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FOREST VEGETATION, FUEL, AND FIRE HAZARD DEVELOPMENT IN STANDS
TREATED TO RESIST CROWN FIRE

By

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Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Forest & Conservation Sciences - Silviculture

The University of Montana
Missoula, MT

December 2017

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Forest vegetation, fuel, and fire hazard development in stands treated to resist crown fire

Chairperson: Christopher R. Keyes

Land management agencies across the western U.S. have urgently sought to restore forests with non-stand-replacing fire regimes to facilitate stand resistance to crown fire. Although silvicultural restoration has been shown to immediately reduce the probability of widespread crown fire, little is known about the mid- to long-term impacts of restoration on vegetation, fuel, and crown fire hazard development. This study examined mid-term (10-14 years) experimental restoration treatment effects in two different non-stand-replacing fire regimes: a frequent, low-severity regime, and an infrequent, mixed-severity regime. Restoration of frequent, low-severity fire regime was represented by fuel reduction treatments in the ponderosa pine/Douglas-fir forest type, whereas restoration of infrequent, mixed-severity fire regime was represented by retention harvesting in the lodgepole pine forest type. After restorative fuel reduction treatments, the experimental ponderosa pine/Douglas-fir stands were also impacted by mountain pine beetle outbreak. The combined effects of fuel reduction and beetle outbreak in these stands resulted in forest structure that converged across treatments for many ecological and fuel attributes, though thinning and burning together demonstrated the greatest treatment longevity. Retention harvesting in lodgepole pine created variable canopy conditions that affected growth and reduced the probability of crown fire spread, but treatment increased surface fireline intensities and susceptibility to torching. Overall, this study highlights that stands treated to restore resistance to crown fire change in structure and fire hazard over time due to overstory mortality and understory growth.

Acknowledgements

Many people have made assembling this dissertation possible. However, the lion's share of gratitude goes to my advisor, Christopher Keyes. I would like to thank Chris for taking a risk and bringing me out to Montana, for providing instruction and guidance in my studies and career path, and for his friendship. I also would like to thank my committee members, David Affleck, Andrew Larson, Sharon Hood, and Anna Sala, for all of the time and direction they gave me. The Tenderfoot chapters were made possible through collaboration with Elaine Sutherland, David Wright, and Joel Egan. Bob Keane and Duncan Lutes provided some important analytical guidance in the Tenderfoot analysis. Tom Perry, Helen Smith, and Kerry Metlen were the key holders to the historical data that I used; they each provided me with important insight into those data. A number of field technicians helped me collect data, including Fred Lauer, Max Keegan, Shea Kennedy, Chris Johnson, Jacob Rex, Curtis Flolid, and Kevin Young. Applied Forest Management Program graduate students Woongsoon Jang, Kate Clyatt, Haley Anderson, Katelynn Jenkins Bowen, and Ben O'Connor provided me with support, labor, and friendship that was most welcome. Folks in the FCFC administration made sure to take care of me whenever I needed a classroom, equipment, or budgetary help. Finally, my family and especially my wife Sarah has provided me with enormous support in this endeavor, without whom this would not be.

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Introduction

Stand-replacing crown fire (i.e., high-severity fire) has a severe impact on forest biota. It rapidly consumes large quantities of biomass and kills living organisms as it advances. Crown fire is also a major threat to the health, safety, and socio-economic security of nearby human communities. Although infrequent crown fire is expected and typical in forest types associated with stand-replacing fire regimes, crown fire is atypical in forests with historically non-stand-replacing (NSR) fire regimes (Agee 1993). Past management strategies in forests with NSR fire regimes have created dense stands with continuous fuels (Covington and Moore 1994; Keeling et al. 2006), and when combined with dry and arid climate in recent decades (Westerling et al. 2006), those conditions have led to more frequent crown fire and greater crown fire contiguity than in years past (Miller et al. 2009, 2012).

Over the last two decades there has been an urgent call to reduce the probability of uncontrollable and widespread crown fire through active forest management (e.g., FIFB 2017), especially in systems with historically NSR fire regimes (Arno and Brown 1991). One of the foremost methods for crown fire mitigation is to emulate forest structure associated with intact NSR fire regimes (Perera et al. 2004). Forests with intact NSR fire regimes – whether they be frequent, low-severity or an infrequent, mixed-severity fire regimes – are resistant to crown fire because past fires maintain low surface fuel loads and low overstory fuel contiguity. Although frequent, low-severity and infrequent, mixed-severity fire regimes can both produce crown fire resistant stands, they create distinctly different stand structures, and therefore require different silvicultural techniques to emulate those structures (Brown et al. 2004). Two such silvicultural techniques include fuel reduction treatment and retention harvesting. Fuel reduction treatments can emulate the low overstory density, single-stratum, park-like stands associated with frequent,

low-severity fire regimes. Similarly, retention harvesting can emulate the multi-storied, heterogeneous stands associated with infrequent, mixed-severity fire regimes. These treatments are not only a means to mitigate crown fire, but they are strategies to restore the natural biodiversity and function of crown fire resistant stands.

Restorative treatments that disrupt fuel contiguity and emulate structure associated with NSR fire regimes should immediately improve resistance to crown fire, especially when combined with prescribed burning to reduce surface fuels (Agee and Skinner 2005). There is an abundance of anecdotal evidence of resistance to crown fire shortly after treatment in forests with low-severity fire regimes (Ritchie et al. 2007; Waltz et al. 2014; Kalies and Yocom Kent 2016), though anecdotal evidence is lacking in forests with mixed-severity fire regimes. Yet forest managers must also consider the long-lasting responses to crown fire mitigation treatments because forests are dynamic and economics limit frequent retreatment (Keyes and Varner 2006). Forest overstories, advance regeneration, seedlings, and shrubs grow in response to increased availability of light, water, and nutrients following silvicultural treatment. In turn, vegetation growth in vertical and horizontal dimensions affects potential fire behavior by increasing fuel load and contiguity. However, it is unclear to what extent vegetation, fuel, and crown fire hazard develop over time in response to restorative crown fire mitigation treatments.

In this study, my overarching research question is: what effect do restorative crown fire mitigation treatments have on mid-term vegetation, fuel, and crown fire hazard development? Since restoration of stand structure varies with the specific type of NSR fire regime being emulated, I answer this question using two different NSR fire regimes: frequent, low-severity, and infrequent, mixed-severity.

I used fuel reduction treatments in a ponderosa pine/Douglas-fir forest to represent restorative crown fire mitigation treatments in the frequent, low-severity fire regime. Fuel reduction treatments are the most common form of crown fire mitigation, and ponderosa pine forests are the archetype for this type of NSR regime in the western United States. This combination of treatment and forest type is valuable to study because of its wide geographic representation. However, this facet of the study became even more valuable because a beetle outbreak affected the study area following treatment, which granted me the opportunity to address the novel conditions that arose from treatment combined with beetle outbreak. My overarching research question takes the form of three more specific questions (each a chapter below) for the low-severity system in light of beetle outbreak.

Next, I used retention harvests in a lodgepole pine forest to represent restorative crown fire mitigation treatments in the infrequent, mixed-severity fire regime. Retention harvesting is infrequently used in most parts of the United States. Furthermore, lodgepole pine forests are typically managed as dense, even-aged stands throughout its expansive range. This combination of treatment and forest type demonstrates an under-utilized management strategy that can moderate potential fire behavior. My overarching research question is manifested by two specific questions (each a chapter) for the mixed-severity system.

Treatment in the frequent, low-severity fire regime

Chapters 1 through 3 focus on a ponderosa pine/Douglas-fir forest with a historically frequent, low-severity fire regime. These chapters utilize a designed experiment at Lubrecht Experimental Forest with four treatment levels to test impacts of various types of fuel treatments: no-action Control, Burn-only, Thin-only, and Thin+Burn. Vegetation and fuels were sampled

immediately following treatment. Beetle outbreak occurred between 5 and 10 years following treatment. Vegetation and fuels were sampled again 14 years after treatment.

Chapter 1 research question: What effect does restorative fuel reduction and beetle outbreak have on overall vegetation dynamics?

Chapter 1 is a stand scale analysis of overstory and understory vegetation dynamics. I identified various treatment effects by year on regeneration density and composition; overstory density, composition, and structural variability; understory cover; and understory diversity. I also conducted multivariate analyses on the overall vegetation community structure and composition. I found that communities became more similar over time, but that Control and Thin+Burn treatments were still differentiable 14 years after treatment.

Chapter 2 research question: What effect does restorative fuel reduction have on large overstory tree growth?

Chapter 2 is an individual scale analysis of growth and other attributes of large overstory trees. I used linear modeling to test for treatment differences in growth and attributes that improve resistance to disturbance. An estimate of beetle outbreak severity was included in the models in an attempt to account for the effect of beetle outbreak. I found that diameter and crown growth was accelerated by restorative thinning treatments, especially for ponderosa pine. Both thinning and burning treatments affected attributes that improve resistance to disturbance, but in various ways.

Chapter 3 research question: What effect does restorative fuel reduction and beetle outbreak have on fuel and fire hazard development?

Chapter 3 is a stand scale analysis of fuel and fire hazard development. Treatment caused differences in absolute value by year and in the change between measurement years for fuel and

fire hazard responses. I also performed mediation analysis to determine the impact that beetle outbreak had on treatment differences. Beetle outbreak was the main reason for an observed treatment effect in downed woody debris and probability of torching, but diminished silvicultural treatment effect on canopy fuel, canopy bulk density, and crowning index.

Treatment in the infrequent, mixed-severity fire regime

Chapters 4 and 5 address a lodgepole pine forest that was historically maintained by infrequent, mixed-severity fire. Both chapters employ a retention harvesting experiment used to restore multi-aged stand structure and avoid high-severity disturbance. Treatments were designed to test the impacts of two levels of retention harvest spatial pattern (aggregated and dispersed) and two levels of prescribed fire (burned and unburned). Including the no-action treatment, there were five treatment levels: Control, Aggregated Burned, Aggregated Unburned, Dispersed Burned, and Dispersed Unburned. Vegetation and fuels were sampled immediately after treatment and again 12 years after treatment.

Chapter 4 research question: What effect does retention harvesting have on stand dynamics?

Chapter 4 is a stand and individual scale analysis of overstory and regeneration dynamics. I identified treatment differences in stand structure over time, and discussed the impact that post-treatment mortality had on stem density and variability. I used generalized linear models to determine if overstory growth, overstory mortality, regeneration stocking, and regeneration growth was best predicted treatment factor or by local conditions. After accounting for competitive covariates, treatment was only useful in predicting overstory growth, indicating that most stand dynamics processes transcend the stand scale impact of treatment and are attributable to local conditions in these highly variable treatments.

Chapter 5 research question: What effect does retention harvesting have on fuel and fire hazard development?

Chapter 5 is a stand scale analysis of fuel and fire hazard development. Fuel development was affected by both retention harvest and burning, especially because of the high post-treatment mortality in the Dispersed treatment and after burning. I created custom fire behavior fuel models that incorporated the dense regeneration cohort in the surface fuel profile to predict fire behavior and crown fire hazard. In contrast to the Control, which had high fire hazard due to low crowning index, crown fire hazard was lowest for the sparse overstories in Dispersed treatments, and highly variable for clumped overstories in the Aggregated treatments.

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Chapter 1: Vegetation dynamics following restorative fuel treatments and bark beetle outbreak in a ponderosa pine forest

Abstract

Restoration of dry forests with historically frequent, low-severity fire regimes often includes fuel reduction treatment. Restorative fuel treatments reestablish open, early-seral forest structures and communities while reducing fuel continuity and load to reverse past management effects and bolster ecosystem resistance and resilience to fire. Between 2001 and 2016, various forms of restoration and fuel reduction have been implemented on over 26 million hectares on federal lands alone, reflecting the political and managerial urgency to prepare forest communities for the future. However, in the period between 2001 and 2012 nearly 20 million hectares were impacted by mountain pine beetle outbreak (*Dendroctonus ponderosae* Hopkins), overlapping both treated and untreated forest stands. We explore vegetation dynamics in restorative fuel treatments that were subsequently overlapped by regional beetle outbreak. We used an experiment designed to test the effects of thinning and burning (treatment levels: Control, Thin-only, Burn-only, Thin+Burn) on frequent-fire forest ecosystems. Stands were fully treated by 2002, then impacted by regional beetle outbreak from approximately 2005 to 2012. We use overstory and understory (including all non-bryophyte vegetation) measurements from 2002, 2004/2005, and 2016 to assess change in forest community structure, composition, and diversity over time. Univariate ANOVA for a variety of responses demonstrated distinct thinning, burning, and year effects. Multivariate analyses indicated forest communities (i.e., structure and composition) were starkly different after treatment but became more similar over time, though

key attributes still segregate Control and Thin+Burn treatments. We discuss developmental convergence and then highlight a persistent suite of ecological differences that remain between unmanaged stands and stands receiving restorative fuel treatments after beetle epidemic.

Introduction

Fire exclusion in dry forests across much of the United States has caused vegetation structure and composition shifts that can result in uncharacteristically high fire severity (Keane et al. 2002; Miller et al. 2009; Naficy et al. 2010). Recent efforts to restore fire-dependent forests can create conditions that foster low-severity fire and counter the successional effects of past management (Arno et al. 1995; Covington et al. 1997; Brown et al. 2004; Franklin and Johnson 2012); however, these efforts often do not acknowledge the need for maintenance treatments. Though restored stands may be defined by fire-resistant structure and early-seral species (Metlen and Fiedler 2006; Schwilk et al. 2009; Fiedler et al. 2010; Fulé et al. 2012), restoration treatment effects on forest structure and communities will change over time, and may be ephemeral if dense successional communities quickly recover. Additionally, subsequent disturbances such as beetle outbreaks play an important role in vegetation dynamics (Bigler et al. 2005; Pec et al. 2015), but these have been poorly characterized in treated stands. Understanding vegetation responses to both time and beetle outbreak is important for evaluating treatment longevity and the relative merits of alternative restoration treatments.

Forest restoration practices in dry and historically frequent-fire forests typically reestablish open, early-seral forest structures and communities to reverse effects of past management, including fire exclusion. Silvicultural practitioners inform their restoration targets using the historical range of variability of stand structure and disturbance (Landres et al. 1999;

Keane et al. 2009), or future desired structure and function (Fulé 2008; Janowiak et al. 2014). In general this equates to removing species or individuals of lesser fire tolerance, and creating open stands with burning or mechanical treatment, thereby stimulating diverse understory regrowth with increased understory light and water availability (Anderson et al. 1969; Ellison et al. 2005). The long term restoration goal in these forest types is to reestablish overstory resistance and community resilience to disturbance. However, it is not entirely evident whether single-entry burning or mechanical treatment better stimulate communities, nor how long restoration benefits endure.

