Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience

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Abstract. Fire frequency in low-elevation coniferous forests in western North America has greatly declined since the late 1800s. In many areas, this has increased tree density and the proportion of shade-tolerant species, reduced resource availability, and increased forest susceptibility to forest insect pests and high-severity wildfire. In response, treatments are often implemented with the goal of increasing ecosystem resilience by increasing resistance to disturbance. We capitalized on an existing replicated study of fire and stand density treatments in a ponderosa pine (*Pinus ponderosa*)–Douglas-fir (*Pseudotsuga menziesii*) forest in western Montana, USA, that experienced a naturally occurring mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak 5 yr after implementation of fuels treatments. We explored whether treatment effects on tree-level defense and stand structure affected resistance to MPB. Mortality from MPB was highest in the denser, untreated control and burn-only treatments, with approximately 50% and 39%, respectively, of ponderosa pine killed during the outbreak, compared to almost no mortality in the thin-only and thin-burn treatments. Thinning treatments, with or without fire, dramatically increased tree growth and resin ducts relative to control and burn-only treatments. Prescribed burning did not increase resin ducts but did cause changes in resin chemistry that may have affected MPB communication and lowered attack success. While ponderosa pine remained dominant in the thin and thin-burn treatments after the outbreak, the high pine mortality in the control and burn-only treatment caused a shift in species dominance to Douglas-fir. The high Douglas-fir component in the control and burn-only treatments due to 20th century fire exclusion, coupled with high pine mortality from MPB, has likely reduced resilience of this forest beyond the ability to return to a ponderosa pine-dominated system in the absence of further fire or mechanical treatment. Our results show treatments designed to increase resistance to high-severity fire in ponderosa pine-dominated forests in the Northern Rockies can also increase resistance to MPB, even during an outbreak. This study suggests that fuel and restoration treatments in fire-dependent ponderosa pine forests that reduce tree density increase ecosystem resilience in the short term, while the reintroduction of fire is important for long-term resilience.

Key words: delayed mortality; Dendroctonus ponderosae; fire-adaptations; fuel treatment; Montana, USA; oleoresin; Pinus ponderosa; plant defense; silviculture; succession.

INTRODUCTION

Forest land management goals often include increasing ecosystem resilience (Hobbs et al. 2014), yet actual management prescriptions rarely examine potential effects from multiple threats to resilience such as wildfire, insects, disease, and drought. In ecosystems shaped by frequent natural disturbance, altered disturbance regimes are likely to affect responses to other overlapping natural disturbances (Buma 2015), potentially yielding "ecological surprises" (Paine et al. 1998) and reduced ecosystem resilience (Folke et al. 2004). Limited resources for implementing treatments heighten the need to develop treatment prescriptions in the context of historical disturbance regimes from a social-ecological resilience perspective (sensu Folke 2006). We examined the impacts of forest fuel treatments on resistance to a subsequent disturbance and the implications to ecosystem resilience. Resilience and resistance have been defined numerous ways and are often ambiguous concepts (Holling 1973, Pimm 1984, Standish et al. 2014). We defined resilience as the capacity of the system to persist after a disturbance, such that the variables and processes that control ecosystem functions remain intact (Holling 1973, Gunderson 2000, Suding and Hobbs 2009). Resilience can be measured in terms of the intensity of a disturbance required to switch the system to another state (Standish et al. 2014). Resistance is an attribute of ecosystem resilience, defined as the difficulty to change the system (Folke et al. 2004) and measured by the degree of change

in ecosystem variables before and after a disturbance (Pimm 1984, Standish et al. 2014).

Wildfire and bark beetles (Coleoptera: Curculionidae, Scolytinae) are two of the most influential disturbance agents in temperate coniferous forests worldwide and have interacted for millennia to drive forest composition and structure (McCullough et al. 1998, Parker et al. 2006). As such, they provide an ideal system to study disturbance interactions and how altered regimes of one disturbance may affect resistance to another disturbance. Anthropogenic changes to historical fire regimes have altered ecosystem flammability, changing the frequency, intensity, extent, and effects of fire in regions around the world (Bond and Keeley 2005, Flannigan et al. 2009, Ryan et al. 2013). Many North American forests are dependent on fire for persistence on the landscape (Agee 1998), but factors such as domestic livestock grazing, road building, cessation of Native American burning, and organized fire suppression since the late 1800s have greatly reduced fire frequency, with the most striking impacts on ecosystems dependent on frequent, low-severity fire (Pyne 1982, Keeley et al. 2009). Widespread exclusion of wildfire in these areas with historical low- and mixed-severity fire regimes poses serious concerns from both an ecological and social viewpoint because of the risk of increased fire severity when wildfire does occur due to increased tree density and, in some areas, to species composition shifts to shade-tolerant species (Hanberry 2014, Hessburg et al. 2015).

Native bark beetles are the largest cause of tree mortality in North American coniferous forests (Logan et al. 2003). Bark beetles typically occur at low population levels, causing limited tree mortality due to specialized host tree physical and chemical defenses that reduce attack success (Franceschi et al. 2005, Seybold et al. 2006). Beetles can overcome host defenses through pheromone-mediated cooperative behavior, in which beetles mass attack trees to exhaust defenses to success-fully reproduce, killing the trees in the process (Berryman 1972, Six and Wingfield 2011). These defenses include resin, a complex mixture of terpenoid compounds, which serve as physical and chemical defenses from attacking beetles (Raffa 2014), and resin ducts, a network of spe-cialized canals that synthesize, store, and deliver resin to attack sites (Hood and Sala 2015). Periodically, wide-spread regional climatic and other factors can trigger populations to irrupt to outbreak levels during which beetles kill large extents of coniferous forests (Raffa et al. 2008). Relative to previously recorded outbreaks, recent bark beetle outbreaks are more synchronous and are causing more tree mortality over larger areas (Bentz et al. 2009). These higher severity outbreaks have been attributed to direct and indirect effects of climate change and past land management practices (Bentz et al. 2009, 2010). Land management practices that reduced forest heterogeneity such as widespread harvesting in the early 1900s and fire exclusion also increase host availability and susceptibility to outbreaks (Parker et al. 2006, Bentz et al. 2009).

Areas with an historical, frequent, low-severity fire regime have been most affected by past wildfire exclusion, and beginning in 2000 the USA enacted several policies to fund treatments designed to foster resilient landscapes resistant to high-severity wildfire and insects and disease (Stephens and Ruth 2005, USDOI and USDA 2014). Many studies have reported the effects of fuel treatments in reducing potential high-severity fire (reviewed in Fulé et al. 2012, Stephens et al. 2012*b*), and the effects of forest management on bark beetle attack patterns also have been widely studied (reviewed in Fettig et al. 2007, 2014*b*). However, the broader ecological impacts of fuel reduction treatments to disturbances other than wildfire and long-term ecosystem resilience are unknown in many areas (Omi 2015). Past studies show strong, consistent patterns that slower growing, less vigorous trees are more likely to be attacked (Waring and Pitman 1985, Kolb et al. 2007) and that higher density forest stands are more susceptible to beetle-caused mortality (Larsson et al. 1983, Negrón and Popp 2004, Fettig et al. 2007, 2014*b*). However, bark beetle attack patterns and preferences depend on bark beetle population size (Boone et al. 2011), and earlier studies with replicated density and fire treatments almost exclusively have been done during relatively low bark beetle population densities (Fulé et al. 2012, Six et al. 2014), limiting inference about treatment effectiveness during a severe outbreak. These limitations and uncertainties highlight the need for a better under-standing of how forest management actions affect resistance from multiple threats and under intense bark beetle pressures to ultimately impact forest resilience (Millar et al. 2007, Schoennagel and Nelson 2010).

