	-0.42	0.37	0.263	
Moderate+TSI	0.96	0.27	0.000	**	1.33	0.40	0.001	**	-0.89	0.42	0.032	*
Heavy	0.53	0.24	0.028	*	0.71	0.36	0.049	*	-0.46	0.37	0.219	
Heavy+TSI	0.80	0.24	0.001	**	1.07	0.36	0.003	**	-0.70	0.36	0.053	+
Clearcut	1.17	0.28	0.000	**	1.52	0.41	0.000	**	-1.57	0.52	0.003	**
Clearcut+TSI	0.83	0.26	0.002	**	1.26	0.40	0.002	**	-0.98	0.43	0.023	*
TSI effects												
Moderate:TSI	0.35	0.29	0.229		0.59	0.42	0.166		-0.47	0.46	0.305	
Heavy:TSI	0.26	0.25	0.300		0.35	0.36	0.325		-0.24	0.40	0.545	
Clearcut:TSI	-0.34	0.30	0.270		-0.26	0.43	0.550		0.59	0.55	0.282	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.8. Model outputs for post-outbreak canopy bulk density, canopy base height, and foliar moisture by thinning treatment.

Treatment	Canopy bulk density			Canopy base height				Foliar moisture			
	β	SE	*P*	β	SE	*P*		β	SE	*P*	
Treatment effect											
Light+TSI	-0.12	0.16	0.484	0.77	0.55	0.158		0.12	0.74	0.872	
Moderate	-0.22	0.18	0.214	1.59	0.59	0.007	*	-0.36	0.72	0.621	
Moderate+TSI	-0.22	0.18	0.214	1.83	0.59	0.002	**	0.42	0.77	0.588	
Heavy	-0.16	0.16	0.344	1.30	0.55	0.018	*	-0.69	0.71	0.331	
Heavy+TSI	-0.21	0.16	0.207	1.20	0.55	0.028	*	0.71	0.79	0.366	
Clearcut	-0.25	0.18	0.162	1.27	0.59	0.032	*	0.44	0.76	0.564	
Clearcut+TSI	-0.13	0.18	0.470	1.27	0.59	0.032	*	0.87	0.85	0.305	
TSI effect[1]											
Moderate:TSI	0.00	0.19	1.000	0.24	0.63	0.703		0.77	0.81	0.337	
Heavy:TSI	-0.05	0.16	0.752	-0.10	0.55	0.862		1.40	0.71	0.051	+
Clearcut:TSI	0.12	0.19	0.528	0.00	0.63	1.000		0.44	0.89	0.625	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.9. Summary of fine-scale spatial heterogeneity in post-outbreak fuel profiles by thinning treatment. Values are the mean (standard error) of within-stand coefficient of variation (%).

Characteristic	Control (n = 4)		Light+TSI (n = 4)		Moderate (n = 3)		Moderate+TSI (n = 3)		Heavy (n = 4)		Heavy+TSI (n = 4)		Clearcut (n = 3)		Clearcut+TSI (n = 3)	
FWD	79.1	(6.9)	55.4	(8.1)	88.8	(14.4)	75.8	(9.5)	86.4	(7.4)	73.9	(9.5)	75.7	(11.9)	63.4	(12.8)
CWD	76.4	(17.2)	111.0	(15.6)	92.8	(36.1)	113.5	(16.5)	71.9	(7.0)	70.1	(16.7)	82.9	(9.5)	106.7	(12.2)
Fuel depth	69.1	(4.6)	71.3	(4.7)	81.3	(16.7)	57.9	(2.2)	77.3	(6.3)	66.8	(11.1)	55.6	(4.5)	55.9	(6.5)
Canopy cover																
Total	27.2	(4.4)	20.5	(5.1)	18.2	(5.5)	16.7	(2.6)	24.7	(5.8)	16.7	(4.5)	11.6	(1.4)	22.2	(4.2)
Live	54.7	(4.9)	35.0	(8.5)	33.3	(17.1)	30.8	(6.9)	43.2	(13.0)	25.3	(7.8)	21.5	(9.1)	35.4	(7.4)
Dead	53.3	(3.2)	89.9	(7.3)	54.9	(8.9)	119.6	(5.4)	79.4	(10.4)	73.0	(9.7)	99.4	(34.1)	114.1	(18.9)
CBH	103.8	(11.8)	99.6	(11.6)	86.5	(8.1)	98.3	(10.6)	92.4	(8.9)	82.0	(8.7)	70.7	(11.0)	73.4	(6.0)
ACFL, horizontal																
Top	43.1	(8.9)	72.5	(1.9)	46.5	(8.4)	65.3	(10.1)	63.1	(11.6)	45.6	(9.0)	46.2	(7.8)	57.4	(6.4)
Middle	62.1	(3.8)	62.9	(8.9)	65.1	(10.6)	70.6	(6.5)	67.4	(5.9)	60.1	(5.1)	79.5	(8.7)	71.5	(8.8)
Bottom	82.6	(12.4)	96.9	(10.9)	98.7	(2.4)	115.6	(17.0)	138.0	(34.4)	114.4	(15.7)	117.3	(22.9)	130.4	(10.6)
ACFL, vertical	79.4	(9.7)	82.7	(7.5)	88.1	(0.9)	77.5	(10.1)	94.8	(4.7)	104.6	(6.7)	99.8	(4.9)	103.7	(2.4)