One crucial element in the restoration of dry forests is fuel reduction, which is not synonymous with restoration, but has compatible management goals and resultant forest structure. Fuel reduction treatments increase resistance to crown fire by retaining large, fire-resistant trees and reducing surface, ladder, and canopy fuel continuity and loads (Agee and Skinner 2005). Whether intended to restore native ecosystem structure and process (Larson and Churchill 2012), provide a defensive framework to protect forests and properties (McKelvey et al. 1996; Schoennagel et al. 2009), or an intermediate point on this continuum, fuel reduction treatments have been widely implemented across the West over recent decades. Various forms of fuel reduction were applied to over 26 million acres between 2001 and 2016 on federal land alone (Forests & Rangelands 2017). As these underlying motives indicate, fuel treatments may not aim to influence vegetation dynamics and biodiversity, but they directly modify overstories and perturb understories in ways that are sure to inculcate community response.

As recent preventative forestry targeted one disturbance agent – fire – another agent swept across the West. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) outbreaks affected nearly 20 million hectares and killed many more trees between the years 2001

to 2012 (Karel and Man 2017). These beetles have selectively altered multiple forest types, including many dry forests with frequent, low-severity historical fire regimes. The MPB outbreaks also spanned multiple management strategies, killing trees in both unmanaged and managed stands, but preferring stands with greater host densities (Klenner and Arsenault 2009; Klutsch et al. 2009; Egan et al. 2010; Hood et al. 2016). Akin to restorative fuel treatment practices, MPB outbreaks reduce live overstory cover and fuel, transferring the balance of resources and productivity from dense overstories to understories (Brown et al. 2010; Griffin et al. 2011; Pec et al. 2015). Simard et al. (2011) argued that beetle outbreaks in untreated stands have the same effect as active management because of change to canopy density (but see Moran and Cochrane 2012, e.g.), which may negate the benefits conferred by silvicultural practices. But unlike silvicultural practices, which remove or volatilize biomass in a short pulse and retain early seral trees, beetle outbreak preferentially kills large trees of early seral species over a lengthier period. Furthermore, silvicultural practices scarify forest understories with machinery or prescribed fire, whereas beetle outbreaks slowly add foliar and woody biomass to the forest floor as beetle-killed trees decompose and fall (Page and Jenkins 2007). Where silvicultural practices such as restorative fuel reduction have subsequently been impacted by beetle outbreaks, community effects may be a composite of both sources, and the effects of either source may mask the other.

In this study we opportunistically focus on treated (with restorative fuel reduction) and untreated stands that were completely overlapped by a regional MPB outbreak. The unique combination of restoration treatment and beetle outbreak have created novel forest stands that have been heretofore undocumented. Little is known about mid-term vegetation and community

dynamics after restorative fuel treatments, and even less is known about the combined impact of these treatments and beetle outbreak on vegetation structure, composition, and dynamics.

We use the northern Rocky Mountains installment of the Fire & Fire Surrogate Study (McIver and Weatherspoon 2010) as a balanced experimental design to contrast restorative fuel reduction treatments (no-action Control, Burn-only, Thin-only, Thin+Burn). Our *Pinus ponderosa/Pseudotsuga menziesii* stands were fully treated by 2002, approximately five years before a widespread MPB outbreak that overlapped all experimental units. We analyze data from 14 years after silvicultural treatment with the broad research question: what impact does the combination of restorative fuel reduction and beetle outbreak have on vegetation dynamics? More specifically, we sought to understand how the combination of treatment and beetle outbreak affected overstory, understory, and total forest community structural and compositional dynamics. We expected that overstory structure, composition, and structural variability would respond differently across treatments over time because post-treatment structure impacts growth and beetle-caused mortality, which in turn also impacts residual growth. In tandem with overstory dynamics, we expected that understory functional composition and diversity would develop on different trajectories across treatments because of changes to resource availability. Finally, we anticipated that the development of the forest community as a whole (both overstory and understory) would segregate by treatment, but that treatment communities may become more similar if the beetle outbreak reduced overstory competition and stimulated understory development as expected by restorative fuel treatments. To our knowledge, this opportunistic study is unprecedented. None have ever revealed the cumulative effects of restorative fuel treatment modified by a beetle outbreak on forest vegetation dynamics, therefore our results are relevant for managers dealing with this novel condition.

Methods

Study site

This study was conducted at the University of Montana's Lubrecht Experimental Forest (46°53'N, 113°26'W), an 11,300 ha forest in western Montana's Blackfoot River drainage of the Garnet Range. Study sites range in elevation from 1,230 m to 1,388 m ASL, and are comprised of *Pseudotsuga menziesii/Vaccinium caespitosum* and *Pseudotsuga menziesii/Spiraea betulifolia* habitat types (Pfister et al. 1977). Soils are fine or clayey-skeletal, mixed, Typic Eutroboralfs, as well as loamy-skeletal, mixed, frigid, Udic Ustochrepts (Nimlos 1986).

Climate in this study area is maritime-continental. Annual precipitation is approximately 460 mm (PRISM Climate Group, 4 km resolution), nearly half of which falls as snow. Mean temperatures range from -6°C in December and January to 17°C in July and August. Average plant growing season is between 60 and 90 days. Grissino-Mayer et al. (2006) identified that historic fire frequency at Lubrecht prior to the 20th century ranged from 2 to 14 years, with a mean composite fire return interval of 7 years, but the last fire prior to treatment was approximately 70 years ago.

Twentieth century forest management in the study area was similar to much of the accessible, pine-dominated intermountain West: selective logging and clearcutting followed by fire exclusion. The overstory is dominated by second-growth ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), and western larch (*Larix occidentalis* Nutt.), naturally regenerated in the 1920s to 1940s after harvesting. Overstories were mostly continuous, with stem densities near 400 trees ha⁻¹ and basal area of 22.1 m² ha⁻¹. Stands were dense (5,000 to

11,000 stems ha⁻¹) with advance regeneration of Douglas-fir, and occasional thickets of ponderosa pine regeneration.

Silvicultural treatment and natural disturbance

Lubrecht Experimental Forest was selected as a site for the Fire & Fire Surrogate Study, a multidisciplinary research project that aimed to quantify the short-term effects of restorative fuel reduction treatments in frequent-fire forests across the US (Weatherspoon 2000; McIver and Weatherspoon 2010). The Fire & Fire Surrogate Study provides a framework to examine the effects of restorative fuel treatments on vegetation dynamics as it has a balanced experimental design and was specifically created to test for differences among treatments. At Lubrecht, treatments were implemented in each of three blocks using a randomized factorial design: two levels of thinning (thinned and unthinned) by two levels of prescribed burning (burned and unburned), for a total of four treatment levels (no-action Control, Burn-only, Thin-only, and Thin+Burn). Prescription intensity was intended to maintain 80% overstory tree survival given a wildfire in 80th percentile weather conditions (Weatherspoon 2000).

Stands were cut in 2001 and burned in 2002, creating twelve 9 ha experimental units. The cutting prescription was a combined low thinning and improvement cut to a residual basal area of 11.5 m² ha⁻¹, favoring retention of large ponderosa pine and western larch over Douglas-fir. Burning treatments were conducted in the spring with windspeeds less than 13 km hr⁻¹. Burns were generally low severity, with pockets of high severity in two of the Thin+Burn treatments. Metlen and Fiedler (2006) and Dodson et al. (2007) analyzed immediate treatment effect on vegetation communities, and Fiedler et al. (2010) discussed treatment effect on stand structure and short-term growth. Six and Skov (2009) report short-term bark beetle activity and emphasize

the pulse of activity associated with burning. Finally, Schwilk et al. (2009) compared this site's vegetative and fuel responses were with the national Fire & Fire Surrogate Study.

Not long after researchers completed measurements of short-term treatment responses, beetle populations (primarily MPB) rose to outbreak levels in Montana, including at Lubrecht (Gannon and Sontag 2010). This MPB outbreak enabled an unprecedented opportunity to study beetle outbreak impact on restorative fuel treatments, shedding light on treatment effectiveness, resilience to disturbance, and vegetation development in novel but increasingly common conditions in the western U.S. Beetle-caused overstory mortality levels were high in Control and Burn-only units over the course of 2006 to 2012 (Hood et al. 2016), leading to similar live ponderosa pine basal area across all treatments. After the outbreak, therefore, changes in vegetation dynamics are no longer a pure effect of restorative fuel reduction treatments, but rather of the combination of restoration and beetle-caused mortality. Therefore, the meaning of “treatment” in this study changes with measurement year. Before beetle outbreak, “treatment” refers to the restorative fuel reduction treatment. Afterwards and unless otherwise noted, “treatment” refers to fuel reduction followed by MPB outbreak.

Field Methods

We measured all live aboveground forest vegetation lifeforms at our study site except for bryophytes. We divided lifeforms into two broad classes for measurement and analysis: tree and non-tree (hereafter, “understory”) vegetation. The tree class was then subdivided by size into overstory (diameter at breast height [dbh] ≥ 10.16 cm) and regeneration (height ≥ 10 cm and dbh < 10.16 cm), the latter comprised of five subclasses (seedling: $10 \text{ cm} \leq \text{height} < 50 \text{ cm}$; large seedling: $50 \text{ cm} \leq \text{height} < 137 \text{ cm}$; small sapling: $0.1 \text{ cm} \leq \text{dbh} < 3 \text{ cm}$; medium sapling: $3 \text{ cm} \leq \text{dbh} < 6 \text{ cm}$; large sapling: $6 \text{ cm} \leq \text{dbh} < 10.16 \text{ cm}$). The understory vegetation class was

subdivided into three mutually exclusive functional classes: graminoid, forb, and shrub. In accordance with previous classification (Metlen and Fiedler 2006), graminoids were defined as species of the families *Graminaceae*, *Poaceae*, *Cyperaceae*, and *Juncaceae*; forbs were non-woody, non-graminoid broadleaf plant species; and shrubs were woody species that do not exceed 10 m in height. In addition to these functional classes, we subsequently characterized vegetation by origin as either native or exotic using the PLANTS database (USDA and NRCS 2017).

The full suite of vegetation data was sampled on permanently monumented 0.10 ha rectangular modified-Whittaker plots (Shmida 1984; Metlen and Fiedler 2006). These were 10 randomly selected plot locations from 36 systematically located grid points within each of the twelve treatment units, making for a total of 120 plot locations. Species, dbh, total height, and crown width were recorded for overstory trees on a 0.04 ha subplot per Whittaker plot. Saplings were tallied on five, 100 m² subplots per plot; seedlings were tallied on twenty, 1 m² subplots per plot. Understory vegetation was identified by species (or by genus for difficult to identify species) and cover was estimated on twelve, 1 m² subplots per plot.

Overstory trees were measured in 2001, immediately after harvest, and trees in burned treatments were revisited in 2002 to identify fire-killed trees and establish the live post-treatment dataset; overstory was then remeasured in 2005 and 2014. Regeneration was measured in 2002 and 2016. Understory vegetation was measured in 2002, 2004, and 2016.

Additionally, a subset of vegetation was measured on each of the 36 grid point locations per unit to assess the spatial variability within treatments (432 plots). In that sample, overstory species, dbh, and height were recorded on 0.04 ha circular plots. Trees were measured in 2000,

prior to treatment, then revisited in 2001 and 2002 to identify removed or fire-killed trees and establish the live post-treatment dataset. Trees were then remeasured in 2015.

For simplicity's sake, we will refer to the earliest datasets (2000, 2001, 2002) as “2002” to represent the collective immediate post-treatment dataset, and most recent datasets (2014, 2015, 2016) as “2016” for the post-outbreak dataset. By the time of final measurement, stands were in the post-MPB-epidemic, leaf-off, gray phase (Jenkins et al. 2008).

Analytical and statistical methods

To understand how the combination of restorative fuel treatment and beetle outbreak affected overstory structure and composition we first analyzed treatments by diameter distribution. We subsequently tested structure and composition using stand scale stem density, ponderosa pine composition, quadratic mean diameter, volume, relative stand density index, and canopy cover. Quadratic mean diameter (QMD) was calculated as the dbh of the overstory tree of average basal area. Volume was estimated with overstory tree dbh and height using regional equations by species for total tree cubic volume (Faurot 1977). We used relative stand density index (rSDI) as a density metric that incorporates overstory tree size and density, scaled by an a priori maximum stocking value for ponderosa pine of 900 (Reineke 1933; Cochran and Barrett 1998). Additionally, we calculated percent canopy cover of overstory trees using measured crown widths (corrected canopy cover in Crookston and Stage 2000).

We made use of the more spatially intensive dataset to address spatial variability of stand structure within treated areas. We summed tree volumes at each of the 36 plots per unit and characterized structural variability with three metrics: in-stand standard deviation, coefficient of variation, and structural complexity index. In-stand standard deviation is simply the standard deviation of volume within each experimental unit, labeled “in-stand” to differentiate it from

treatment scale standard deviation. Coefficient of variation, a standardized measure of variability, was calculated as standard deviation divided by mean volume per experimental unit. Third, we calculated the structural complexity index (SCI) for each unit (introduced by Zenner and Hibbs 2000; del Río et al. 2016). This index is a measure of attribute (e.g., height, volume, etc.) spatial variability, and is also known as the rugosity of a three-dimensional surface. It is calculated using a spatially explicit irregular network of non-overlapping triangles, generated using a Delaunay triangulation algorithm (Turner 2017). Triangle vertices are three-dimensional (X, Y, Z) spatial data points: X and Y are the easting and northing, while the accessory coordinate (i.e., Z) may be any attribute of interest. The SCI is the sum of all triangle areas in the network divided by the total projected (two-dimensional) area. Spatially homogeneous attributes yield low indices (near 1), while greater values (unbounded) reflect spatial heterogeneity. In this study, we used the gridded X and Y coordinates of our measured plot centers (in m) and considered volume as the Z coordinate (m^3ha^{-1}) (see Appendix 1 for an example). We present SCI as percent greater than 1.

We analyzed understory vegetation total percent cover and cover by class to understand how the combination of restorative fuel treatment and beetle outbreak affected understory dynamics. We also calculated and analyzed three measures of diversity: richness, Shannon's H, and Simpson's evenness. Richness was the count of total genera present; we used genus instead of species to avoid identification inconsistencies since entirely different field crews sampled vegetation over the years. Shannon's H was the Shannon-Weiner diversity index (Shannon and Weaver 1949), an unbounded metric that increases with richness and cover. Simpson's evenness, when scaled by richness, is a diversity metric that identifies imbalanced (0) or balanced (1) communities (Smith and Wilson 1996).