Definitions and interpretation of ecological resistance and resilience must be placed in the context of the local disturbance regime and successional dynamics. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests occur over a large geographic range where historical fire regimes vary regionally from low-severity surface fires to more infrequent, mixed-severity fires (Arno et al. 1995, Brown and Sieg 1996, Swetnam and Baisan 1996, Moore et al. 1999, Sherriff and Veblen 2007, Taylor 2010, Perry et al. 2011), as do the successional patterns and species associa-tions (Oliver and Ryker 1990). Our study focuses on ponderosa pine-dominated forests in the U.S. Northern Rockies. Here, at low-to-mid elevations, the historical, frequent, low- and mixed-severity surface fire regimes created low-density forests dominated by ponderosa pine, with an association of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco) (Keeling et al. 2006). Ponderosa pine develops resistance to fire more quickly than Douglas-fir, allowing a higher proportion of ponderosa pine to establish (Keane et al. 1990). Where ponderosa pine is seral to shade-tolerant species, as in the Northern Rockies and many other loca-tions, such as California, the Pacific Northwest, and the Colorado Front Range, fire exclusion leads to both increased tree density and establishment of shade-tolerant species (Arno et al. 1995, Allen et al. 2002,

Keeling et al. 2006). Frequent fire regulates tree density by killing seedlings and saplings still susceptible to fire because the bark is not yet thick enough to prevent cambium kill. Decades of fire exclusion in many areas has allowed enough time for some shade-tolerant species to develop thick bark and become resistant to fire, such that even if fire is reintroduced survival is much higher (Hood 2010). In contrast, in areas such as the southwestern USA and Black Hills Region, ponderosa pine is not seral to other tree species and lack of fire increases tree density, but generally does not cause a change in forest species composition (Covington and Moore 1994, Allen et al. 2002, Shepperd and Battaglia 2002). How the interaction between fire and bark beetles under changing climate and disturbance regimes will alter forest structure and dynamics and subsequent ecosystem processes over the landscape will therefore likely vary regionally due to differences in successional patterns.

A resilient forest ecosystem in a landscape with a historical fire regime of frequent, low-severity fire is one that can withstand disturbance and persist in a forested state dominated by shade-intolerant tree species and maintain ecological processes (fire regime, hydrology, nutrient cycling, etc.). In contrast, this same landscape is not resilient if a disturbance moves the system to a new state, such as a change in species dominance or forest structure to such a degree that ecological processes are altered. Using ponderosa pine-dominated forests in the Northern Rockies as an example, higher resistance to a wildfire or mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) outbreak would translate to low tree mortality

and continued dominance of shade-intolerant, larger trees. While a shift in dominance of these forests to Douglas-fir would increase resistance to MPB, it would lower resistance to other irruptive insect species, while also increasing the potential of high-severity fire. Therefore, the historical fire regime for ponderosa pine forests in the Northern Rockies, likely fostered conditions resistant to high-severity fire and MPB outbreaks, creating a landscape resilient to both disturbances.

We capitalized on an existing, replicated study originally designed to test treatment efficacy in increasing resistance of a ponderosa pine forest to potential high-severity wildfire. The area experienced a naturally occurring MPB outbreak approximately 5 yr after treatment, allowing us to test treatment effectiveness in resisting MPB (e.g., lower tree mortality and fewer changes in forest structure and composition) and the consequences to ecosystem resilience (i.e., capacity to absorb disturbance and persist as a ponderosa pine-dominated forest; Table 1). Treatments included prescribed burning, mechanical thinning, thinning and burning, and an untreated control. Historically, the area burned very frequently, but prior to treatment implementation, the study site had not burned in over 100 yr (Gundale et al. 2005, Grissino-Mayer et al. 2006). This offered a unique opportunity to explore the underlying tree-level physiological effects and stand-level ecological effects of treatments on resistance to bark beetle attack with far-reaching management implications for the resiliency of fire-dependent coniferous forests to multiple threats. We hypothesized that trees in the control

TABLE 1. Definitions, context, and criteria used for determining forest management effects on ecological resistance and resilience of a ponderosa pine ecosystem in the Northern Rockies, USA, subject to a mountain pine beetle outbreak.

Concept	General definition	Specific context	Measurement and decision criteria
Resistance	The difficulty in changing the system (Folke et al. 2004). An attribute of resilience.	How do fuel treatments in ponderosa pine forests in the Northern Rockies affect the degree of change in forest structure and species composition after a mountain pine beetle outbreak?	Change before and after the outbreak (less change equals more resistance) • Beetle-induced mortality • Host and non-host basal area • Host and non-host density • Host and non-host mean size Overall change • Resistant treatments will exhibit little change when variables listed above are combined using multivariate analysis
Resilience	The capacity of system to persist even when affected by disturbance such that the variables and processes that control ecosystem behavior remain intact (Holling 1973, Gunderson 2000).	How do fuel treatments in ponderosa pine forests in the Northern Rockies affect the ability of the ecosystem to remain dominated by ponderosa pine after a mountain pine beetle outbreak?	Species dominance • Treatments dominated by larger ponderosa pine after the outbreak are more resilient Trajectories • After the outbreak resilient treatments will be associated with ponderosa pine and lower forest density in the multivariate analysis

treatments would have the least resistance (highest mortality from bark beetles), followed in order by the burn-only, thin-only, and thin-burn treatments in response to changes in tree density. We reasoned that the burn-only treatment would reduce tree density but not near to historical levels due to the atypically long time since prior wildfire, but confer some increased long-term resistance to bark beetles due to fire-caused stimulation of host-tree defenses (Hood et al. 2015). The thin-only treatment would increase resistance to bark beetles by reducing tree density, and the thin-burn would be most resistant due to both decreasing density and the fire-caused stimulation of tree defense. Lastly, we predicted that the low-density thin-only and thin-burn would be most resilient and remain dominated by ponderosa pine due to increased resistance to the outbreak.

METHODS

Site and treatment description

Our study site is located on the University of Montana's Lubrecht Experimental Forest in western Montana, USA (46°53′ N, 113°26′ W) and is part of a national program to study the effects of silvicultural methods designed to reduce fire hazard in forests with a historical, frequent, low-to-moderate severity fire regime (Stephens et al. 2009). Mean annual temperature is 7°C, ranging from a mean minimum of 0°C and maximum of 13°C. The area receives an average of 50 cm precipitation annually, about half in the form of snow (Fiedler et al. 2010). Our study site is located in a second-growth forest that established after widespread harvesting in the late 1800s–early 1900s. The forest is dominated by ponderosa pine and Douglas-fir, with scattered western larch (*Larix occidentalis* Nutt) and lodgepole pine (*Pinus contorta* Douglas ex Louden). The historical mean fire return interval was 7 yr (range of 2–14 yr), but fire frequency greatly declined after 1871 (Grissino-Mayer et al. 2006). The study site had not burned since the late 1800s, although there was moderate grazing throughout the 1900s (Gundale et al. 2005).

Three 36-ha blocks consisting of four, 9-ha units each were established in 2000. Each unit within a block was assigned one of four treatments: control, burn-only, thin-only, and thin-burn (see Gundale et al. 2005, Fiedler et al. 2010 for detailed treatment prescriptions and pre-treatment conditions). In each unit, 10 plots, 20 × 50 m (0.1 ha), were established for sampling trees > 10 cm diameter at breast height (DBH; 1.37 m above ground). Control treatments were not manipulated. Thinning and burning treatments were designed to restore stands toward historical conditions by reducing tree density, particularly shade-tolerant Douglas-fir, and encourage shade-intolerant species such as ponderosa pine, while also reducing hazard of stand-replacing wildfire. The goal of all treated units was to create fire-resistant forests in which 80% of basal area of overstory trees would

survive a wildfire burning under 80th percentile weather conditions (Fiedler et al. 2010). In the thin-only and thin-burn units, a low thinning with improvement/selection cutting to favor ponderosa pine ≥ 40 cm DBH reduced average residual basal area to a target of 11 m²/ha. Thinning was conducted in the winter of 2001. Burn-only and thin-burn units were broadcast burned in May and June 2002. The prescribed burns were designed to reduce surface fuel loading and ladder fuels consisting of seedling and saplings.