Notes: FWD, fine woody debris. CWD, coarse woody debris. Fuel depth, sum of litter and duff depths. CBH, crown base height. ACFL, available canopy fuel load. Top strata, height ≥ 16 m; middle strata, 8 m ≤ height < 16 m; bottom strata, height < 8 m.

Table H.10. Model outputs for within-stand coefficient of variation in post-outbreak fuel profiles by thinning treatment.

Treatment	FWD				CWD				Fuel depth				CBH			
	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Treatment effect																
Light+TSI	-0.34	0.14	0.013	*	0.39	0.19	0.039	*	0.03	0.13	0.817		-0.04	0.12	0.719	
Moderate	0.14	0.15	0.337		0.22	0.21	0.290		0.16	0.14	0.260		-0.19	0.13	0.146	
Moderate+TSI	-0.03	0.15	0.846		0.34	0.21	0.106		-0.18	0.14	0.219		-0.07	0.13	0.603	
Heavy	0.09	0.14	0.512		-0.03	0.19	0.885		0.11	0.13	0.402		-0.11	0.12	0.343	
Heavy+TSI	-0.08	0.14	0.582		-0.07	0.19	0.726		-0.03	0.13	0.799		-0.24	0.12	0.044	*
Clearcut	-0.01	0.15	0.952		0.03	0.21	0.901		-0.22	0.14	0.133		-0.41	0.13	0.002	**
Clearcut+TSI	-0.21	0.15	0.151		0.28	0.21	0.185		-0.21	0.14	0.142		-0.37	0.13	0.005	**
TSI effect[1]																
Moderate:TSI	-0.17	0.16	0.289		0.12	0.23	0.598		-0.34	0.15	0.028	*	0.12	0.14	0.387	
Heavy:TSI	-0.16	0.14	0.228		-0.04	0.19	0.835		-0.15	0.13	0.275		-0.13	0.12	0.286	
Clearcut:TSI	-0.20	0.16	0.195		0.25	0.22	0.251		0.00	0.15	0.975		0.04	0.14	0.765	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. FWD, fine woody debris. CWD, coarse woody debris. Fuel depth, sum of litter and duff depths. CBH, crown base height. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.11. Model outputs for within-stand coefficient of variation in post-outbreak canopy cover by thinning treatment.

Treatment	Total				Live				Dead			
	β	SE	*P*		β	SE	*P*		β	SE	*P*	
Treatment effect												
Light+TSI	-0.30	0.24	0.208		-0.48	0.29	0.103		0.51	0.15	0.001	**
Moderate	-0.47	0.27	0.082	+	-0.67	0.32	0.038	*	0.01	0.16	0.959	
Moderate+TSI	-0.50	0.26	0.058	+	-0.66	0.32	0.041	*	0.85	0.16	0.000	**
Heavy	-0.10	0.24	0.686		-0.17	0.29	0.563		0.35	0.15	0.025	*
Heavy+TSI	-0.51	0.24	0.035	*	-0.84	0.29	0.004	**	0.29	0.15	0.055	+
Clearcut	-0.85	0.26	0.001	**	-0.99	0.32	0.002	**	0.62	0.16	0.000	**
Clearcut+TSI	-0.21	0.26	0.415		-0.49	0.32	0.126		0.79	0.16	0.000	**
TSI effect[1]												
Moderate:TSI	0.0	0.3	0.905		0.0	0.3	0.955		0.8	0.2	0.000	**
Heavy:TSI	-0.4	0.2	0.093	+	-0.7	0.3	0.028	*	-0.1	0.2	0.704	
Clearcut:TSI	0.6	0.3	0.022	*	0.5	0.3	0.137		0.2	0.2	0.323	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Table H.12. Model outputs for within-stand coefficient of variation in post-outbreak available canopy fuel load by thinning treatment.