We used univariate repeated measures ANOVA to test treatment influences on vegetation structure, composition, diversity, and variability (i.e., all variables listed above except tree size class distributions). ANOVA models had the form:

$$\hat{y}_{ijkl} = \mu + \alpha_i + \beta_j \times \gamma_k + \varepsilon_{(1)ijk} + \alpha_i \times \delta_l + \beta_j \times \gamma_k \times \delta_l + \varepsilon_{(2)ijkl}$$

where \hat{y} is the mean response variable at the experimental unit-scale (n per year = 12), μ is the grand mean, α_i is the block effect (levels 1-3), β_j is the prescribed burn effect (levels not burned and burned), γ_k is the thinning effect (levels not thinned and thinned), and δ_l is the year effect (levels 2002, 2004 or 2005 [if response was measured], and 2016). We identified two random error terms: $\varepsilon_{(1)ijk}$ was the between unit error term for testing treatment effect (i.e., burning and thinning), and $\varepsilon_{(2)ijkl}$ was the within unit error term for testing the effect of time on treatment. Within-unit error was assigned a continuously declining autocorrelation structure to reflect the unequal correlation between measurement years 2002, 2004/2005, and 2016. We used a logarithm transformation to normalize non-normal responses. Treatment effects were considered to have strong evidence of significance at the 95% confidence level, and marginal evidence of significance at the 90% level.

Finally, we identified change to overall forest communities by treatment. This was done in multivariate space, using nonmetric multidimensional scaling, multi-response permutation procedure, and canonical discriminant analysis. Nonmetric multidimensional scaling (NMDS) is a distance-based ordination method that maximizes correlation between groups in n -dimensional space and ordination space, making no assumptions about data normality. We ran NMDS with Bray-Curtis distance in R using the *vegan* package (Oksanen et al. 2017) to reduce multivariate experimental unit data to 2 dimensions, first for the overstory community (16 dimensions) and then the understory (9 dimensions). Both 2002 and 2016 measurements were included in this

operation for a total of 24 data points per analysis. We separated those same data by year (back to $n = 12$) and tested for treatment differences using multi-response permutation procedure (MRPP), which is a non-parametric alternative to multivariate ANOVA. Whereas NMDS and MRPP were used to illustrate and test the similarities and differences between treatments at the experimental unit scale, we also wanted to highlight multivariate attributes that best segregate treatment groups at the plot scale for a better understanding of fine scale ecological relationships ($n = 120$). We did this with canonical discriminant analysis (CDA), which is a principal component technique that derives canonical variables to maximize variation between specified treatment groups. Since CDA requires multivariate normality, we reduced data to 11 normally-distributed dimensions split across tree and understory vegetation metrics. We analyzed change in treatment segregation by performing CDA on 2002 and 2016 plot scale data separately (ignoring data nesting structure of plot within unit within block), then comparing attribute ‘loadings,’ or correlations.

Results

Overstory structure, composition, and structural variability

In 2002, diameter distributions on the Whittaker plots varied by treatment (Figure 1). In particular, unthinned treatment (Control and Burn-only) distributions had high densities of small overstory trees and low densities of large trees. Thinned treatment (Thin-only and Thin+Burn) densities were lower, especially for trees smaller than 40 cm dbh. Thinned treatments also had notably less Douglas-fir than unthinned treatments. Regeneration size-class distribution also varied by treatment in 2002 (Figure 2). Small regeneration was less frequent in burned treatments than unburned treatments, and density across all classes in the Thin+Burn treatment was much lower than other treatments.

By 2016, changes to diameter distributions were most evident in the unthinned treatments, where the beetle outbreak caused sizable mortality to ponderosa pine trees from 10 to 55 cm dbh (Figure 1). Changes from 2002 to 2016 were also evident in the Thin-only treatment, where regeneration grew into overstory size classes. Douglas-fir ingrowth into the overstory and ascension through diameter classes was greater in unthinned than in thinned treatments where Douglas-fir was targeted for removal, and also greater in the Thin-only than the Thin+Burn treatment where small Douglas-fir was killed by fire. Regeneration distributions in 2016 reflect active recruitment in all treatments but the Control (Figure 2). We observed greater decline across regeneration classes in the unthinned treatments than the thinned treatments likely due to overstory competition and spruce budworm (*Choristoneura occidentalis* Freeman), which severely affected Douglas-fir regeneration. This was in sharp contrast to change in the Thin-only treatment, where Douglas-fir increased across size classes. The Thin+Burn treatment had the most notable influx of seedlings, evidence that all tree species responded well to the combination of thinning and burning.

We also used the Whittaker plots to test stand structure and composition metrics by year (Figure 3). In 2002, the average stand across all treatments had 242 overstory trees ha⁻¹, with a QMD of 29 cm, volume of 102 m³ha⁻¹, rSDI of 31%, 25% canopy cover, and was comprised of 60% ponderosa pine. The regenerating cohort had 5,275 trees ha⁻¹ and was 39% ponderosa pine. Year or Year interaction with treatment (i.e., change over time) were significant factors for all responses except regeneration pine composition. Thinning was a significant factor for each response variable except regeneration pine composition, and burning was a significant factor for overstory density, regeneration density, QMD, and canopy cover; the interaction between thinning and burning was not significant for any responses.

Overstory density, regeneration density, volume, rSDI, and canopy cover all behaved similarly over time. Thinning immediately reduced responses between 46% and 61% over the unthinned treatments ($P \leq 0.090$). Burning reduced overstory density, regeneration density, and canopy cover between 15% and 54% over unburned treatments ($P \leq 0.054$). Responses decreased 6% to 22% in unthinned treatments over time (2002 to 2016) whereas they increased 22% to 50% in thinned treatments ($P \leq 0.027$).

Overstory and regeneration composition did not respond the same across treatment and year. Across all years, thinning increased overstory ponderosa pine composition 40% over unthinned treatments ($P \leq 0.001$). Overstory ponderosa pine composition declined across all treatments from 2002 to 2016 ($P < 0.001$), but the decline was 4.5 times greater in the unthinned than thinned treatments ($P = 0.008$). Combined seedling and sapling ponderosa pine composition did not exhibit any significant change due to treatment or time, although only the Thin+Burn treatment had greater than 50% ponderosa pine composition by 2016.

Structural variability (i.e., variability of overstory volume) generally increased over time across treatments. We calculated and tested structural variability with our more spatially intensive dataset of 36 plots per stand. Treatment and Year had nearly identical effects on in-stand standard deviation and structural complexity index (SCI; Figure 4). Those two metrics show that thinning reduced structural variability ($P < 0.006$): thinned treatments had 27% to 34% lower structural variability than unthinned treatments (Control and Burn-only). Variability across all treatments, however, increased 21% to 27% over time ($P < 0.073$). Although the gap between thinned and unthinned treatments closed by 2016, lack of a significant interaction term shows these statistical differences persist over time. The striking similarity between in-stand standard deviation and SCI indicates that spatial referencing provided little additional information to

variability, at least when summarized to the stand scale. Coefficient of variation (variability relative to the mean) showed a slightly different relationship of thinning and time on structural variability. Relative variability in thinned treatments declined 2% from 2002 to 2016 (19% in Thin-only alone), whereas it increased 29% in unthinned treatments ($P = 0.026$).

Understory cover and diversity

We calculated understory cover and diversity metrics from Whittaker plots across all units to determine and test treatment effects over time (Figure 5). In 2002, the average stand across all treatments had 2.3% graminoid cover, 7.6% forb cover, 6.8% shrub cover, 0.3% exotic cover, 17.4% total cover, a richness of 27.7 species, Shannon's H of 2.6, and an evenness index of 0.37. Change by year was significant for every response, but not always monotonic. Thinning or thinning interaction was a significant factor for graminoid cover, exotic cover, richness, and Shannon's H. Burning or burning interaction was a significant factor for graminoid cover, shrub cover, exotic cover, total cover, richness, and Simpson's evenness; it was not significant for forb cover nor Shannon's H. The interaction between thinning and burning was not significant for any response.

All functional types (graminoids, forbs, and shrubs) grew in cover over time, increasing between 102% and 558% from 2002 to 2016 ($P < 0.001$). Graminoids were the only functional type influenced by thinning. The thinning \times year interaction on graminoid cover was primarily significant ($P = 0.017$) because of the 2004 response, where cover in Thin-only and Thin+Burn treatments were 34% and 54% greater than combined unthinned treatments (Control and Thin-only), respectively. The burning \times year interaction on graminoid cover was significant ($P = 0.050$) because burning immediately reduced graminoid cover by 21% in 2002, but that difference faded with time. Shrub and total cover were 52% and 41% lower, respectively, in

burned treatments than unburned (Control and Thin-only) treatments in 2002 ($P \leq 0.005$), but those differences were also ephemeral. Exotic species cover was greater in thinned than unthinned treatments ($P = 0.020$). Overall, exotic species cover was low in 2002, spiked in burned treatments especially in 2004 ($P = 0.064$), but then declined across all treatments by 2016 ($P < 0.001$).

Richness also spiked across treatments in 2004, where it was 27% greater than pooled 2002 and 2016 values ($P < 0.001$). Across years, richness was 13% greater in thinned than unthinned treatments (Control and Burn-only; $P = 0.040$), but the difference was greatest in 2004 ($P = 0.040$). Burning initially (2002) reduced richness 16% over unburned units (Control and Thin-only), but the effect was transient and not evident in subsequent years ($P = 0.001$). Evenness declined 41% over time across all treatments ($P < 0.001$). The initially positive effect of burning ($P = 0.026$) on evenness also declined over time ($P = 0.001$): in 2002 burned treatments had 43% greater richness than unburned treatments (Control and Thin-only) but only 8% greater in 2016.

Dominant understory vegetation species (by cover) and their temporal trends appeared to be influenced primarily by experimental block rather than by treatment (summarized by treatment in Appendix 2). In one block, burned treatments in 2002 were dominated by *Berberis repens* and unburned treatments by *Arnica cordifolia*. By 2016 all treatments in that block were dominated by *Calamagrostis rubescens*. In the second block, 2002 Burn-only and Thin-only treatments were dominated by *Berberis repens* while Control and Thin+Burn were dominated by *Symphoricarpos albus*. By 2016, vegetation in that block had reorganized such that thinned treatments were dominated by *Arctostaphylos uva-ursi* and unthinned treatments were dominated by *Symphoricarpos albus*. In the third block, Burn-only and Thin-only treatments were

dominated by *Spirea betulifolia* in 2002 and 2016. However, the Control treatment in that block transitioned from *Spirea betulifolia* to *Arnica cordifolia* dominance, and the Thin+Burn treatment shifted from *Apocynum androsaemifolium* to *Calamagrostis rubescens* dominance. Overall, 121 genera were identified 2002 to 2004. Twenty-six genera identified in 2002 to 2004 were not found or identified in 2016, most of which were forbs; five of these were or included exotic forbs. Nine new genera were identified in 2016, of which only one was exotic.

Overall forest vegetation community

We used NMDS and MRPP to demonstrate the multivariate change in overstory and understory vegetation communities across treatment units over time (Figure 6). Overstory communities exhibited strong separation by treatment in 2002 ($A_{2002}=0.273$, $P_{2002}=0.002$), but by 2016 they were more similar ($A_{2016}=0.086$, $P_{2016}=0.188$). The developmental vectors shown in the NMDS projection illustrate downward directionality in the thinned treatments toward the unthinned treatment centroids over time, whereas unthinned treatment vectors expanded to the right. Movement toward the lower right sector of the projection is best interpreted as an increase in overall tree and sapling densities, and especially Douglas-fir volume and tree densities. Some of the downward changes on the left side of the figure (e.g., left-most Thin+Burn unit) are better interpreted as increasing in ponderosa pine sapling and seedling densities. Understory communities likewise exhibited strong separation by treatment in 2002 ($A_{2002}=0.322$, $P_{2002}=0.011$) but became more similar by 2016 ($A_{2002}=-0.132$, $P_{2002}=0.953$). These developmental vectors demonstrate a consistent pattern across all treatments. As communities move toward the right in this projection and away from the various measures of understory diversity, they show an increase in understory cover, especially shrub and graminoid cover.

The CDA likewise shows treatments were well differentiated in 2002 (P for canonical axes 1 and 2 < 0.001; Figure 7). By 2016, however, treatments were only differentiated along one axis ($P_{\text{axis1}} < 0.001$ and $P_{\text{axis2}} = 0.163$), meaning that treatments grew more similar over time. In 2002, tree densities (-) and diversity metrics (+) comprised the first axis that best differentiated between Control and Thin+Burn treatments, respectively (Table 1). Cover and richness (-) and overstory densities (+) best differentiated between Thin-only and Burn-only treatments in 2002. These canonical loadings were mostly stable over time, many of them repeating for the same differentiating effects in 2016 (albeit opposite signs). However, shrub cover and richness replaced evenness (-) and regeneration density became less informative than overstory density (+) in the differentiation of Control and Thin+Burn. The second canonical axis for the 2016 data did not significantly differentiate the Thin-only and Burn-only treatments though two-thirds of the most negative and most positive influential loadings were the same as in 2002.

Discussion

Our analysis of short-term vegetation dynamics corroborate prior findings at Lubrecht Forest's Fire & Fire Surrogate Study. Of the restorative fuel reduction treatments, the thinning treatments had the greatest immediate impact on overstory structure – they reduced densities, shifted composition toward ponderosa pine, and contracted canopy cover (as in Fiedler et al. 2010). Understory cover was immediately reduced by burning treatments, though the reduction concomitantly increased species evenness (also in Metlen and Fiedler 2006). In the first few years after treatment, overstory trees grew because of thinning, cover (especially forb and shrub cover) and richness increased in response to all active treatments, and exotic cover increased in

response to the Thin+Burn treatment (Metlen and Fiedler 2006; Fiedler et al. 2010; Hood et al. 2016).

After a period of 14 years since treatment, and at least four years after beetle outbreak, we report that vegetation structure and functional composition across treatments became more similar in 2016 than in 2002. However, there were still key differences that distinguish treatments in 2016, especially between the no-action Control and the Thin+Burn treatment. The Thin+Burn was the most intensive of the silvicultural treatments because of the overstory (thinning) and understory (burning) treatment, but this study shows that combined treatment of both vegetation strata is necessary to meet structural and compositional restoration goals.