Data collection and tissue preparation

Treatment resistance to mountain pine beetle outbreak.—Pre-harvest measurements were completed in 2000, with annual measurements for the first 4 yr post-treatment. Initial treatment effects through 2005 have been reported (Gundale et al. 2005, Metlen and Fiedler 2006, Six and Skov 2009, Stephens et al. 2009, Fiedler et al. 2010); hence, we only present data collected between 2005 and 2012. In 2005 and 2010, we measured DBH for all trees ≥ 10 cm DBH in each treatment and assessed bark beetle attack status and tree mortality. During the 2010 assessment, we observed increasing MPB activity in many units in conjunction with a large-scale regional outbreak in western Montana (Montana DNRC 2010). Bark beetle activity was low during the first several years after treatment implementation, at least through 2004 (Six and Skov 2009). We therefore sampled the site again in 2012, during which time we also collected additional data to quantify potential treatment differences in tree growth and defense-related traits to further examine mechanisms associated with stand-level resistance to bark beetles.

We calculated several forest structural and species composition attributes using the tree data (> 10 cm DBH) from the 2005 and 2012 plot surveys, including basal area (i.e., cross-sectional area of living trees per hectare; m²/ha), density (living trees/ha), quadratic mean diameter (QMD, i.e., average diameter [cm²] of the mean basal area; Curtis and Marshall 2000) by host (ponderosa) and non-host (Douglas-fir) species for each plot for each time step. We also calculated the percent of host basal area and density per plot for each time step. Analysis only included living trees.

Tree growth and axial resin ducts.—We randomly selected three plots in each unit. One ponderosa pine, between 27 and 36 cm DBH with no sign of bark beetle attack, was selected in each plot in 2012. We collected resin flow samples on the west and east aspects of each tree at approximately 1.37 m above ground by removing a 2.5 cm circular section of the bark and phloem and using a silicone funnel to channel resin into a 50-mL vial attached to the tree below the tapping site. After 24 h, we measured the volume of resin to the nearest 0.25 mL.

To quantify annual tree growth and axial resin duct production, we extracted two 5 mm wide increment cores from each tree in October 2013 using a manual increment

borer to obtain a cross section of wood containing annual rings from 2013 to the tree pith. Cores were collected at approximately 1.37 m above the ground, below and within 3–6 cm the resin flow tapping site. We prepared cores using standard techniques (mounted and sanded until cellular structure was visible through a binocular microscope) and assigned the correct calendar year to each tree ring (i.e., crossdated; Grissino-Mayer 2001). We scanned all cores using an Epson platform scanner at 2400 dpi and measured ring widths to the nearest 0.001 mm using CooRecorder v7.7 (Cybis Elekronik & Data AB, Saltsjöbaden, Sweden). We measured individual resin duct area in ImageJ (version 1.46r; National Institutes of Health, Bethesda, Maryland, USA) to the nearest 1×10^{-7} mm^2 using the ellipse tool and assigned the calendar year in which each duct formed. We measured ducts formed from 1996 (five growing seasons pre-treatment) to 2011 (10 growing seasons post-burn and year prior to resin flow sampling).

We calculated basal area increment (BAI), duct size, duct production, and total duct area for each core based on raw ring width values and calculated the average annual value per tree from the two collected cores. We observed no age-related decline in ring widths for the section of the chronology we used for analyses (the most recent 16 yr); therefore, we did not detrend raw ring width values. We calculated BAI from ring widths and the tree diameter inside bark using the dplR package, version 1.6.0 in R, version 3.0.1 (Bunn 2008). From the resin duct area measurements, we calculated the following additional metrics, based on the methods of Hood and Sala (2015) and Kane and Kolb (2010): (1) duct size (mean size of all ducts per annual ring; mm^2); (2) duct production (total number of ducts per annual ring; number/yr); and (3) total duct area (sum of duct size per annual ring; mm^2/yr).

Constitutive resin flow and monoterpene composition.— We measured resin flow on an additional 6–11 trees in each unit using the same methods as described above to increase sample size ($n = 128$). To quantify constitutive monoterpene composition, we collected phloem tissue from 9 to 24 trees in each unit, including all trees sampled for resin flow ($n = 199$). We extracted 2×5 cm samples of phloem approximately 1.37 m high on the east of each tree using a chisel. Tissue was placed in 15-mL plastic vials and stored on dry ice in the field and then in a $-80°C$ freezer in the laboratory until chemical analysis. Chisels were rinsed in 70% ethanol between samples.

We extracted monoterpenes from phloem tissue and analyzed by gas chromatography (GC) using methods based on Powell and Raffa (2011). We placed finely chopped tissue into 2-mL glass GC vials with 1 mL hexane and agitated for 24 h. We then filtered the hexane solution through glass wool into a second GC vial, rinsed the first vial with 0.25 mL hexane twice, and added the filtered solution into the second vial for a final volume

of 1.5 mL. We added 10 µl 0.01% isobutylbenzene (IBB) to the vial as an internal standard. Phloem samples were dried for one week at 25°C and weighed.

Samples were analyzed using a Hewlett Packard 5890 Series II gas chromatograph (Palo Alto, CA, USA) with an Agilent Technologies Cyclodex-B column (0.25 mm diameter × 30 m) Santa Clara, CA, USA with helium as the carrier gas. The oven temperature program was 60°C for 10 min, with a 5°C rise per minute to 160°C, held at 160°C for 10 min, for a total run time of 40 min. We ran seven GC-grade standards (Sigma-Aldrich, St. Louis, Missouri, USA) of known ponderosa pine monoterpenes, using the method described previously to determine retention times, for identification of the peaks in the phloem sample chromatograms. We calculated absolute concentration of each monoterpene (mg) by integrating the area under each peak, dividing by the IBB peak area, and multiplying by the density of IBB.

Data analysis

We used general linear mixed models (GLMM) with a randomized block design for all analyses of treatment effects on MPB-induced tree mortality, growth, and resin defenses (ducts, flow, and total monoterpene composition) in SAS 9.4 (SAS Institute, Cary, North Carolina, USA). Treatment units were the experimental unit ($n = 3$) and block and block × treatment were random effects (SAS, version 9.3). For the mortality data GLMM, we used events/trials syntax (number of trees killed/total number of trees) with a binomial distribution. For the dependent variables of BAI and resin ducts, we used the most recent 5 yr average prior to resin flow sampling (2007–2011) with a lognormal distribution to stabilize residuals. Binomial and log-normal model estimates were back-transformed for the purpose of reporting mean and standard error. Pairwise differences in categorical variables were tested using Tukey's post hoc test ($\alpha = 0.05$). We used the average resin flow per tree for the resin flow dependent variable. For monoterpenes, we standardized monoterpene concentrations by mass of the phloem sample (g) to calculate absolute concentration (mg/g phloem) for each compound and summed the concentration of the seven compounds for total concentration. For individual monoterpenes, we calculated the relative concentration of each compound as percent of the total concentration. Due to non-normally distributed data, we tested for treatment differences in individual monoterpenes using Friedman's nonparametric test to account for block effects, followed by a GLMM of the rankings for post hoc multiple comparisons.