Treatment	Horizontal profile												Vertical profile			
	Top strata (height ≥ 16 m)				Middle strata (8 ≤ height < 16 m)				Bottom strata (height < 8 m)							
	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Treatment effect																
Light+TSI	0.60	0.15	0.000	**	0.01	0.12	0.963		0.16	0.18	0.369		0.04	0.09	0.630	
Moderate	0.14	0.17	0.390		0.04	0.13	0.747		0.19	0.20	0.350		0.10	0.10	0.290	
Moderate+TSI	0.52	0.17	0.002	**	0.11	0.13	0.365		0.33	0.20	0.091	*	-0.03	0.10	0.785	
Heavy	0.41	0.15	0.007	**	0.07	0.12	0.523		0.51	0.18	0.005	*	0.18	0.09	0.047	*
Heavy+TSI	0.07	0.15	0.644		-0.04	0.12	0.743		0.33	0.18	0.074	+	0.28	0.09	0.002	**
Clearcut	0.17	0.17	0.307		0.23	0.13	0.064	+	0.35	0.20	0.083	+	0.23	0.10	0.021	*
Clearcut+TSI	0.41	0.17	0.015	*	0.13	0.13	0.289		0.45	0.20	0.023	*	0.27	0.10	0.007	**
TSI effect[1]																
Moderate:TSI	0.38	0.18	0.035	*	0.07	0.13	0.586		0.15	0.22	0.494		-0.13	0.11	0.216	
Heavy:TSI	-0.34	0.15	0.026	*	-0.11	0.12	0.334		-0.18	0.18	0.316		0.10	0.09	0.281	
Clearcut:TSI	0.24	0.18	0.178		-0.10	0.13	0.452		0.11	0.21	0.611		0.04	0.10	0.703	

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. FWD, fine woody debris. CWD, coarse woody debris. Fuel depth, sum of litter and duff depths. CBH, crown base height. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

Appendix I. Q2 – POST-OUTBREAK ABOVEGROUND CARBON STORAGE

Table I.1. Summary of post-outbreak aboveground carbon biomass by thinning treatment. Values are the mean (standard error).

Carbon (Mg/ha)	Control (n = 4)		Light+TSI (n = 4)		Moderate (n = 3)		Moderate+TSI (n = 3)		Heavy (n = 4)		Heavy+TSI (n = 4)		Clearcut (n = 3)		Clearcut+TSI (n = 3)	
Total	113.2	(13.4)	112.0	(13.5)	85.4	(7.0)	103.4	(16.1)	101.2	(3.2)	99.6	(13.4)	103.8	(6.3)	82.2	(3.3)
Live	20.0	(2.8)	48.0	(8.4)	31.4	(8.3)	54.0	(11.8)	33.6	(6.0)	46.6	(12.6)	53.7	(19.5)	43.3	(5.3)
Dead	93.2	(10.7)	64.0	(9.6)	53.9	(1.6)	49.4	(4.6)	67.6	(3.2)	53.0	(2.3)	50.1	(13.2)	38.9	(2.2)

Table I.2. Model outputs for post-outbreak aboveground carbon storage variables as a function of thinning treatment.

Treatment	Total				Live				Dead			
	β	SE	*P*		β	SE	*P*		β	SE	*P*	
Treatment effect												
Light+TSI	0.00	0.09	0.971		0.87	0.21	0.000	**	-0.38	0.12	0.001	**
Moderate	-0.26	0.10	0.007	**	0.48	0.23	0.033	*	-0.55	0.13	0.000	**
Moderate+TSI	-0.03	0.10	0.736		1.10	0.23	0.000	**	-0.62	0.13	0.000	**
Heavy	-0.09	0.09	0.302		0.51	0.21	0.014	*	-0.31	0.12	0.007	**
Heavy+TSI	-0.13	0.09	0.139		0.81	0.21	0.000	**	-0.56	0.12	0.000	**
Clearcut	-0.01	0.10	0.939		1.15	0.23	0.000	**	-0.63	0.13	0.000	**
Clearcut+TSI	-0.24	0.10	0.012	*	0.91	0.23	0.000	**	-0.86	0.13	0.000	**
TSI effect[1]												
Moderate:TSI	0.23	0.11	0.031	*	0.62	0.25	0.013	*	-0.07	0.14	0.603	
Heavy:TSI	-0.04	0.09	0.656		0.29	0.21	0.159		-0.25	0.12	0.036	*
Clearcut:TSI	-0.24	0.10	0.021	*	-0.24	0.24	0.316		-0.23	0.14	0.094	+

Notes: Coefficient estimates (β), standard error (SE), and *P* values are reported for each predictor variable. Symbols indicate strength of evidence of an effect according to $P < \alpha = 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive). TSI, timber stand improvement.