Treatment convergence

The NMDS analyses concisely synthesized and summed up the abundance of ecological responses in this study: namely, that stands across all treatments are converging toward a similar forest structure and composition with high overstory Douglas-fir densities and understory cover. This was supported by our analysis of individual forest components. For instance, overstory tree density metrics showed thinned stands increased in density over time while unthinned stands decreased, closing the gap between treatments from both sides. Overstory ponderosa pine also gave way to Douglas-fir across all treatments, demonstrating a link between treatment convergence and the structural and compositional changes ushered by shade-tolerant succession of the Interior Ponderosa Pine forest type (Eyre 1980). Treatment differences for understory cover and diversity metrics either diminished with time (e.g., decline in effect of burning on evenness) or were of minimal perceptible consequence (e.g., 2016 richness of 27.7 genera in Thin-only and Thin+Burn versus 25.3 genera in Control and Burn-only). Whereas small differences in treatment, environment, or species assemblages can escalate community

uniqueness and divergence over time (Samuels and Drake 1997), this study suggests that structural and functional developmental trajectories were not sufficiently modified by treatment to initiate such differentiation. In this sense, the successional pathway of these ecological systems have demonstrated resilience to silvicultural disturbance, a result not unique to fuel treatments and ponderosa pine ecosystems (e.g., Haeussler et al. 2004; Jang et al. 2016).

Growth was not the only driver of between-treatment homogeneity in vegetation. Development during our measurement period was driven by the combination of growth (greater in thinned stands than unthinned) and beetle-induced overstory mortality (greater in unthinned stands than thinned). As the foundational units of the ecosystem, growth and mortality of the overstory trees has a profound impact on the ecosystem function and composition, especially on the understory light environment and water balance (Anderson et al. 1969; Ellison et al. 2005). Restorative thinning to reduce crown fire hazard (a more intensive treatment than prescribed burning alone) removes overstory competition and temporarily reduces fuels (Stephens et al. 2009; Fulé et al. 2012), but this study corroborates that treatment also stimulates tree growth and recruitment (Keyes and Varner 2006). Thus, thinning as a restorative fuel treatment initially creates open forest structure, but new and advance regeneration develop increasingly dense stands. With various caveats, beetle outbreak and subsequent overstory mortality has emulated the silvicultural thinning treatment in the unthinned units, following a five to seven year lag period. Similar to the post-thinning environment, post-outbreak stands were undoubtedly subject to a change in light and water conditions because of overstory loss, which would have stimulated both residual overstory and understory growth (Heath and Alfaro 1990; Stone and Wolfe 1996). Therefore, thinned and unthinned treatments have become more similar in 2016 structure (e.g., overstory tree density, total understory cover) and diversity (e.g., evenness) because of parallel

overstory reductions; if beetles had not reduced overstory densities in unthinned stands then structure and diversity may have diverged according to prior differences (e.g., those identified by 2004 in Metlen and Fiedler 2006).

Convergence due to overstory mortality is just one explanation of the trends we observed. Cattle grazing is another explanation of convergence, though it does not exclude the influence of beetle-caused mortality on overstory and understory dynamics. Similar to many low elevation public lands in the West, cattle have grazed Lubrecht Experimental Forest for at least half a century. However, fenced exclosures were installed around the entire Fire & Fire Surrogate Study immediately after treatment implementation in order eliminate cattle pressure and isolate treatment responses. Understory development across all treatment levels has been generally unhindered by cattle grazing, explaining the overall increase of understory cover across functional classes since treatment. Similar gains in understory cover and production were identified after excluding cattle in ponderosa pine forests in Idaho and Arizona, especially for graminoid species (Zimmerman and Neuenschwander 1984; Strahan et al. 2015). It is also possible that major increases in cover by 2016 were due to favorable growing season climate. Lubrecht had a relatively dry spring in 2015 (PRISM Climate Group), but received average precipitation in spring 2016 (measurement in June 2016). The two-fold increase in March to June precipitation from 2015 to 2016 may have stimulated a widespread understory growth response. Thus, understory convergence across treatments may be attributable to overstory loss from mountain pine beetle, change in grazing pressure, a wet spring prior to measurement, or some combination thereof.

Treatment convergence provides an important cue to managers, especially when developing silvicultural timelines and weighing treatment alternatives. Although convergence

conveys a number of developmental pointers when paired with supplemental information, the most important message is that successional development has decreased treatment longevity and made treated stands more similar to untreated stands. Of all treatments, Burn-only communities are most similar to the 2016 Control treatment centroid in the overstory NMDS analysis. But in the upcoming decade, Thin-only stands will rapidly advance toward the Control centroid because of the deluge of Douglas-fir saplings that will soon be promoted to the overstory stratum. These similarities demonstrate that treated stands are due for follow-up treatment (as expected in fuel management regimes in Reinhardt et al. 2008) to reestablish desired conditions with open, early-seral communities and low surface fuel loads. Finally, convergence indicates that vegetation has generally become more similar across treatments over time, but it does not invalidate specific and nuanced differences between treatments. Subtle differences in specific vegetation components may account for large effects on habitat use, forest productivity, or fire behavior.

Persisting and emerging differences

By 2016, some key differences remained between treatments. The persisting and emerging differences between Control and Thin+Burn treatments emphasize the tradeoffs between managing for dense or sparse overstories. Simply put, dense overstories like the Control prioritize total tree biomass and canopy cover but limit understory biomass and diversity, while sparse overstories like the Thin+Burn restore understory development at the overstory's expense. These distinctions were highlighted in our plot-scale canonical discriminant analysis, which nuanced differences between treatments after NMDS analysis suggested experimental units were overall more similar to each other in 2016. In 2016, CDA showed the Control and Thin+Burn were still significantly different from each other after positively weighted overstory density, canopy cover, and rSDI (greater in Control), and negatively weighting Shannon's H, richness,

and shrub cover (greater in Thin+Burn). Our univariate analyses of these variables supported that the overstory attributes were a persistent difference between Control and Thin+Burn over the course of the study. The suite of understory variables showed only minor differences between treatments by 2016 in univariate analyses, but when combined into multivariate space they emerged as an important means to segregate Control and Thin+Burn treatments.

Past Fire & Fire Surrogate studies have emphasized the positive effects of combined thinning and burning on understory cover and diversity relative to the Control (summarized in Schwilk et al. 2009). Likewise, traditional silvicultural knowledge identifies the structural tradeoffs between maintaining dense overstories versus thriving understories (Oliver and Larson 1996). However, there is little empirical evidence of the mid-term effects of burning on understory cover and diversity in the U.S. West; most understory studies are limited to less than 6 years since burning treatment. One study in the western United States did examine process-based restoration by burning in long-unburned stands (Webster and Halpern 2010). In that study, the authors found that single burns increased forb and shrub richness over the course of 10 years; two burns increased richness of a broader suite of functional classes through 20 years. In the Thin+Burn treatment, it is likely that the structural and process-based modifications (thinning and burning treatments, respectively) combined to positively affect understory cover and diversity and set the Thin+Burn apart from the Control. However, as treatment differences due to burning have declined with time, additional burning will be necessary in the Thin+Burn to maintain differences from the Control.

Treatment differences in structural variability persisted through the 14 year measurement period. Thinning reduced absolute structural variability (Thin-only and Thin+Burn vs. Control and Burn-only). This was an expected finding since many forest treatments tend to simplify

forest structure (Puettmann et al. 2009). Variability was lowest for the Thin-only treatment, and variability relative to the mean decreased over time in this treatment as advance regeneration filled in canopy gaps. In contrast, canopy gaps were created in unthinned treatments by the beetle outbreak. The MPB outbreak made treatments more similar in a number of ways, but spatial variability was not one of them. Rather, increases in structural variability via canopy gap creation (as in Dordel et al. 2008) proved to be a unique way that beetle outbreak actually perpetuated differences between treatments.

Tree size distributions also exhibited key dissimilarities between treatments. Overstory and regeneration distributions in 2002 and 2016 did illustrate that treatments became more similar with time in some ways. But differences in the distribution of structure, recruitment, and species composition between the Control and Thin+Burn are especially evident in 2016, and will surely continue to perpetuate themselves over the next decades in the absence of future disturbance. In the Control, gains in density were heavily weighted toward Douglas-fir as they steadily advanced size classes, and away from ponderosa pine as they were killed by beetles. Without fire or cutting treatment, we expect the composition and structure of Control stands to more rapidly diverge from the Thin+Burn as shade-tolerant Douglas-fir continues to dominate multiple canopy strata and restrict stand openings (Habeck 1994; Keeling et al. 2006). This successional trajectory is also a concern for all three active treatments since the restorative fuel treatments aimed to create open, fire-tolerant stands, but structure will become more dense and less resistant to fire with successional shifts toward Douglas-fir (Arno et al. 2008). Combined thinning and burning best delays succession, but maintenance treatments will be needed to perpetuate open stands and forestall dominance by dense Douglas-fir.

The catalog of differences between stands years after treatment and beetle outbreak emphasizes that although the treatments have amassed similarities, these stands are still unique in meaningful ways. Promoting seral overstory trees and diversifying understory cover are two common management objectives in treatments such as these that double as forest restoration and fuel reduction (Laughlin et al. 2004; Mitchell et al. 2006; Kolb et al. 2007). Since seral overstory composition and a more diverse understory cover continue to distinguish Thin+Burn from the Control treatments even years after beetle outbreak, we conclude that the combination of restorative thinning and burning treatments has the most persistent and enduring treatment effectiveness. Managers weighing treatment options in these forest types should consider that (1) MPB outbreaks reduce overstory densities, but cannot meet the early-seral composition and structure goals that silvicultural thinning accomplishes, and (2) understory treatment (broadcast burning, especially) is needed to reduce shade-tolerant species advance regeneration and promote diverse understories in the years ensuing treatment. Thinning results in forest structure and composition that can immediately meet most restoration goals, but following thinning with burning delays succession and ensures that restoration goals are met for years to come.

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Table 1. Variable abbreviations and loadings from canonical discriminant analysis of plot-scale multivariate communities in 2002 and 2016 at Lubrecht Forest's Fire & Fire Surrogate Study. First two canonical axes (Can1 and Can2) are shown for each year (axis p-values < 0.05 except Can2 in 2016). Up to three most positive loadings are portrayed in boldface, and three most negative loadings are portrayed in italic.

Vegetation type	Variable	Abbreviation	2002		2016	
			Can1	Can2	Can1	Can2
Tree	Overstory density	OvDens	-0.567	0.531	0.785	-0.376
	Total volume	Vol	-0.581	0.459	0.332	-0.090
	Canopy cover	CC	<i>-0.614</i>	0.534	0.582	-0.049
	Stand density index	SDI	<i>-0.618</i>	0.538	0.508	-0.277
	Regeneration density	RegDens	<i>-0.741</i>	0.048	0.452	0.616
Understory	Total cover	TotCov	-0.570	<i>-0.748</i>	-0.157	0.191
	Forb cover	Forb	-0.300	-0.594	0.118	-0.020
	Shrub cover	Shrub	-0.526	<i>-0.651</i>	<i>-0.291</i>	0.213
	Richness	Rich	-0.212	<i>-0.657</i>	<i>-0.316</i>	0.301
	Shannon's H	ShanH	0.137	-0.056	<i>-0.362</i>	0.056
	Simpson's Evenness	SimpEv	0.394	0.500	-0.076	<i>-0.339</i>

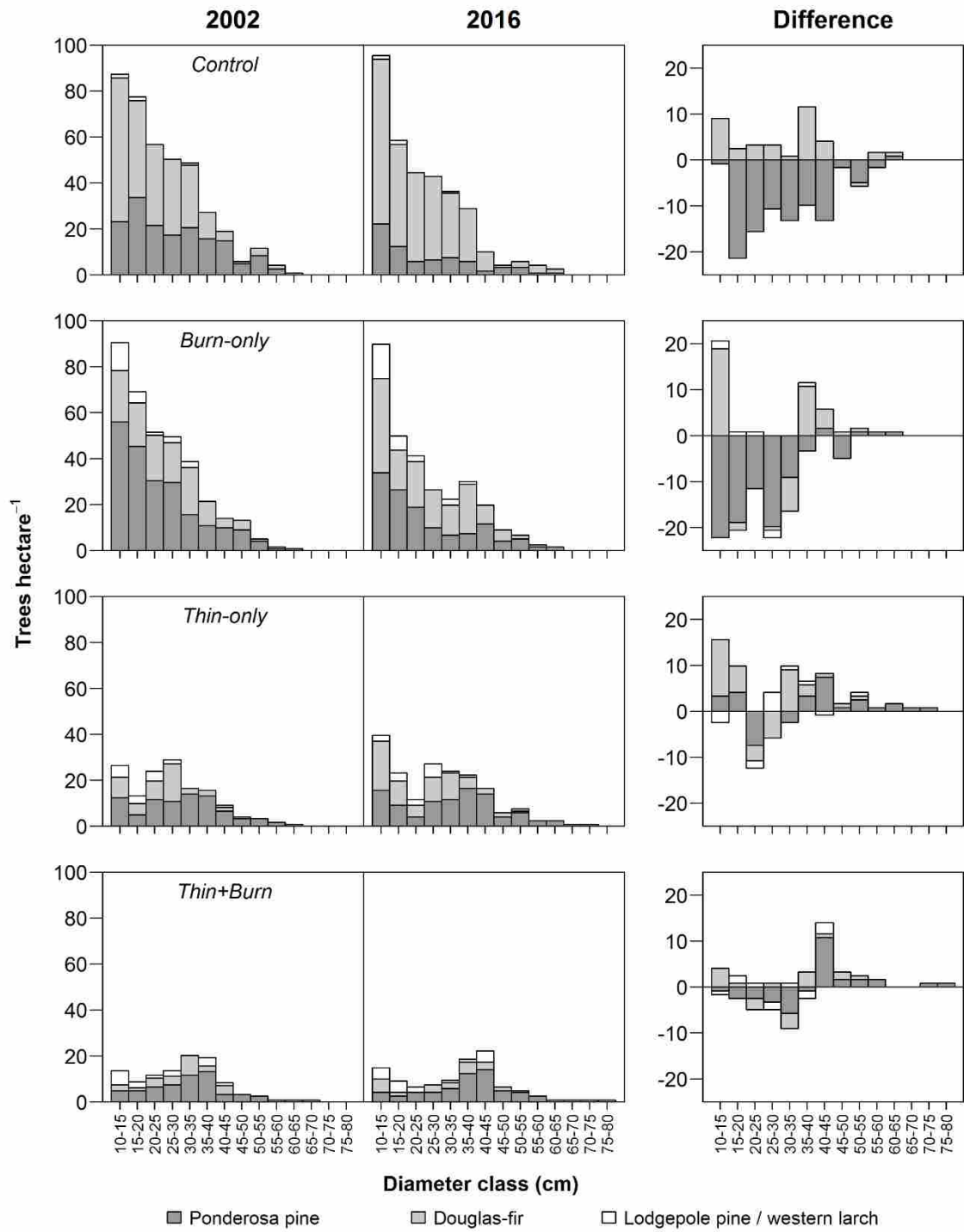


Figure 1. Overstory diameter distribution by species after treatment at Lubrecht Forest's Fire & Fire Surrogate Study. From left to right panels show distribution in 2002 (immediately after treatment), 2016, and gains/losses per class between 2002 and 2016.