Lastly, we examined treatment differences in resistance to the MPB outbreak using both linear models and ordination. We used a repeated measures general linear mixed model to test within and among treatment differences in basal area, tree density, and QMD by MPB host species before and after the outbreak. We specified

treatment, year (2005, 2012), MPB host, and the three-way interaction of treatment, year, and host as fixed effects, with residuals as random effects and experimental unit as treatment × block. We used non-metric multidimensional scaling (NMS) using the vegan library (version 2.0-10) in R, version 3.0.1, to both visualize how treatments had changed in structure and composition after the outbreak and also to quantitatively test resistance to the outbreak. We used 2005 (before outbreak) and 2012 (after outbreak) plot average total basal area, density, DBH, QMD, and the percentages of host and non-host basal area and density before and after the outbreak to determine how treatments and time correlated with forest structure, with the Bray-Curtis dissimilarity index as the multidimensional distance measure of plots from 2005 to 2012. We used stress values as a measure of the goodness-of-fit for the final NMS configuration. Stress values <0.05 indicate the ordination provides an excellent representation of the data with no prospect of misinterpretation, and values <0.1 indicate a good representation with little risk of false inferences (Clarke 1993). Treatment by time 95th percentile confidence interval ellipses allowed testing of statistical differences ($\alpha = 0.05$) of resistance, in which no ellipse overlap indicate a treatment changed significantly from before to after the outbreak (Oksanen et al. 2013). We used the general location of treatments in ordination space and the degree of ponderosa pine dominance after the outbreak to make
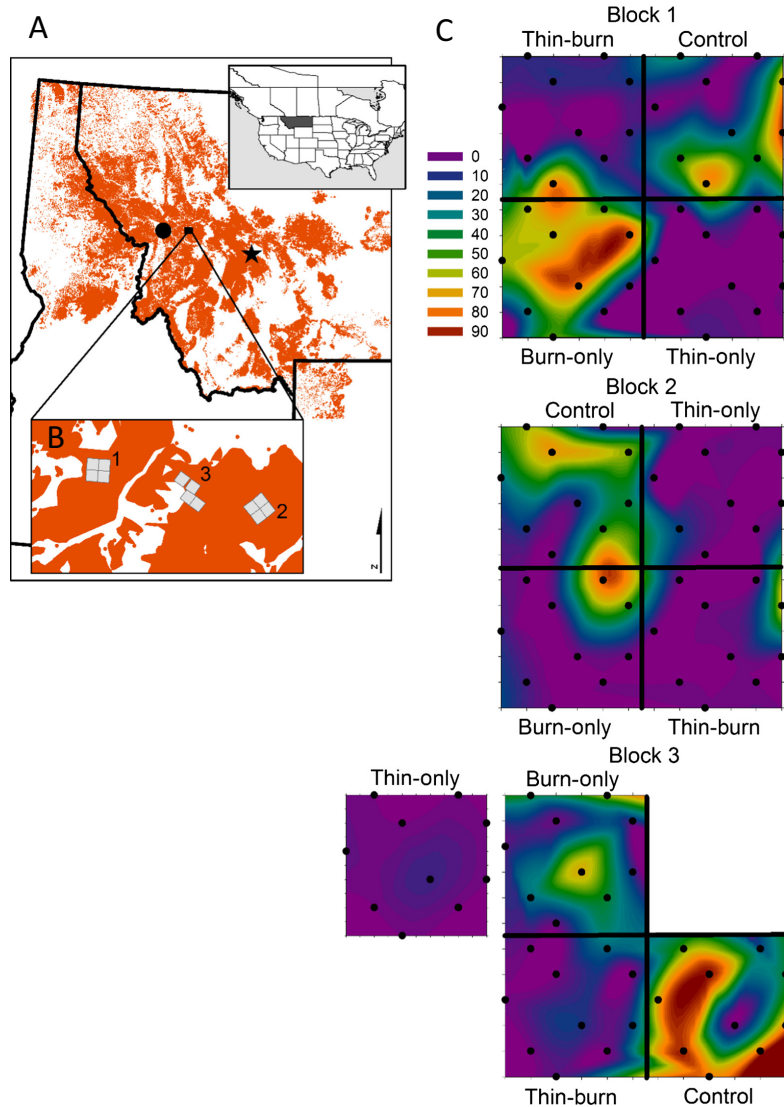

Fig. 1. (A) An area in western Montana impacted by mountain pine beetle between 2000 and 2013. Source: USDA Forest Service Aerial Detection Survey Data (http://www.fs.usda.gov/detailfull/r1/landmanagement/gis/?cid=stelprdb5430191&width=full). The black square shows the study site, the black star shows Helena, state capital of Montana, and the black circle shows Missoula. The upper right box shows the location of Montana in relation to USA and Canada. (B) The inset shows the location of the Fire and Fire Surrogate study site on Lubrecht Experimental Forest. (C) MPB attack intensity (% of MPB host trees killed by MPB) patterns shown in each block by treatment. Black circles indicate location of 0.1-ha plots where attack data was collected.
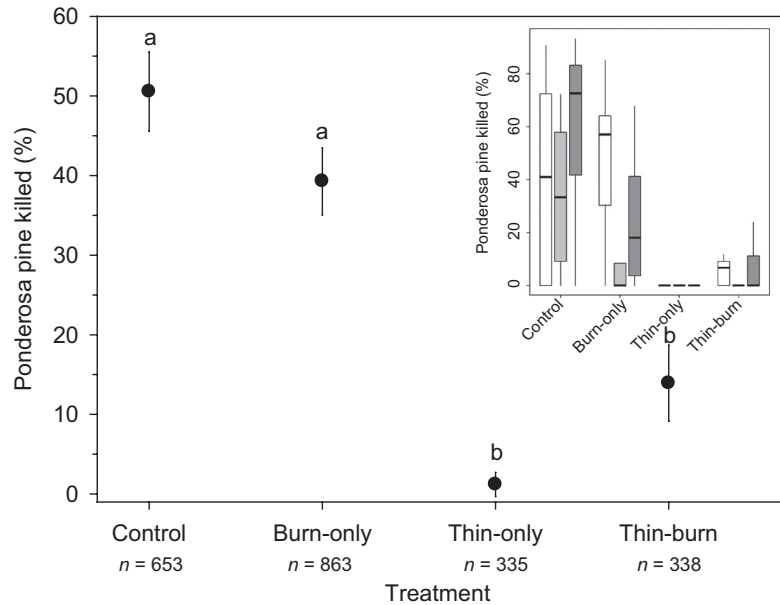
FIG. 2. Mean (SE) of percent of ponderosa pine killed by mountain pine beetle between 2005 and 2012. Different letters indicate mortality is significantly different between treatments ($\alpha = 0.05$). Study total number of host trees noted below treatment. The inset shows the percentage of ponderosa pine killed by mountain pine beetle between 2005 and 2012 by experimental block. Block 1 is white; block 2, light gray; and block 3, dark gray. Boxes denote first and third quartiles, lines the median, and whiskers the 1.5 inter-quartile range (IQR).

inferences about short and long-term resilience to disturbance in ponderosa pine ecosystem in the Northern Rockies. In 2005, ponderosa pine and Douglas-fir comprised 96% of the trees sampled; therefore, for simplicity we refer to these two species only instead of host and non-host in the results and discussion.

RESULTS

Treatment resistance to mountain pine beetle outbreak

During the outbreak, 33% (720 of 2189 trees) of the total number of ponderosa pine trees were killed from MPB, but mortality was markedly different between treatments (Figs. 1 and 2; $X^2_{(3,166)} = 9.02$, $P < 0.0001$). The treatments divided into two groups, with the control and burn-only treatments having significantly higher mortality than the thin-burn and thin-only treatments (Fig. 2). In the control and the burn-only treatments 50% ($\pm 5\%$ SE) and 39% ($\pm 4\%$ SE) of the ponderosa pine > 10 DBH were killed, respectively. Mortality was much lower in the thin-burn (14% $\pm 5\%$ SE) and virtually nonexistent in the thin-only (1% $\pm 2\%$ SE). Mortality was variable, but almost all plots in the control had some mortality from MPB and responses were generally consistent across blocks, indicating one block was not driving the combined study results (Fig. 2, inset). In the control, median MPB-caused mortality exceeded 30% in all blocks. It was near 0% in all but one block of the thin-only and thin-burn treatments (the one block with higher

MPB-kill in the thin-burn was still less than 10% mortality). The burn-only treatment had the largest variation among blocks, ranging from a median of 0% to almost 60% MPB kill.

The MPB outbreak had a large effect on basal area and density (Table 2, Fig. 3). The high mortality from

TABLE 2. Model F statistics and significance of basal area, density, and quadratic mean diameter.