[1] TSI effect isolates the difference between stands with and without TSI within the same major treatment.

CONCLUSIONS

Climate-mediated increases in disturbance activity create challenges for forest managers tasked with maintaining ecological resilience and ecosystem services. Through empirical examination of historical thinning legacies on forest response to a severe mountain pine beetle outbreak, this work provides critical observations of effects and longevity of past forest management on components of resilience, fuel profiles, and aboveground carbon storage. Findings from both chapters demonstrate that stand-thinning treatments present a series of management tradeoffs by influencing post-outbreak stand structure, fuel profiles, and carbon storage.

Mixed-species subalpine forests are naturally positioned to be resilient (i.e., recover essential structure and function; Walker et al. 2004) to outbreaks without management intervention due to the selective nature of bark beetles as a mortality agent (i.e., only killing the largest individuals of a single tree species) (Safranyik and Carrol 2006, DeRose and Long 2014). Managing for resistance to outbreak may even compromise resilience to a second outbreak, since repeated heavy stand thinning necessary for reducing stand susceptibility to mountain pine beetle attack (DeRose and Long 2014) favors the creation of even-age stands dominated by host lodgepole pine trees (Kashian et al. 2011). While effects of thinning on resistance to outbreak are transient, historical treatments had lasting effects on increasing live (and decreasing dead) post-outbreak stand components (e.g., density, basal area, canopy fuel, aboveground carbon biomass) into the gray stage. These findings suggest past management activities may drive potential differences in fire hazard, resistance to control, and carbon dynamics between thinned and uncut stands following outbreak. Yet, alteration of forest structure and composition by stand-thinning treatments has additional consequences for post-outbreak biodiversity and ecosystem services (Thom and Seidl 2016) including wildlife habitat (Saab et al. 2014), biogeochemical cycling

(Mikkelson et al. 2013), and human dimensions (e.g., timber harvest, recreation, property value; Flint and others 2009). These tradeoffs highlight the importance of recognizing potential consequences of management actions on other critical ecosystem components, rather than adhering to a single objective (D'Amato et al. 2011), and suggest limitation of thinning treatments to high-value areas, such as built environments (Baker 2009).

This research provides a foundation upon which to build further exploration of interactions between forest management and natural disturbances. Both chapters examined legacies of 60-year-old stand-thinning treatments on forest attributes measured 8 years after mountain pine beetle outbreak. Since disturbance and forest dynamics unfold over multiple decades to centuries (Carpenter and Turner 2001), using a simulation modeling approach to examine forest structure and function over longer time since outbreak could extend our research insights on resilience and disturbance interactions. Simulation of successional dynamics over time could enhance our understanding of thinning effects on resilience to outbreak by allowing differences in species composition (or lack thereof) among treatments to emerge. Modeling stand development under different climate change scenarios could also provide insights into thinning effects on climate-adaptability following outbreak. Additionally, simulation could be used to model interactions with fire or subsequent beetle outbreaks, enriching our understanding of thinning effects on fire hazard, carbon storage, and resilience beyond the gray stage post-outbreak. Ultimately, continuing to monitor and maintain long-term experimental research sites such as the Fraser Experimental Forest will provide critical opportunities to empirically measure legacies of past management on forest response to disturbance events and changing climate conditions decades into the future.

REFERENCES

Baker, W. L. 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington D.C.

Carpenter, S. R., and M. G. Turner. 2001. Hares and tortoises: interactions of fast and slow variables in ecosystems. Ecosystems 3:495–497.

D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. Forest Ecology and Management 262:803–816.

DeRose, R. J., and J. N. Long. 2014. Resistance and resilience: a conceptual framework for silviculture. Forest Science 60:1205–1212.

Flint, C. G., B. McFarlane, and M. Müller. 2009. Human dimensions of forest disturbance by insects: an international synthesis. Environmental Management 43:1174–1186.

Kashian, D. M., R. M. Jackson, and H. D. Lyons. 2011. Forest structure altered by mountain pine beetle outbreaks affects subsequent attack in a Wyoming lodgepole pine forest, USA. Canadian Journal of Forest Research 41:2403–2412.

Mikkelson, K. M., L. A. Bearup, R. M. Maxwell, J. D. Stednick, J. E. McCray, and J. O. Sharp. 2013. Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. Biogeochemistry 115:1–21.

Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60:539–559.

Safranyik, L., and A. L. Carrol. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 *in* L. Safranyik and W. R. Wilson, editors. The Mountain Pine Beetle - A Synthesis of Biology, Management, and Impacts in Lodgepole Pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Thom, D., and R. Seidl. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews 91:760–781.

Walker, B., C. S. Holling, S. R. Carpenter, and A. P. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9:5.