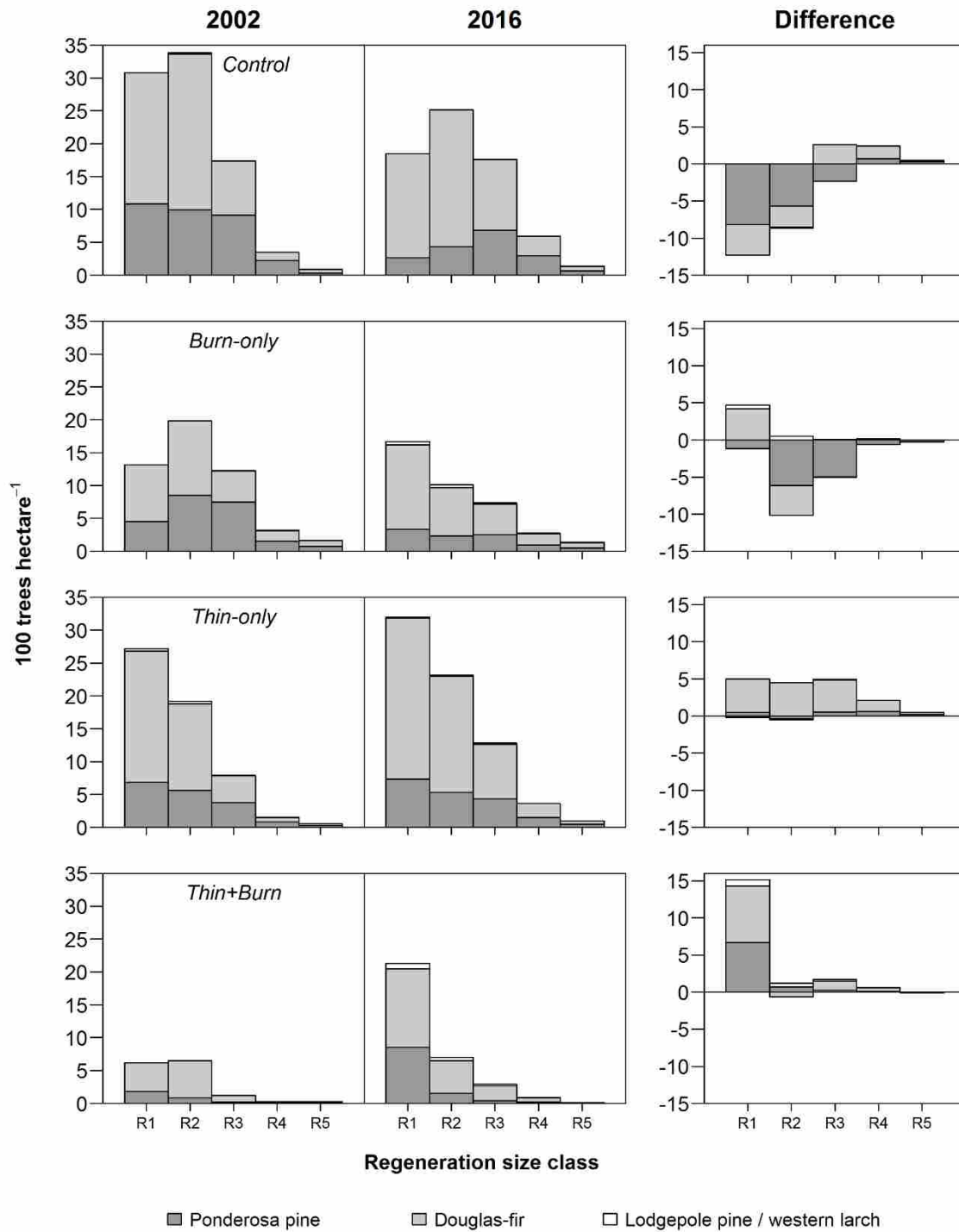


Figure 2. Regeneration size class distribution by species after treatment at Lubrecht Forest’s Fire & Fire Surrogate Study. From left to right panels show distribution in 2002 (immediately after treatment), 2016, and gains/losses per class between 2002 and 2016. Regeneration size classes are: R1=“seedling” (10 cm ≤ height < 50 cm), R2 =“large seedling” (50 cm ≤ height < 137 cm), R3=“small sapling” (0.1 cm ≤ dbh < 3 cm), R4=“medium sapling” (3 cm ≤ dbh < 6 cm), and R5=“large sapling” (6 cm ≤ dbh < 10.16 cm).

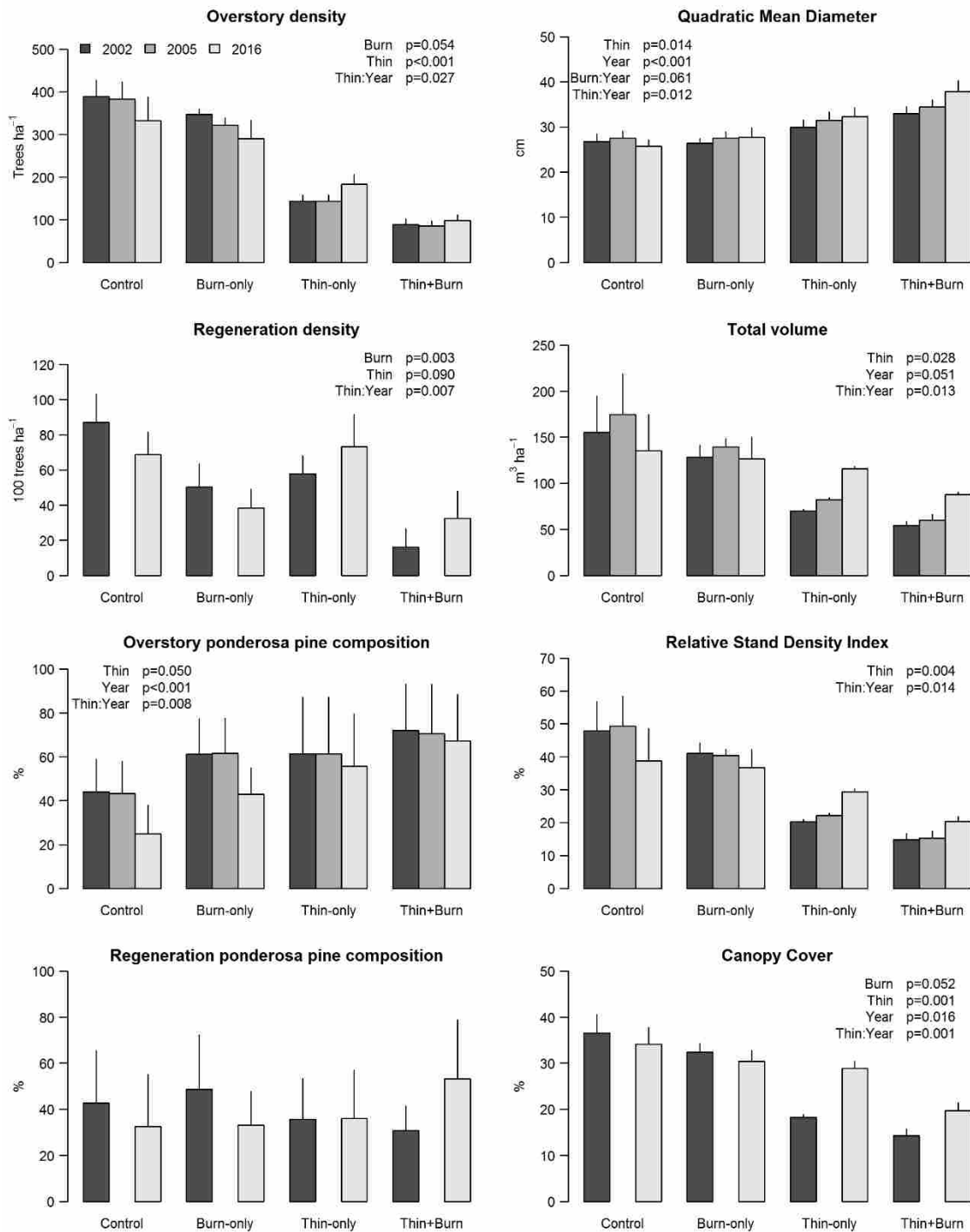


Figure 3. Forest structure and composition at Lubrecht Forest's Fire & Fire Surrogate Study. Bars show treatment means and standard error by year: 2002 (immediately after treatment), 2005, and 2016. Regeneration density, regeneration composition, and canopy cover were not measured in 2005. Significant ANOVA factors (p-values < 0.1) are shown with text at the top of each panel.

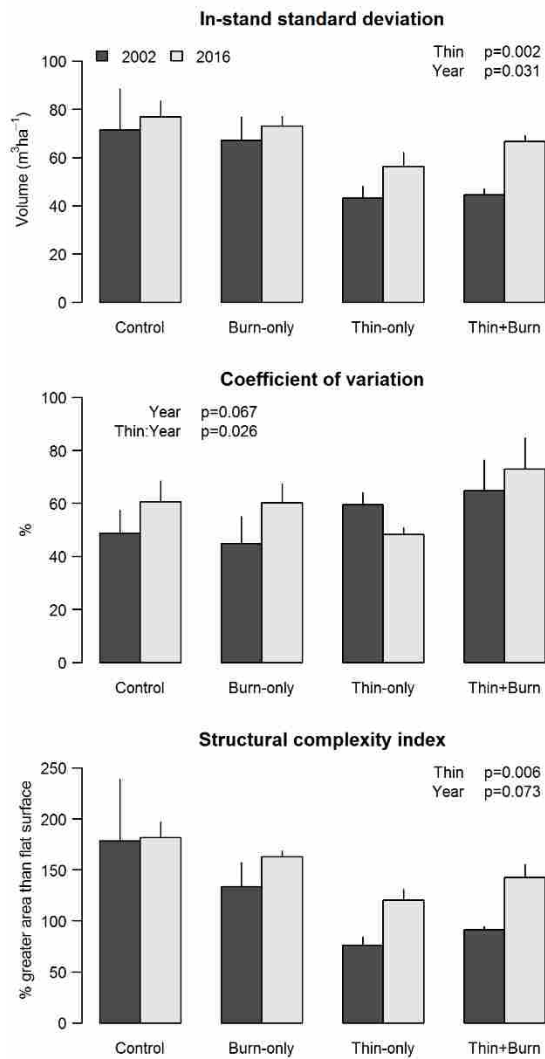


Figure 4. Structural variability at Lubrecht Forest’s Fire & Fire Surrogate Study. Bars show treatment means and standard error by year: 2002 (immediately after treatment) and 2016. Significant ANOVA factors (p -values < 0.1) are shown with text at the top of each panel.

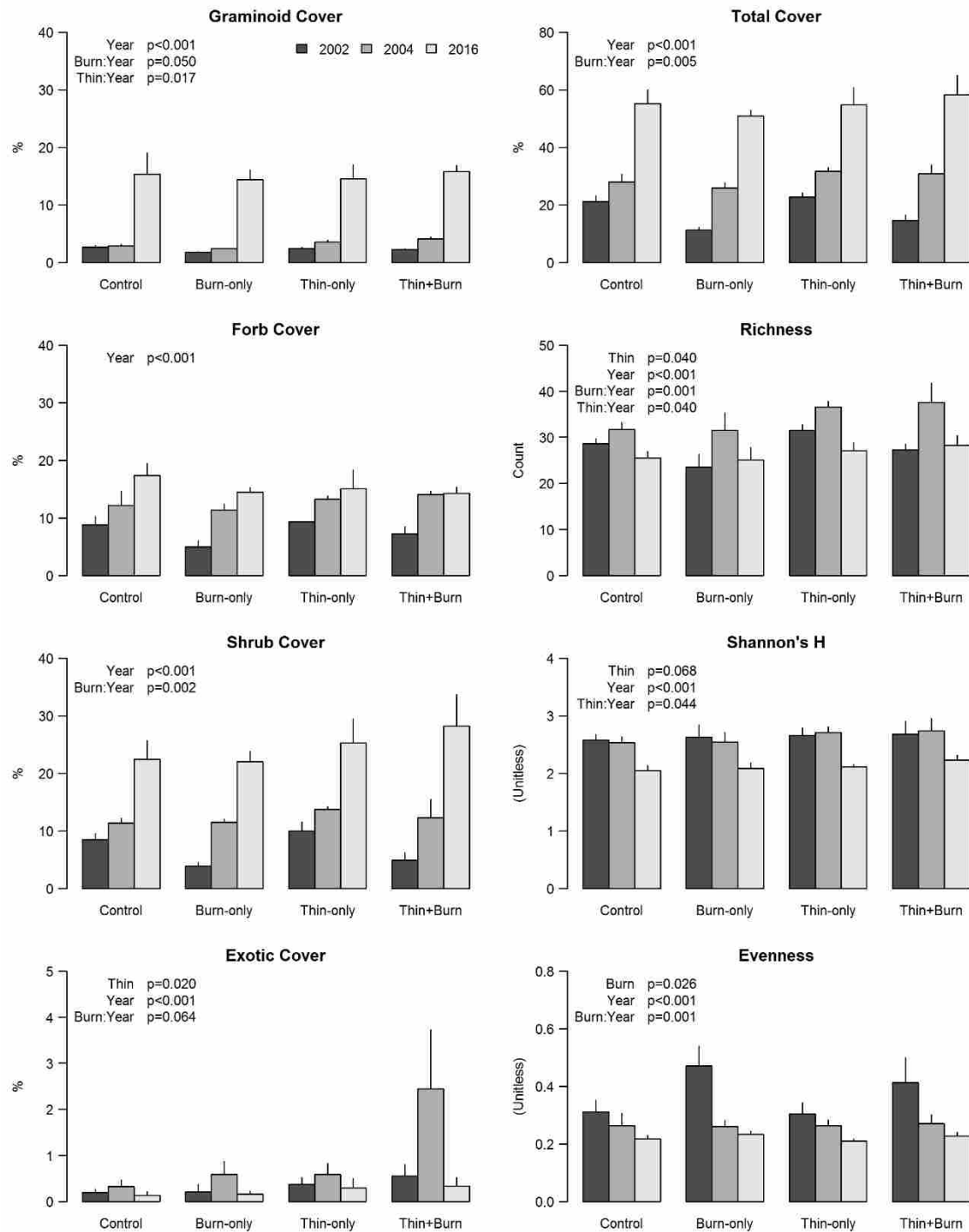


Figure 5. Understory vegetation cover and species diversity at Lubrecht Forest's Fire & Fire Surrogate Study. Bars show treatment means and standard error by year: 2002 (immediately after treatment), 2004, and 2016. Significant ANOVA factors (p-values < 0.1) are shown with text at the top of each panel.