Effect	Num df, Den df	F	P
Basal area			
Treatment	3, 8	5.42	0.0249
Year	1, 456	1.31	0.2532
MPB host	1, 456	111.64	<0.0001
Treatment × year × host	10, 456	7.90	<0.0001
Density			
Treatment	3, 8	19.24	0.0005
Year	1, 456	3.39	0.0660
MPB host	1, 456	37.23	<0.0001
Treatment × year × host	10, 456	6.87	<0.0001
Quadratic mean diameter			
Treatment	3, 7.929	2.48	0.1357
Year	1, 405.1	3.48	0.0627
MPB host	1, 406.6	126.69	<0.0001
Treatment × year × host	10, 405.4	5.45	<0.0001

Notes: Treatments included control, burn-only, thin-only, and thin-burn. Years include 2005 (before outbreak) and 2012 (after outbreak). Mountain pine beetle (MPB) host = 1 (host) or 0 (nonhost).
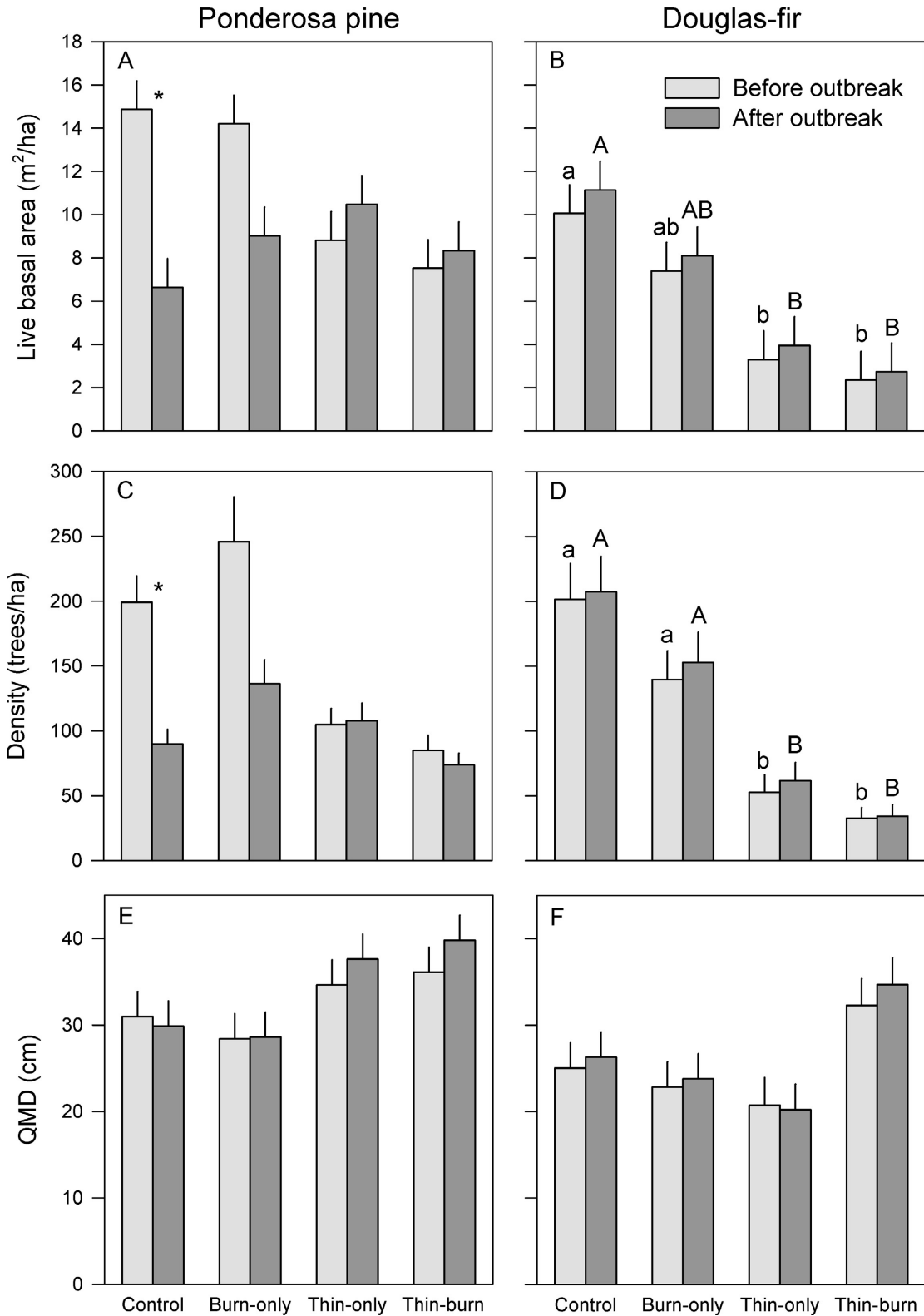
Fig. 3. Mean (SE) of forest attributes before (2005) and after (2012) the mountain pine beetle outbreak by host (ponderosa pine) and non-host (Douglas-fir). (A and B) shows basal area, (C and D) shows density, and (E and F) shows quadratic mean diameter (QMD). The asterisk denotes a significant difference before and after the outbreak within a treatment. Lower case letters denote significant treatment differences before the outbreak, and uppercase letters denote significant treatment differences after the outbreak.
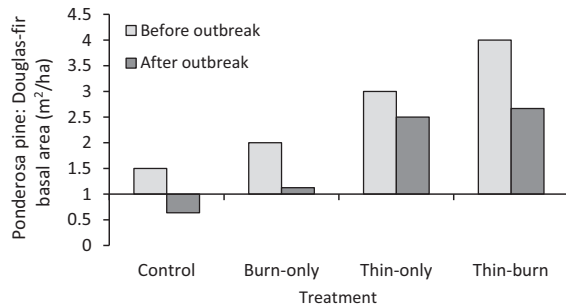
FIG. 4. The ratio of host (ponderosa pine) to non-host (Douglas-fir) basal area before (2005) and after (2012) the mountain pine beetle outbreak.
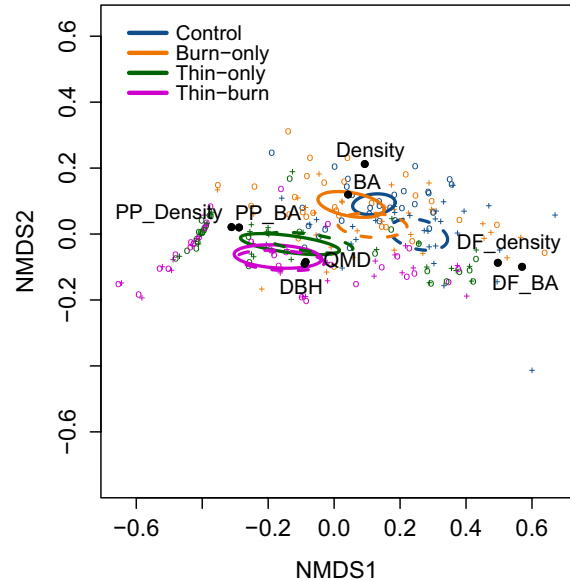

FIG. 5. Non-metric multidimensional scaling (NMDS) of treatments before (solid line) and after (dashed line) the mountain pine beetle outbreak showing association with forest structural attributes. Ellipses are 95th percentile confidence intervals of each treatment and time step centroid. Individual plots show before outbreak (o) and after (+) outbreak. Black circles show the location of forest structural and composition variables in ordination space relative to plots, where density is total trees per hectare, all species; BA is basal area (m²/ha), all species; DBH is diameter at breast height (cm), all species; QMD is quadratic mean diameter (cm), all species; PP_Density is percentage of density composed of ponderosa pine; PP_BA is percent of BA composed of ponderosa pine; DF_Density is percentage of density composed of Douglas-fir; and DF_BA is percentage of BA composed of Douglas-fir. Stress = 0.0536, two dimensions.

MPB in the control reduced pine basal area and density by over half, from 14.9 m²/ha in 2005 to 6.6 m²/ha in 2012 ($P = 0.0033$) and from 199 trees/ha in 2005 to 90 trees/ha in 2012 ($P = 0.0046$; Fig. 3A, C). Though ponderosa pine basal area and density was also greatly reduced in the burn-only treatment, these differences were not statistically significant due to high block variability in the burn-only (Fig. 2, inset). Ponderosa pine in the thin-only and thin-burn treatments and Douglas-fir in all treatments showed little change before and after the outbreak (Fig. 3). There were more Douglas-fir trees in the control and burn-only compared to the thin-only and thin-burn treatments (Fig. 3B, D), reflecting the thinning treatment prescription of removing Douglas-fir to promote ponderosa pine. Douglas-fir tended to be larger in diameter in the thin-burn treatments compared to the other treatments, from the combination of thinning to remove Douglas-fir and the prescribed burn killing smaller, less fire-tolerant trees.

The outbreak caused a shift in species dominance in the control and burn-only treatments (Fig. 4). Before the outbreak, all treatments had more ponderosa pine than Douglas-fir, though the difference was not significant in the control (basal area, $P = 0.6384$; Fig. 4). After the outbreak, ponderosa pine remained the dominant species in terms of both basal area and density only in the thin-only ($P < 0.0001$, $P = 0.0195$) and thin-burn ($P < 0.0001$, $P = 0.0044$) treatments, while Douglas-fir density was higher than ponderosa pine in the control ($P = 0.0241$).

The ordination analysis supported the individual tests of changes in structure before and after the outbreak (Fig. 5). The final 2D ordination configuration suggested excellent representation of the data (stress = 0.0536). Axis 1 shows a species composition gradient from ponderosa pine to Douglas-fir dominance. Axis 2 shows a tree density and size gradient from larger trees with lower density to smaller trees with higher density. Before the outbreak, the four treatments were clustered into two groups: (1) the control and burn-only and (2) the thin-only and thin-burn (Fig. 5, based on overlap of solid line 95th percentile confidence ellipses). The control and burn-only were associated with more Douglas-fir, higher total tree density, and smaller trees, whereas the thin-only and thin-burn were associated with more ponderosa pine, lower total density, and larger trees. After the outbreak, the control exhibited the largest change (least resistance) of the treatments (Fig. 5), shifting toward Douglas-fir dominance and reduced total density. The burn-only shifted similarly to the control, but not as dramatically. The thin-only and thin-burn treatments showed high resistance to the outbreak, with very little change occurring in either treatment.

Tree growth and axial resin ducts

Treatment effects emerged for growth and resin ducts variables between the thinned and unthinned treatments within 1 yr of implementation (Table 3, Fig. 6). Annual growth (BAI) during the most recent 5 yr was 2.4 times higher in the thin-only and thin-burn treatments than the control and burn-only ($F_{3,32} = 18.42$, $P < 0.0001$). BAI began increasing 2 yr after thinning and remained higher than the control and burn-only treatments throughout the study, which concluded 10 yr post-burning (Fig. 6A).

TABLE 3. Mean (SE) of growth and defense variables by treatment at Lubrecht Experimental Forest, Montana, USA.

	df	Control	Burn-only	Thin-only	Thin-burn
BAI_5 (cm^2)†	3	5.8 (0.7)a	7.5 (0.9)a	16.5 (2.0)b	15.1 (1.8)b
Duct size$_5$ (mm^2)†	3	0.03 (0.002)a	0.03 (0.002)a	0.04 (0.002)b	0.04 (0.002)b
Duct production$_5$ (no. ducts)†	3	3.2 (0.4)a	4.1 (0.5)a	7.3 (0.9)b	7.4 (0.9)b
TDA_5 (mm^2)†	3	0.09 (0.01)a	0.11 (0.02)a	0.27 (0.04)b	0.27 (0.04)b
Resin flow (mL)	3	6.3 (0.8)a	4.1 (0.5)b	4.8 (0.6)ab	4.9 (0.6)ab

Notes: Growth and resin duct characteristics are based on a 5 mm wide sample collected from three trees per unit (total = 36 trees). Resin flow collected from 9 to 24 trees per unit (total = 128 trees). Different letters within a row denote significant treatment differences (α = 0.05).

†Yearly average from most recent 5 yr (2007–2011) prior to resin flow sampling. Abbreviations are BAI, basal area increment; TDA, total duct area per year; duct production, number of ducts per year.

Resin duct size in the thin-only and thin-burn treatments averaged 33% larger than the control and burn-only treatments during the most recent 5 yr ($F_{3,32.02}$ = 9.76, P = 0.0001). In the thin-only and thin-burn treatments, duct production was approximately double the production of the control and burn-only treatments ($F_{3,31.8}$ = 12.46, P < 0.0001). Producing larger and more ducts in the thin treatments resulted in a 2.7 fold increase in total duct area per ring compared to the unthinned treatments ($F_{3,31.9}$ = 13.75, P < 0.0001). The increase in resin duct area began immediately after the thinning treatment and has persisted for the 11 yr since treatment, while duct area in the unthinned treatments has declined slightly (Fig. 6B).

Constitutive resin flow and monoterpene composition

Resin flow varied by treatment ($F_{3,131.2}$ = 2.77, P = 0.0447) and was positively related to DBH ($F_{1,122}$ = 7.89, P = 0.0058). Ten years after the burning treatments, resin flow was higher in the control than the burn-only treatment (P = 0.0280). Resin flow in the thin-only and thin-burn treatments was intermediate and did not differ from either the control (P = 0.3135, P = 0.3871, respectively) or the burn-only (P = 0.7555, P = 0.6678, respectively).

Total monoterpene concentration (mg/g) differed by treatment ($F_{3,10.58}$ = 4.38, P = 0.0306) and was lower in the burn-only compared to the thin-only and thin-burn (P = 0.0502, P = 0.0688, respectively), but not the control (Table 4). This pattern was driven by four of the seven monoterpenes tested: (−)-α-pinene, myrcene, 3-carene, and terpinoline concentrations were each lower in the burn-only compared to the thin-only and thin-burn but not different from the control (Table 4). The exception to the pattern was limonene, which was lowest in the control compared to the thin-burn concentrations. The concentration of (+)-α-pinene and β-pinene did not differ by treatments.

Monoterpene composition consisted of approximately 50% 3-carene for all samples. Terpinoline, limonene, (+)-α-pinene, and β-pinene each comprised about 10% of the total monoterpene content, followed by myrcene (7%) and (−)-α-pinene (3%; Table 4). Relative concentration (%) differed by treatment only for (−)-α-pinene ($X^2_{(3, N = 199)}$ = 8.9552, P < 0.0299; Table 4). The burn-only treatment was lower in (−)-α-pinene relative concentration compared to the other treatments, but this difference was only significant for the thin-burn.
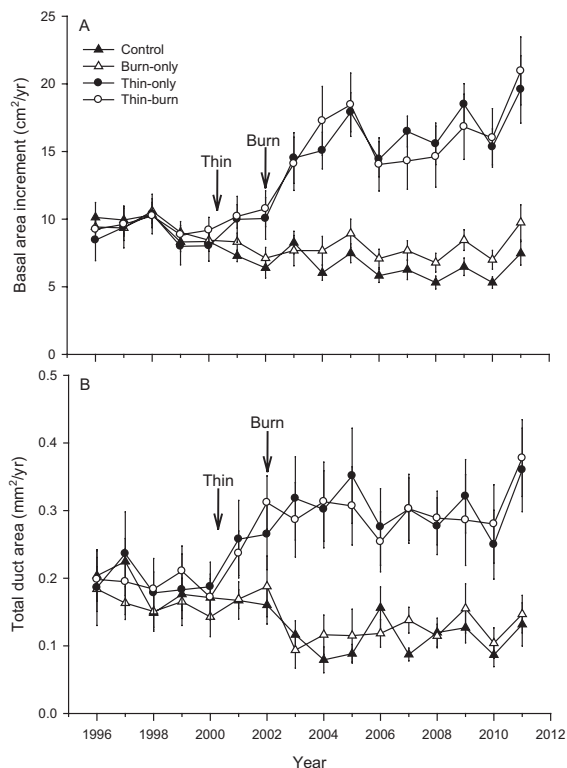

FIG. 6. (A) Yearly mean basal area increment and (B) total duct area by treatment. Error bars are standard error. Arrows denote year of thinning (winter 2000/2001) and prescribed burn (Spring 2002).