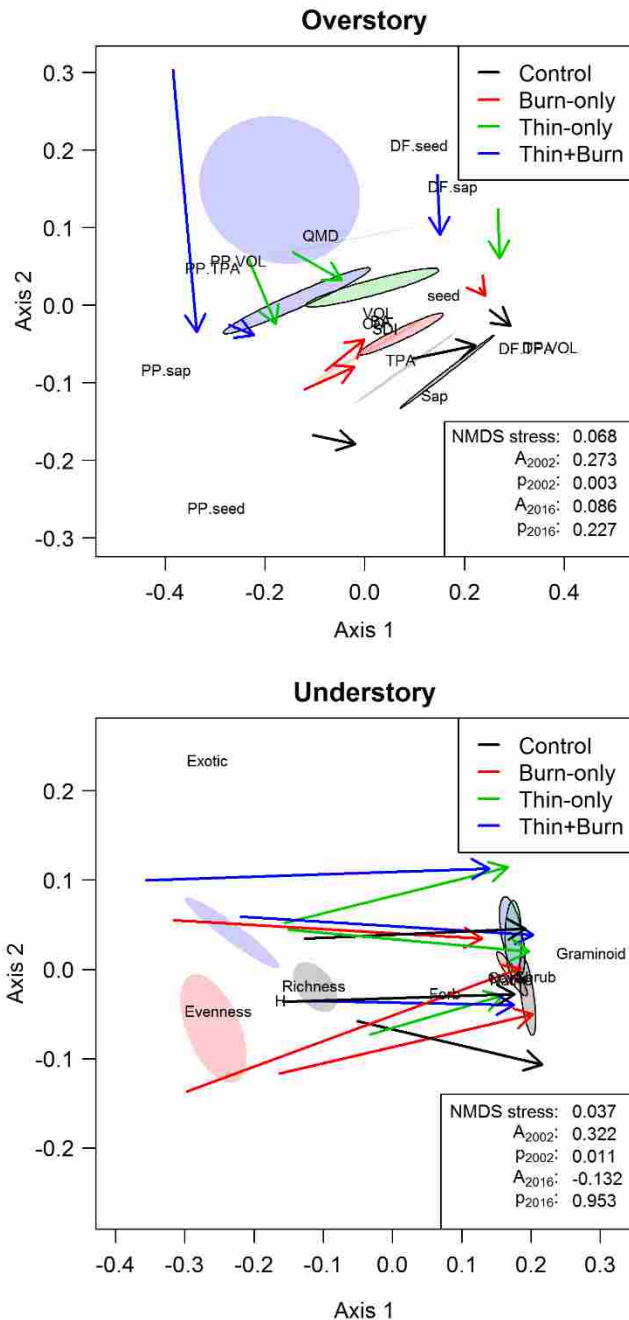


Figure 6. Two-dimensional projection of nonmetric multidimensional scaling ordinations, showing overstory (top panel) and understory (bottom panel) community shifts by experimental unit from 2002 (arrow tail) to 2016 (arrow head) at Lubrecht Forest’s Fire & Fire Surrogate Study. Projected treatment standard errors are shown with ellipses, 2002 values denoted by ellipses without outlines and 2016 values denoted by ellipses with outlines. On-figure text demonstrates the influence of each community response (16 and 9 responses for overstory and understory, respectively). Total configuration stress, test statistic (A) for multi-response permutation procedure by year, and p-value for test statistic by year are shown in bottom right of panels.

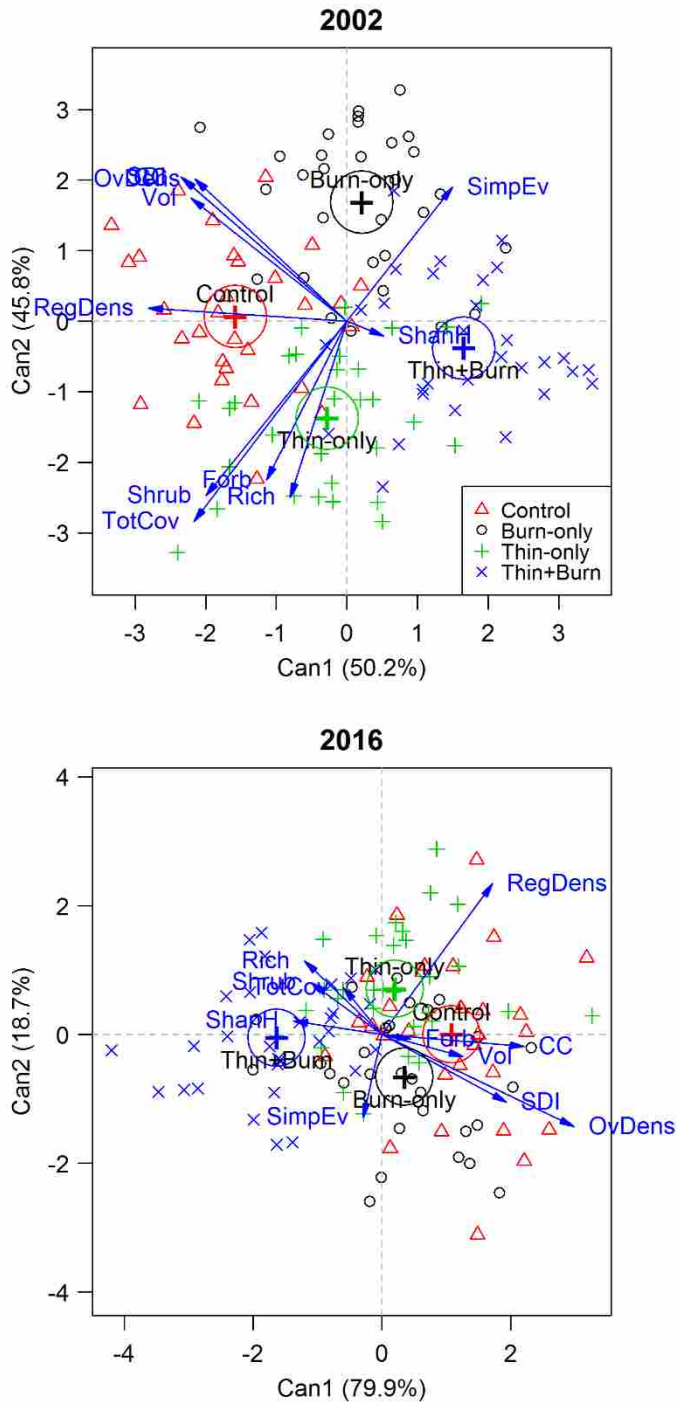
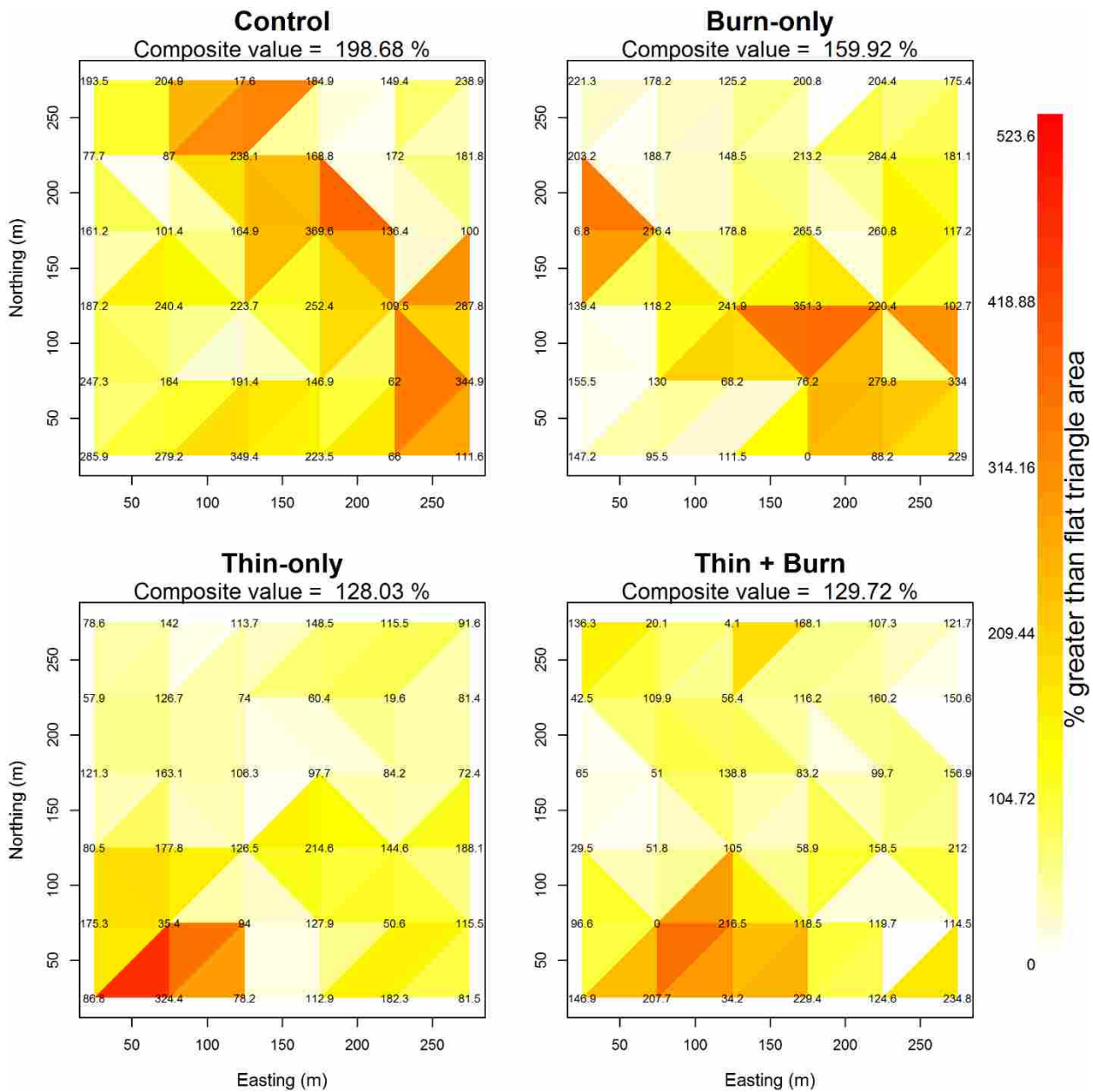


Figure 7. Canonical discriminant analysis of plot-scale multivariate communities in 2002 (top panel) and 2016 (bottom panel) at Lubrecht Forest’s Fire & Fire Surrogate Study. First two canonical axes are shown for each year (p -value < 0.05 except Can2 in 2016), labeled with percent variance explained by axis. Treatment mean centroids are labeled with black text and symbolized by circle and crosshairs. Labeled arrows show direction and relative magnitude of variable loading in canonical space (see Table 1 for attribute names and loadings by axis).

Appendix



Appendix 1. Figure demonstrating spatial variability in stand structure by experimental unit using the Structural Complexity Index (SCI). Sampled grid points are labeled with total overstory tree volume estimates ($m^3 ha^{-1}$). Triangles are colored according to the percent greater than flat triangle area, that is, their three-dimensional size. Red triangles represent high structural complexity; white or yellow colors represent low structural complexity. This study analyzed the composite, or total SCI, which is the average of all individual triangles within the unit. This example showcases the treatments from Block 2 in 2002.

Appendix 2. Species ranked abundances by treatment and year. Treatment levels are: C=Control, BO=Burn-only, TO=Thin-only, TB=Thin+Burn. Rank “1” is most abundant within treatment.

Species	2002				2016				Lifeform	Origin
	C	BO	TO	TB	C	BO	TO	TB		
<i>Achillea millefolium</i>	13	8	12	7	14	12	15	13	Forb	Native
<i>Agoseris glauca</i>	68.5	47.5	78	70.5	-	-	-	-	Forb	Native
<i>Agropyron repens</i>	-	-	-	-	-	68.5	-	70.5	Forb	Exotic
<i>Agrostis interrupta</i>	-	-	108.5	88	-	-	-	-	Graminoid	Exotic
<i>Agrostis scabra</i>	94	-	74	106	-	-	-	-	Graminoid	Native
<i>Allium spp</i>	42	38.5	50	36	43	37	58	57	Forb	Native
<i>Amelanchier alnifolia</i>	44	42.5	27.5	37	32	38.5	32	30	Shrub	Native
<i>Anaphalis margaritacea</i>	94	-	-	-	-	49	-	-	Forb	Native
<i>Anemone multifida</i>	55	29	64	30.5	58	26	64	37	Forb	Native
<i>Antennaria anaphaloides</i>	67	-	85.5	95.5	-	-	-	-	Forb	Native
<i>Antennaria racemosa</i>	24	21.5	32.5	39	24	24.5	25	38	Forb	Native
<i>Antennaria spp</i>	16	12	13	11	20	15	17	15	Forb	Native
<i>Apocynum androsaemifolium</i>	9	6	8	1	18	8	9	7	Forb	Native
<i>Arabis holboellii</i>	94	84	-	88	-	-	-	-	Forb	Native
<i>Arabis microphylla</i>	-	-	-	-	-	-	-	55.5	Forb	Native
<i>Arabis spp</i>	-	70	85.5	-	-	-	-	91	Forb	Native
<i>Arctostaphylos uva-ursi</i>	8	14	6	8	6	4	2	2	Shrub	Native
<i>Arnica cordifolia</i>	-	-	-	-	1	2	4	5	Forb	Native
<i>Arnica spp</i>	1	3	2	3	-	-	-	-	Forb	Native
<i>Artemisia tridentata</i>	-	53.5	-	-	-	-	-	-	Shrub	Native
<i>Aster conspicuus</i>	49.5	59	36.5	42.5	-	-	-	-	Forb	Native
<i>Aster meritus</i>	-	-	-	88	-	-	-	-	Forb	Native
<i>Aster occidentalis</i>	31	16.5	29	21	-	-	-	-	Forb	Native
<i>Aster spp</i>	-	-	-	-	28	23	19	25	Forb	Native
<i>Astragalus miser</i>	49.5	-	85.5	65	-	-	-	-	Forb	Native
<i>Astragalus spp</i>	-	-	-	-	26	-	75	26	Forb	Native
<i>Balsamorhiza sagittata</i>	11	11	16	53.5	15	21	21	42	Forb	Native
<i>Berberis repens</i>	4	4	4	4	7	6	7	6	Shrub	Native
<i>Bromus anomalus</i>	85	-	108.5	95.5	-	-	-	-	Graminoid	Native
<i>Bromus tectorum</i>	-	-	-	79.5	-	-	38	78	Graminoid	Exotic
<i>Calamagrostis purpurascens</i>	-	59	-	-	-	-	-	-	Graminoid	Native
<i>Calamagrostis rubescens</i>	5	5	7	6	2	1	1	1	Graminoid	Native
<i>Calochortus spp</i>	37	64	32.5	57	38	32	35	29	Forb	Native
<i>Camassia quamash</i>	-	-	108.5	-	-	-	-	-	Forb	Native