DISCUSSION

There is widespread concern about maintaining forest resilience in the face of multiple threats, such as wildfires,

TABLE 4. Mean (SE) of absolute and relative concentration of individual and total constitutive ponderosa pine monoterpenes by treatment.

Treatment	N	(−)-α-pinene	(+)-α-pinene	Myrcene	3-carene	β-pinene	Limonene	Terpinoline	Total
Absolute concentration (mg/g phloem)									
Control	40	23.6 (8.8)ab	49.0 (12.5)	39.2 (13.2) ab	274.7 (73.3)ab	91.0 (59.2)	39.3(9.0)a	48.4 (9.8)ab	565.1 (159.0)ab
Burn-only	62	14.6 (3.1)a	54.1 (15.7)	22.0 (3.4)a	176.9 (29.2)a	23.9 (3.4)	43.3 (7.7)a	44.7 (7.4)a	379.6 (64.4)a
Thin-only	30	23.5 (3.8)b	57.6 (11.5)	33.5 (3.9)b	331.0 (48.5)b	34.3 (7.4)	66.1 (11.2) ab	74.8 (10.8)b	620.8 (85.1)b
Thin-burn	67	26.7 (3.9)b	76.3 (16.4)	34.6 (4.0)b	301.1 (41.6)b	34.9 (6.0)	77.4 (13.9) b	80.5 (14.0)b	631.6 (90.9)b
P		0.0014	0.0595	0.0022	0.0002	0.6437	0.0063	0.0031	0.0306
Relative concentration (%)									
Control		3.5 (0.4)ab	10.7 (1.6)	7.3 (0.9)	51.1 (1.8)	9.4 (1.7)	8.5 (0.9)	9.6 (0.9)	Na
Burn-only		2.7 (0.4)a	10.2 (1.1)	7.0 (0.8)	49.7 (1.6)	10.0 (1.2)	9.7 (0.7)	10.7 (0.7)	Na
Thin-only		3.4 (0.4)ab	8.1 (1.2)	7.0 (0.7)	53.7 (1.7)	6.2 (1.3)	9.9 (0.9)	11.8 (0.5)	Na
Thin-burn		4.1 (0.3)b	10.7 (1.0)	6.4 (0.4)	49.4 (1.6)	7.1 (0.9)	10.8 (0.6)	11.4 (0.5)	Na
P		0.0381	0.6994	0.9660	0.1912	0.3794	0.3321	0.3978	Na

Notes: Different letters within a column denote significant ($\alpha = 0.05$) treatment differences using Friedman's test of post hoc comparisons. If no letters are present, treatment was not a significant factor.

bark beetles, and climate change (Dale et al. 2001, Millar et al. 2007, Allen et al. 2010, Bentz et al. 2010). Altered natural disturbance regimes may further decrease ecosystem resilience and create novel conditions that complicate restoration efforts (Folke et al. 2004, Suding and Hobbs 2009). We found that thinning treatments designed to increase resistance from potential high-severity wildfire were also more resistant to a MPB outbreak. Approximately 50% of the ponderosa pine in the control treatments were killed from MPB during the outbreak compared to 39% in the burn-only and almost no mortality in the thin-burn and thin-only treatments, even though the units were surrounded by intense bark beetle attack levels (Fig. 1). Consistent with this, and with previous studies showing positive effects of reduced tree density in water- and nitrogen-limited forests (Smith et al. 1997, Warren et al. 2001, Agee and Skinner 2005, Sala et al. 2005, Fettig et al. 2007, Kolb et al. 2007), we found a strong density effect at the individual level, where trees in the thinned treatments had increased growth (BAI) and resin ducts compared to those in the control and burn-only treatments (Table 3, Fig. 6). This supports past research that management treatments in ponderosa pine that reduce tree density can increase resistance to bark beetles and drought due to increased growth and defenses (reviewed in Kolb et al. 2007, Fettig et al. 2014b). Bark beetle attacks are spatially dependent, with the probability of a new attack increasing around existing attacks (Raffa and Berryman 1983). Our results also suggest dense forests are more susceptible to initial attacks which can then expand. Trees in open forests have fewer stressed, less defended trees and allow faster diffusion and subsequent loss of beetle-produced aggregation pheromones, thus lessening the chance of MPB patch establishment (Logan et al. 1998).We expect growth and resin ducts will now begin to increase in the control

and burn-only treatments due to thinning effects caused by mountain pine beetle, though competition with the developed Douglas-fir midstory and understory could inhibit this response (Romme et al. 1986, Hansen 2014). Therefore, any release to the remaining living ponderosa pine trees will likely be short-lived in these treatments, as the existing high Douglas-fir component likely also will be released and outcompete residual ponderosa pine.

Burning did not increase resin duct area, contrary to our hypotheses and the results of Hood et al. (2015) where resin duct area increased following wildfires. In addition, resin flow was higher in the control treatment 10 yr post-fire compared to the burn-only treatment. Burning has been shown to increase resin flow (Santoro et al. 2001, Wallin et al. 2004, Lombardero et al. 2006, Cannac et al. 2009, Perrakis et al. 2011), a response that can last for up to four years (Perrakis et al. 2011). This long-term increase apparently can occur because low-severity fire induces the production of resin ducts (Hood et al. 2015), which can then contribute to resin flow as long as 10 years afterwards (Hood and Sala 2015). At our study site, resin flow was highest in the burn-only and thin-burn treatments immediately after the prescribed fires (Six and Skov 2009). However, in 2012 the control had higher resin flow. It is possible that bark beetles attacked and killed trees with lower resin flow in the control units, such that surviving trees in 2012 were those with higher resin flow. The lack of long-term increase in resin flow in the burning treatments is consistent with the lack of resin duct induction. However, resin flow is inherently highly variable (Gaylord et al. 2007, 2011, 2013) and may not be a reliable metric for defense compared to resin ducts (Hood and Sala 2015).

Two possible reasons may explain why burning treatments did not induce resin ducts, as reported in Hood

et al. (2015): fire type and season of fire. Conditions under which the treatments were prescribed burned (see Gundale et al. 2005 Table 1 for burning conditions) may have been too mild relative to the wildfires examined by Hood et al. (2015) and may have been insufficient to stimulate the induction. Further, the prescribed fires in this study were set in the late spring, yet wildfires in the Northern Rockies typically occur under drier conditions later in the growing season (Heyerdahl et al. 2008). Following the logic of the growth-differentiation balance hypothesis (Lorio 1986, Herms and Mattson 1992), trees may only be able to respond to a fire stimulus and increase in resin duct production later in the growing season, when defense costs are lower due to water limitations to tree growth. Further research is needed to determine the impacts of fire intensity and burning season on fire-induced resin duct formation.

The burn-only treatment also tended to have lower and more variable mortality than the control, suggesting that burning alone confers some resistance to MPB. Resin chemistry may explain the reduced mortality in the burn-only treatments compared to the control. The burn-only treatment had lower levels of several specific monoterpenes known to benefit MPB, including $(-)$-α-pinene, myrcene, and 3-carene. MPB uses $(-)$-α-pinene and myrcene as a precursor and synergist, respectively, to the production of aggregation pheromone, and high rates of 3-carene and myrcene have been shown to increase flight response to aggregation pheromone (Seybold et al. 2006). Limonene, the most toxic monoterpene to bark beetles (Raffa 2014), was also lowest in the control treatment. However, the effects of burning and thinning on resin chemistry were variable, suggesting that defense responses are context-specific. For instance, conflicting with our results, Powell and Raffa (2011) found burned lodgepole pine trees had increased proportions of $(-)$-α-pinene compared to unburned trees one year post-fire, but both studies found increased limonene in burned trees. Resin chemistry changes temporally after fire (Campbell and Taylor 2007), so differences in time since burn between our study and Powell and Raffa (2011) may explain contradictory results, as well as species-specific responses. In addition, variability in the prescribed burns could have influenced responses. Though the burns were conducted under the same prescription and methodology, variation in actual weather and fuel consumption between the units were unavoidable (Gundale et al. 2005). We did not measure induced resin chemistry, but it can play a large role in resistance to beetle attack (Raffa and Smalley 1995) and could also possibly explain the differences in attack rates between treatments. Recent work shows ponderosa pine exhibits substantial changes in induced resin chemistry in response to simulated mountain pine beetle attack (Keefover-Ring et al. 2016). Very few studies have examined fire-induced changes in resin chemistry, and more research is needed to fully understand the interactions between thinning and burning treatments, constitutive and induced resin chemistry, and susceptibility to herbivory.