Appendix 1, continued

Species	2002				2016				Lifeform	Origin
	C	BO	TO	TB	C	BO	TO	TB		
<i>Campanula rotundifolia</i>	62.5	53.5	57.5	75.5	58	43	29	82	Forb	Native
<i>Carduus nutans</i>	-	-	-	75.5	-	-	-	-	Forb	Exotic
<i>Carex concinnoides</i>	18	19	18	14	46	30	49	32	Graminoid	Native
<i>Carex geyeri</i>	7	10	10	10	4	7	8	8	Graminoid	Native
<i>Carex nebrascensis</i>	-	-	95	-	-	-	-	-	Graminoid	Native
<i>Carex rossii</i>	35	36	41	32.5	40	57	83.5	-	Graminoid	Native
<i>Carex spp</i>	-	-	-	-	-	-	77.5	-	Graminoid	Native
<i>Castilleja spp</i>	-	-	-	-	60	51	42	63	Forb	Native
<i>Castilleja sulphurea</i>	53	56	43	75.5	-	-	-	-	Forb	Native
<i>Ceanothus velutinus</i>	73	-	-	60	-	68.5	71	23	Shrub	Native
<i>Centaurea maculosa</i>	73	40.5	39	70.5	73	58	55	69	Forb	Exotic
<i>Chimaphila umbellata</i>	85	64	68	-	23	-	73.5	-	Shrub	Native
<i>Cirsium arvense</i>	94	-	59	95.5	-	63	85	80	Forb	Exotic
<i>Cirsium vulgare</i>	-	-	108.5	70.5	-	-	-	-	Forb	Exotic
<i>Claytonia perfoliata</i>	-	64	-	-	-	-	33	-	Forb	Native
<i>Claytonia spp</i>	-	-	-	-	-	68.5	-	-	Forb	Native
<i>Clematis occidentalis</i>	-	-	108.5	-	-	-	-	-	Forb	Native
<i>Collinsia parviflora</i>	26.5	31	23.5	53.5	42	38.5	41	39	Forb	Native
<i>Collomia linearis</i>	40	49	53	57	-	-	-	-	Forb	Native
<i>Comandra umbellata</i>	-	-	-	-	-	-	-	86	Forb	Native
<i>Crataegus douglasii</i>	-	-	-	106	-	-	-	91	Shrub	Native
<i>Crepis spp</i>	-	-	-	-	55	47	61	64	Forb	Native
<i>Cryptantha affinis</i>	94	84	108.5	88	-	-	-	-	Forb	Native
<i>Cynoglossum officinale</i>	-	-	-	-	-	-	-	50.5	Forb	Exotic
<i>Cypripedium montanum</i>	94	-	-	-	-	-	-	-	Forb	Native
<i>Dactylis glomerata</i>	-	-	-	-	-	68.5	-	-	Graminoid	Exotic
<i>Danthonia intermedia</i>	42	23	47.5	30.5	33	46	-	47	Graminoid	Native
<i>Danthonia unispicata</i>	58.5	53.5	108.5	70.5	-	-	-	-	Graminoid	Native
<i>Disporum trachycarpum</i>	-	-	78	79.5	-	-	-	-	Forb	Native
<i>Dodecatheon pulchellum</i>	81	59	64	-	44	56	73.5	89	Forb	Native
<i>Elymus glaucus</i>	-	-	95	106	-	-	-	-	Graminoid	Native
<i>Elymus spp</i>	-	-	-	-	53	42	68.5	61	Graminoid	Native
<i>Epilobium angustifolium</i>	-	84	85.5	106	-	60	80	93	Forb	Native
<i>Epilobium brachycarpum</i>	94	-	108.5	106	-	-	-	-	Forb	Native
<i>Erigeron pumilus</i>	73	84	85.5	75.5	-	-	-	-	Forb	Native
<i>Erigeron spp</i>	-	-	-	-	70.5	74.5	76	75.5	Forb	Native
<i>Erigeron subtrinervis</i>	73	70	95	-	-	-	-	-	Forb	Native
<i>Erythronium grandiflorum</i>	20	25	25	47	30	28	34	34	Forb	Native
<i>Festuca idahoensis</i>	30	24	34	25	-	20	71	24	Graminoid	Native

Appendix 1, continued

Species	2002				2016				Lifeform	Origin
	C	BO	TO	TB	C	BO	TO	TB		
<i>Festuca occidentalis</i>	81	59	60	53.5	-	-	-	-	Graminoid	Native
<i>Festuca saximontana</i>	-	-	-	-	-	-	31	-	Graminoid	Native
<i>Festuca scabrella</i>	-	84	-	-	-	-	-	-	Graminoid	Native
<i>Festuca spp</i>	-	-	-	-	54	62	50	83	Graminoid	Native
<i>Fragaria virginiana</i>	14	9	11	9	17	14	13	17	Forb	Native
<i>Fritillaria pudica</i>	-	-	108.5	-	-	-	-	-	Forb	Native
<i>Galium boreale</i>	25	45	64	23.5	12	34	53.5	14	Forb	Native
<i>Gayophytum decipiens</i>	52	84	64	67	-	76	-	-	Forb	Native
<i>Gentianella amarella</i>	-	-	75.5	79.5	-	-	-	-	Forb	Native
<i>Geranium viscosissimum</i>	42	84	64	57	35	68.5	48	55.5	Forb	Native
<i>Gnaphalium microcephalum</i>	-	-	108.5	-	-	-	-	-	Forb	Native
<i>Goodyera oblongifolia</i>	85	84	-	-	-	-	-	-	Forb	Native
<i>Heterotheca villosa</i>	73	84	95	106	-	-	-	-	Forb	Native
<i>Heuchera cylindrica</i>	58.5	47.5	45	65	52	61	51	73.5	Forb	Native
<i>Hieracium albertinum</i>	23	21.5	23.5	32.5	-	-	-	-	Forb	Native
<i>Hieracium albiflorum</i>	56	42.5	52	44.5	-	-	-	-	Forb	Native
<i>Hieracium caespitosum</i>	-	-	-	-	-	-	71	-	Forb	Exotic
<i>Hieracium canadense</i>	-	-	108.5	106	-	-	-	-	Forb	Native
<i>Hieracium spp</i>	-	-	-	-	29	18	24	28	Forb	Native
<i>Holodiscus discolor</i>	-	-	108.5	-	-	-	-	84.5	Shrub	Native
<i>Juncus balticus</i>	-	-	95	-	-	-	-	-	Graminoid	Native
<i>Juncus spp</i>	-	-	-	-	-	-	45	-	Graminoid	Native
<i>Juniperus communis</i>	17	-	44	-	11	-	23	-	Shrub	Native
<i>Juniperus scopulorum</i>	-	84	-	106	-	-	-	-	Shrub	Native
<i>Koeleria macrantha</i>	77	84	-	48	64	44.5	53.5	48	Graminoid	Native
<i>Leymus spp</i>	-	-	-	-	-	55	-	-	Graminoid	Native
<i>Linanthus septentrionalis</i>	77	-	-	79.5	-	-	-	-	Forb	Native
<i>Linnaea borealis</i>	81	38.5	26	60	31	11	12	22	Shrub	Native
<i>Lithophragma parviflorum</i>	-	-	-	-	66	68.5	65	68	Forb	Native
<i>Lithospermum ruderale</i>	64	64	71	42.5	49	44.5	28	40	Forb	Native
<i>Lomatium triternatum</i>	33	44	30.5	39	48	50	40	46	Forb	Native
<i>Lupinus argenteus</i>	10	15	5	29	-	-	-	-	Forb	Native
<i>Lupinus spp</i>	-	-	-	-	8	9	6	19	Forb	Native
<i>Luzula campestris</i>	81	-	64	95.5	16	17	14	12	Graminoid	Native
<i>Luzula spicata</i>	-	-	-	-	-	68.5	81.5	-	Graminoid	Native
<i>Luzula spp</i>	-	-	-	-	-	-	-	35	Graminoid	Native
<i>Melampyrum lineare</i>	-	-	78	-	-	-	-	-	Forb	Native
<i>Microseris nutans</i>	47.5	46	54	50	-	-	-	-	Forb	Native
<i>Orobanche uniflora</i>	-	-	-	-	70.5	-	-	-	Forb	Native

Appendix 1, continued

Species	2002				2016				Lifeform	Origin
	C	BO	TO	TB	C	BO	TO	TB		
<i>Orthocarpus tenuifolius</i>	94	-	-	-	-	-	-	-	Forb	Native
<i>Osmorhiza berteroi</i>	-	-	95	62.5	-	-	-	-	Forb	Native
<i>Osmorhiza chilensis</i>	-	-	-	-	67	68.5	59	65.5	Forb	Native
<i>Pedicularis bracteosa</i>	-	-	-	-	-	-	-	77	Forb	Native
<i>Pedicularis contorta</i>	94	-	95	106	-	-	-	-	Forb	Native
<i>Penstemon albertinus</i>	28.5	31	20	23.5	62	-	79	70.5	Forb	Native
<i>Penstemon spp</i>	19	13	15	12	21	16	20	21	Forb	Native
<i>Phleum pratense</i>	65.5	84	71	50	51	74.5	56	67	Graminoid	Exotic
<i>Piperia unalascensis</i>	54	37	47.5	62.5	-	-	-	-	Forb	Native
<i>Platanthera hyperborea</i>	-	-	-	-	34	31	30	60	Forb	Native
<i>Poa compressa</i>	-	-	85.5	95.5	-	-	-	-	Graminoid	Exotic
<i>Poa gracillima</i>	70	-	85.5	65	-	-	-	-	Graminoid	Native
<i>Poa palustris</i>	-	70	85.5	88	-	-	-	-	Graminoid	Native
<i>Poa pratensis</i>	77	53.5	71	60	76	-	-	-	Graminoid	Exotic
<i>Poa secunda</i>	-	-	-	-	74.5	59	-	80	Graminoid	Native
<i>Polygonum douglasii</i>	68.5	51	95	88	-	-	-	-	Forb	Native
<i>Potentilla diversifolia</i>	-	-	-	-	-	-	36	-	Forb	Native
<i>Potentilla glandulosa</i>	94	-	75.5	70.5	-	-	57	73.5	Forb	Native
<i>Potentilla gracilis</i>	47.5	27.5	55.5	26	41	36	44	31	Forb	Native
<i>Potentilla recta</i>	58.5	35	57.5	35	61	48	67	36	Forb	Exotic
<i>Prunella vulgaris</i>	-	-	108.5	-	-	-	-	84.5	Forb	Native
<i>Pseudoroegneria spicata</i>	-	84	80	50	-	-	-	-	Graminoid	Native
<i>Pyrola chlorantha</i>	94	-	108.5	-	64	-	-	-	Forb	Native
<i>Pyrola secunda</i>	-	70	108.5	106	-	-	-	-	Forb	Native
<i>Pyrola spp</i>	-	-	-	-	70.5	-	-	-	Forb	Native
<i>Rosa woodsii</i>	32	18	19	13	27	19	22	20	Shrub	Native
<i>Rumex acetosella</i>	-	-	-	106	-	-	-	-	Forb	Exotic
<i>Salix scouleriana</i>	46	70	46	83	50	22	43	75.5	Shrub	Native
<i>Sedum stenopetalum</i>	22	26	27.5	46	37	33	46	62	Forb	Native
<i>Senecio canus</i>	-	-	-	-	-	-	39	-	Forb	Native
<i>Senecio integerrimus</i>	-	-	-	95.5	-	-	-	-	Forb	Native
<i>Shepherdia canadensis</i>	45	-	42	106	-	-	16	33	Shrub	Native
<i>Silene menziesii</i>	38.5	59	71	53.5	25	40	60	58	Forb	Native
<i>Silene spp</i>	-	-	-	-	74.5	54	68.5	50.5	Forb	Native
<i>Sitanion hystrix</i>	34	34	30.5	27	-	-	83.5	-	Graminoid	Native
<i>Smilacina racemosa</i>	-	84	85.5	-	68	52.5	63	88	Forb	Native
<i>Solidago missouriensis</i>	-	-	108.5	-	-	-	-	-	Forb	Native
<i>Solidago multiradiata</i>	-	84	71	88	-	-	-	-	Forb	Native
<i>Spiraea betulifolia</i>	3	1	1	2	5	5	3	4	Shrub	Native

Appendix 1, continued

Species	2002				2016				Lifeform	Origin
	C	BO	TO	TB	C	BO	TO	TB		
<i>Spiranthes romanzoffiana</i>	94	84	-	-	-	-	-	-	Forb	Native
<i>Stipa occidentalis</i>	65.5	50	95	95.5	-	-	-	-	Graminoid	Native
<i>Stipa richardsonii</i>	28.5	16.5	36.5	19	13	27	26	9	Graminoid	Native
<i>Stipa spp</i>	-	-	-	-	-	-	-	65.5	Graminoid	Native
<i>Streptopus spp</i>	-	-	-	-	-	-	77.5	87	Forb	Native
<i>Symphoricarpos albus</i>	2	2	3	5	3	3	5	3	Shrub	Native
<i>Taraxacum officinale</i>	36	31	35	18	47	35	37	59	Forb	Exotic
<i>Thalictrum occidentale</i>	26.5	70	22	16	19	52.5	18	18	Forb	Native
<i>Thlaspi arvense</i>	-	-	-	106	-	-	-	-	Forb	Exotic
<i>Tragopogon dubius</i>	81	64	108.5	83	-	-	81.5	-	Forb	Exotic
<i>Trifolium pratense</i>	-	-	-	-	45	68.5	52	49	Forb	Exotic
<i>Trifolium spp</i>	58.5	84	38	22	-	-	-	-	Forb	Exotic
<i>Trisetum canescens</i>	62.5	84	64	41	-	-	-	-	Graminoid	Native
<i>Trisetum cernuum</i>	-	-	-	-	-	-	62	-	Graminoid	Native
<i>Trisetum spicatum</i>	94	84	108.5	95.5	-	-	-	-	Graminoid	Native
<i>Vaccinium caespitosum</i>	12	20	14	15	9	13	10	10	Shrub	Native
<i>Vaccinium membranaceum</i>	15	27.5	17	20	10	10	11	11	Shrub	Native
<i>Valeriana dioica</i>	61	84	40	44.5	-	-	-	-	Forb	Native
<i>Valeriana occidentalis</i>	-	-	-	-	56	-	27	80	Forb	Native
<i>Valeriana spp</i>	-	-	-	-	-	-	-	72	Forb	Native
<i>Verbascum thapsus</i>	-	-	85.5	34	-	-	-	41	Forb	Exotic
<i>Vicia americana</i>	-	-	-	-	-	-	-	91	Forb	Native
<i>Viola adunca</i>	51	70	50	28	-	-	-	-	Forb	Native
<i>Viola spp</i>	-	-	-	-	39	68.5	66	45	Forb	Native
<i>Zigadenus venenosus</i>	38.5	40.5	50	39	22	29	47	53.5	Forb	Native

Chapter 2: Fuel reduction affects individual tree growth and attributes 13 years after treatment

Abstract

Fuel reduction treatments are commonplace in dry, fire-prone forests of the western United States. The primary objective of fuel treatments is to immediately reduce crown fire hazard. However, information on the effects of these treatments on residual trees is relevant to assess their productivity as well as resistance and resilience to future disturbances. In this study, we evaluate the effects of fuel treatments on retained individual overstory ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees in western Montana, where fuel reduction treatments were implemented 13 years prior as part of a national experiment. We examined tree attributes in response to the following replicated treatments: thin-only, burn-only, thin+burn, and a no-action control. Annual growth of the two species varied by treatment type: thinning-based fuel reduction (thin-only and thin+burn) increased diameter growth for both species, stem volume and crown dimensions in ponderosa pine, and crown length in Douglas-fir relative to unthinned treatments. Burning (burn-only and thin+burn) did not significantly affect tree growth relative to unburned treatments. We analyzed three different tree attributes that confer resistance to common disturbances: height-to-diameter ratio (resistance to wind), bark thickness (resistance to surface fire), and growth efficiency (resistance to bark beetles). Our models suggest that both thinning and burning alter tree attributes relative to the control in a manner that may increase tree resistance to wind and snow breakage, surface fire, and biotic agents such as bark beetles. This study provides much needed insight into the mid-term growth dynamics of trees in response to fuel treatments, and will be

useful to scientists and managers attempting to better grasp the relative merits of fuel treatments types.