Though the thin-only and the thin-burn treatment both had the lowest mortality from MPB, there are other factors to consider when choosing whether to use prescribed burning, either alone or following thinning treatments. Density by species and the ordination results show the largest changes in vegetation occurred in the control (Fig. 5, no overlap in pre vs. post outbreak ellipses), suggesting that the burn-only treatment had higher resistance to the outbreak relative to the control. Further, we note that our analysis of the effects of burning treatments on successional dynamics is conservative because we only included trees larger than 10 cm DBH. However, the thin-burn treatment greatly reduced the number of seedlings and saplings (Metlen and Fiedler 2006), which will increase treatment longevity and alter successional trajectories compared to the thin-only treatment. Therefore, there is a potentially large burning effect on recruitment that is not captured in our analyses because these small trees have not reached census size. In addition, burning also affects nutrient cycling, spatial heterogeneity for wildlife habitat, and resilience from other disturbances that may also be important for perpetuating the ecosystem in the long-term (Bond and Keeley 2005, Gundale et al. 2005, Fiedler et al. 2010, Ryan et al. 2013) and which cannot be replicated by mechanical treatments alone (McIver et al. 2013, Stevens et al. 2014).

Management implications are different in forests where lack of frequent, low-severity fire causes changes in both species composition and forest structure compared to forests where fire exclusion causes structural changes only. Many shade-tolerant species are easily killed by fire as seedlings and saplings but become tolerant to fire as they grow larger (Hood 2010). Therefore, if enough time lapses between fires, the shade-intolerant species will survive fire, resulting in a persistent shift in species composition even if frequent, low-severity fire returns to the system. The burn-only treatment in our study is an example of this situation: reintroducing fire after over 100 years without fire did not reduce stand density and species composition relative to controls because many of the Douglas-fir trees are now fire-tolerant (Hood and Bentz 2007, Hood 2010). This has implications for forest resilience after the beetle outbreak. The large Douglas-fir component in both the control and burn-only due to fire exclusion, coupled with the high pine mortality from MPB has shifted forest dominance to Douglas-fir, a shift that will only increase over time in the absence of further fire. In addition, logging of the study site in the late 1800s–early 1900s may further explain the high density of shade-tolerant Douglas-fir in the control and burn-only treatments. Naficy et al. (2010) found fire-excluded ponderosa pine forests in the Northern Rockies with historical logging were much denser and had a higher component of shade-tolerant species compared to fire-excluded, unlogged ponderosa pine forests. The influence of past management activities on contemporary forest conditions has been documented in other areas with frequent,

low-severity fire regimes as well (Moore et al. 2004, Haugo et al. 2010, Sánchez Meador and Moore 2010).

Burning alone (i.e., no prior mechanical treatment) has been shown to reduce tree density and future fire severity (Pollet and Omi 2002, Finney et al. 2005, Schwilk et al. 2009, Stephens et al. 2009). Reductions in tree density through prescribed burning may take longer to occur than mechanical treatments. For example, reductions in tree density at the Fire and Fire Surrogate site in the Central Sierra Nevada Mountains were not observed until seven years after the burn-only treatment (Stephens et al. 2012*a*), showing the importance of long-term monitoring. Repeated fires and/or higher intensity may also be necessary to achieve objectives relating to reductions in density and maintaining resilient ponderosa pine-dominated forests (Larson et al. 2013). Though shade-tolerant species, such as Douglas-fir, historically occurred to some extent in most ponderosa pine forests of the Northern Rockies, our study supports previous research that fire exclusion can dramatically increase the proportion of Douglas-fir (Brown et al. 1994, Arno et al. 1995, Keeling et al. 2006), which, when combined with pine mortality from MPB, can accelerate succession to Douglas-fir-dominated forests.

Treatments in this study were implemented about five years before the MPB population increased, so there is a possibility of different outcomes if treatments are implemented during a MPB outbreak. There are mixed results of the effectiveness of using treatments to limit bark beetle outbreaks once they begin (Six et al. 2014), but consistent patterns of increased tree resistance if thinning is conducted prior to outbreaks (Fettig et al. 2007, 2014*a,b*, Gillette et al. 2014). The majority of data from replicated, experimental studies supporting thinning as an effective tool for increased resistance to beetles is based on treatment responses to endemic or moderate bark beetle population levels. For instance, 6% of host trees were killed in Larsson et al. (1983) and in Fettig and McKelvey (2014). Our study corroborates these previous results and shows that fuel and restoration treatments in ponderosa pine forests that create low-density, faster-growing stands can increase resistance to MPB even under much higher beetle pressure (33% of the host trees killed by MPB).

While regional weather and climatic variables are clearly linked to the onset of bark beetle outbreaks (Bentz et al. 2010, Preisler et al. 2012, Creeden et al. 2014), attack patterns are also dependent on species-specific host factors and the local fire regime (Littell et al. 2010, Chapman et al. 2012, Simard et al. 2012). Our results suggest that the effects of fire exclusion in ponderosa pine forests may play a large role in fostering outbreaks by promoting dense, continuous forests susceptible to bark beetles. Consistent with the review of Fettig et al. (2007), we show that low density ponderosa pine stands in units as small as 9 ha have higher resistance to MPB during an outbreak due to the combination of increased tree defenses and forest structural changes. Chapman et al.

(2012) found host differences in MPB attack dynamics between lodgepole pine and ponderosa pine during MPB outbreaks and suggested that MPB spread is lower in the more structurally diverse ponderosa pine forests due to a high-frequency, low-severity fire regime compared to the typical high-severity fire regime of lodgepole pine forests. Littell et al. (2010) recommend thinning in forests with historical, frequent, low-severity fire regimes as a climate change adaptation strategy to increase resistance from uncharacteristic, high-severity wildfire and bark beetles. Our findings support this recommendation.

Our study highlights the importance of managing forests for multiple ecological objectives. The treatments in this study were originally designed to increase resistance from wildfire (i.e., create conditions unconducive to high-severity fire that would cause high mortality of overstory trees). However, fire is only one of many possible disturbances, and other disturbances such as insect outbreaks and severe drought are common. When and whether any of these disturbances will affect the treated area is virtually impossible to predict. Therefore, management decisions should be guided by broad ecological factors such as long-term ecosystem resilience in the face of climate change and multiple disturbances. We show mechanical treatments that create low-density ponderosa pine forests are more resistant to mountain pine beetle outbreaks and also that prescribed fire confers additional benefits to resistance. These conclusions are in agreement with the other sites in the National Fire and Fire Surrogate study (McIver et al. 2013) and other areas (Stevens et al. 2014), which show that fire is an important process in frequent, fire-dependent systems that cannot be mimicked through mechanical treatments alone. Our results likely extend to other pine-dominated forests adapted to frequent, low-severity fire and bark beetles, such as occur in other regions of the USA (Shepperd and Battaglia 2002, Varner et al. 2005, Scherer et al. 2016), Mexico (Rodríguez-Trejo and Fulé 2003), and Europe (Lombardero and Ayres 2011). Management that takes into account historical disturbance regimes will likely lead to greater ecosystem resilience and increased resistance to a variety of disturbances and climate change.

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Data Availability