Introduction

Many of today's dry, temperate forests are susceptible to high-severity crown fire due to management history and changing climate (Covington and Moore 1994; Westerling et al. 2006; Miller et al. 2009; Miller et al. 2012). This is a significant problem in the western US because crown fire was historically uncommon in forests with frequent, low-severity fire regimes, and because novel environmental conditions may imbue ecosystem structural and functional properties that are ill-equipped to meet societal needs and desires. Furthermore, crown fire threatens nearby communities and suppression is costly. One common means of mitigating these hazards is with fuel reduction treatment, whereby land managers remove excess live and dead forest fuels while retaining fire resistant trees (Agee and Skinner 2005; Reinhardt et al. 2008). How fuel treatments affect other management objectives not directly related to fire resistance remains unclear, especially individual tree responses that are directly related to multiple-use management objectives.

Fuel reduction treatments manipulate forest structure to limit fire transfer from the surface to the overstory. They are typically evaluated with fire hazard metrics that quantify stand susceptibility to crown fire (e.g., canopy bulk density, canopy base height, potential fire behavior, torching index, crowning index; Scott and Reinhardt 2001; Stephens et al. 2009), but are rarely evaluated in terms of individual tree growth and morphology responses. Yet, individual tree responses have direct implications on fire hazard and other management objectives because individuals are foundational to stand metrics and specific management needs.

For instance, growth of individual trees, particularly of large trees, is essential for future fire resistance (Ryan and Reinhardt 1988; Agee and Skinner 2005), ecological processes (e.g. productivity and carbon storage; Waring 1983; Lutz et al. 2012; Sala et al. 2012), wildlife habitat (Scott 1978; Meyer et al. 2005), and timber products that offset costs of future treatment (Scott 1998; Reinhardt et al. 2008). The growth and persistence of large trees are central goals to many restoration projects as well, which are often comingled with fuel treatments (Kolb et al. 2007). Since fuel reduction treatments are so common in Western landscapes, it is important to assess effects on large tree growth.

Past studies on restorative fuel reduction treatments often document diameter distributions and basal area differences from pre-treatment to immediate post-treatment (e.g., Harrod et al. 2007; Youngblood 2010), with the primary goal to assess changes in stand fire hazard rather than individual-level stem responses. However, Fiedler et al. (2010) documented greater individual basal area increment in thinning and thinning + burning treatments four years after treatment, and Hood et al. (2016) show that these effects persist in the longer term (11 years). Still, there is a shortage of information available on tree height and volume growth, which are expected to improve in response to reductions of stand density (Schubert 1971; Agee 1993; Nyland 2016). Burning may improve stem growth beyond thinning alone because fire mobilizes N, improves nutrient cycling, and modifies the shrub community (Gundale et al. 2006; Metlen and Fiedler 2006; Ganzlin et al. 2016). However, thinning without burning may result, at least in the short term, in better stem growth as it avoids potential for fire injury, does not stimulate heat-scarified understory seed bed, and does not induce soil hydrophobicity as fire does (Nyland 2016). Whatever the mechanism causing stem change, treatment effects on individual stem

responses over time will form the basis of future stand structure and subsequent silvicultural options.

Whereas stem attributes are the most often considered tree attributes in forestry, much of forest health, crown fire hazard, and ecosystem function is tied to a tree's crown attributes (Van Wagner 1977; Waring 1983; Waring and Running 2007). However, fuel reduction and fire modeling studies often fail to report crown morphology or growth (Affleck et al. 2012). Thinning-based fuel reduction treatments often significantly reduce overstory competition by decreasing crown density (Agee and Skinner 2005), and where overstory competition is low, individual tree crowns may be growing more like open canopy trees (free growth) than closed canopy trees (Oliver and Larson 1996). This rapid change in competitive pressure may result in atypical crown structure and growth in residual trees. Prescribed burning also alters expected crown development by causing live crowns to recede due to heat scorch (Van Wagner 1973). Overall then, fuel reduction treatments may have both direct and indirect impacts on crown morphology that have not been adequately quantified.

Fuel reduction and restoration treatments are acutely concerned with large tree persistence (Agee and Skinner 2005). This is intimately tied with the management objective of improved tree growth, but is more focused on morphological attributes that enable trees to survive disturbance (Kolb et al. 2007). Since surviving trees are necessary for diverse management objectives (e.g., to provide expected ecological processes, wildlife habitat, and potential economic return) individual trees must be resistant to natural disturbance agents. Common disturbance agents that trees face in dry forests are surface fire, wind and snow breakage, and insect attack. Given these disturbance agents, bark thickness, height-to-diameter (height:diameter) ratio, and growth efficiency are three measureable attributes related to

resistance to disturbance. The principal advantage of thick bark in fire-prone forests is that bark insulates cambium during surface fires, increasing tree survival (Martin 1963; Jones et al. 2006). Conifer height:diameter ratios have a strong negative relationship with snow and wind damage incidence (Cremer et al. 1982; Wonn and O'Hara 2001). Growth efficiency, here defined as basal area growth per sapwood cross-sectional area, is a metric that quantifies tree vigor (Waring et al. 1980). In theory, more vigorous trees have better capacity to withstand insect and pathogen attack if vigor represents better access to and use of resources. Understanding how these metrics are affected by treatment should help attain resistance-oriented objectives characteristic of fuel reduction and restoration treatments. We could assume that bark thickness, height:diameter, and growth efficiency are equivalent to stands thinned with timber-oriented objectives (e.g., Larsson et al. 1983; O'Hara 1988), but thinning for crown fire resistance often results in lower relative stand densities and thus lower competitive pressure on residual trees.

The primary research goal of this study is to test mid-term effects of restorative fuel reduction strategies (13 years since treatment) on overstory tree growth and attributes. We pose and answer two questions to achieve this goal: what are the treatment effects on stem and crown growth after 13 years?; and what are the treatment effects on tree attributes that have implications for resistance to future disturbance (i.e., bark thickness, height:diameter ratio, and growth efficiency)? We expect that this study will guide researchers, modelers, and managers to better understand the broad reaching effects of fuel treatments on tree-level attributes important to achieving diverse management objectives. The results of this study can be used to improve individual tree growth estimates based on treatment history, and press us to further define fuel reduction treatment effectiveness.

Methods

Study Site

This study was conducted at the University of Montana's Lubrecht Experimental Forest (LEF; 46°53'N, 113°26'W), an 11,300 ha forest in western Montana's Blackfoot River drainage of the Garnet Range. Study sites range in elevation from 1,230 to 1,388 m ASL, and are comprised of *Pseudotsuga menziesii/Vaccinium caespitosum* and *Pseudotsuga menziesii/Spiraea betulifolia* habitat types (Pfister et al. 1977). This forest is generally composed of second-growth ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), with western larch (*Larix occidentalis* Nutt.) regenerated from heavy cutting in the early 20th century. Soils are fine or clayey-skeletal, mixed, Typic Eutroboralfs, as well as loamy-skeletal, mixed, frigid, Udic Ustochrepts (Nimlos 1986).

Climate in this study area is maritime-continental. Annual precipitation is approximately 460 mm (PRISM Climate Group), nearly half of which falls as snow. Mean temperatures range from -6°C in December and January to 17°C in July and August. Average plant growing season is between 60 and 90 days. Grissino-Mayer et al. (2006) identified that historic fire frequency at LEF prior to the 20th century ranged from 2 to 14 years, with a mean composite fire return interval of 7 years.

The LEF was part of the Fire and Fire Surrogate (FFS) Study, a multidisciplinary research project that aimed to quantify the short-term effects of restorative fuel reduction treatments in frequent-fire forests across the US. The FFS Study provides a framework to examine fuel treatment effects on tree growth as it has a balanced experimental design and was specifically created to test for differences among treatments (McIver and Weatherspoon 2010).

As a nationally implemented network, researchers have used the FFS Study to answer a wide gamut of short-term ecological response questions (see McIver et al. 2012). At LEF, treatments were implemented in each of three blocks using a randomized factorial design: two levels of thinning (not thinned and thinned) by two levels of prescribed burning (not burned and burned), for a total of four treatment levels (no-action control, thin-only, burn-only, thin+burn).

Prescription severity was intended to maintain 80% overstory tree survival given a wildfire in 80th percentile weather conditions. Stands were cut in 2001 and burned in 2002, creating twelve 9 ha experimental units. The cutting prescription was a combined low thinning and improvement cut to a residual 11.5 m²ha⁻¹ of basal area, favoring ponderosa pine and western larch over Douglas-fir. Applied burning treatments were low-severity spring burns at windspeeds less than 13 kph. Stand conditions have been documented to assess short-term (up to 4 years) treatment effects (Metlen and Fiedler 2006; Fiedler et al. 2010).

Although LEF's FFS study is a randomized complete block design, bark beetle-induced mortality has complicated the assessment of longer term treatment effects. Beetle populations (primarily *Dendroctonus ponderosae* Hopkins) rose to outbreak levels in Montana between 2006 and 2012. Beetle mortality was highest in control and burn-only units (Hood et al. 2016), leading to similar live ponderosa pine basal area in all treatments. Since Hood et al. (2016) found a treatment effect on beetle-induced tree mortality and stands are more similar now than in the pre-outbreak years, any statistical differences between treatments found in this study will either be due to a combination of treatment and subsequent beetle kill or will be due to a muted treatment effect.

Field Methods

We sampled trees on permanently monumented plots in the FFS Study. We measured previously tagged mature trees in 2014 using 0.04 ha circular plots, measuring a subset of trees from the center of each of the study's rectangular modified-Whittaker plots (Shmida 1984; Metlen and Fiedler 2006). These were 10 randomly selected plot locations from 36 systematically located grid points within each treatment unit, making for a total of 120 revisited points. For each mature tree (diameter at breast height [dbh; 1.37 m] greater than 10.16 cm), we recorded species, dbh, total height, height to the base of live crown, and crown width. Height to the base of live crown was the estimated average branch height of the compacted lower limit of the crown (US Forest Service 2005). Crown width was the projected horizontal distance between live crown edges as visualized by GRS densitometers (Geographic Resource Solutions; Arcata, CA); two measurements were made per tree at right angles. We used a historical dataset from these same plots dating back to 2001 (residual trees) and 2005 (residual trees plus ingrowth). The 2001 data comprised the same measurements as our 2014 dataset, however, crown width was not measured in 2005. Live stand structure metrics are presented in Table 1 and Figure 1.

In 2015 we measured bark thickness and collected tree cores using an increment borer for each of the tagged trees. Trees were cored along two perpendicular axes at breast height. Live sapwood boundaries were located and marked on the cores, then taken back to the lab to measure sapwood length. Sapwood length was then converted to cross-sectional area at breast height (less heartwood area) and used to calculate growth efficiency, which we define as 10-year periodic basal area growth (2005 to 2015) divided by total sapwood area in 2015 (sensu O'Hara 1988).

Statistical Analysis

We considered all live tagged trees in plots when calculating stand summary statistics and diameter distributions. Since we were interested in overstory tree response, subsequent calculations and analyses were performed using data only from trees initially present and greater than 25.4 cm dbh in 2001 and surviving through 2014.

We created two response variable suites each for ponderosa pine with initial dbh ≥ 25.4 cm (the primary species of interest in this study; 161 trees) and Douglas-fir ≥ 25.4 cm dbh (167 trees). These included annualized growth dimensions (periodic annual growth in dbh, height, volume, crown length, crown width, and crown surface area from 2001 to 2014) to answer our first research question, and tree attributes (height:diameter ratio, bark thickness, and growth efficiency in 2015) to answer the second. Volume was calculated from height and dbh as total cubic meters using equations developed by Faurot (1977). Crown surface area was calculated as square meters assuming the shape of a paraboloid. Height:diameter ratio was calculated as height in meters divided by dbh in meters.

We used linear mixed-effects models to test our research questions, which were focused on treatment effect detection in annualized growth and tree attribute responses. In these models, we included non-treatment model terms (i.e., dead basal area on the measured plot in 2014 as a surrogate for beetle severity, 2001 dbh to account for tree size in the annual dbh growth model, 2001 height for the height model, etc.) to isolate treatment effects, not to improve predictive capacity or make extended inference on non-treatment terms. These covariates were specified for inclusion a priori, so there was no model selection routine to remove non-significant covariates. We used AIC for model selection when checking for interaction between tree covariates and treatment, but AIC was always lower for the simpler, non-interactive models. Models were fit in

R (R Core Team 2016) with the `lme` function (Pinheiro et al. 2016). The same model form is used for each of the response variables to be tested:

$$[1] \quad y_{ijklm} = \mu + \alpha_i \times \beta_j + \gamma_k + \varepsilon_{ijk} + \varphi_{ijkl} + \rho_{ijkl} + \tau_{ijklm} + \omega_{ijklm}$$

where, y is the tree response variable of interest, μ is the grand mean, α is the thinning effect (levels i : 1=not thinned, 2=thinned), β is the burning effect (levels j : 1=not burned, 2=burned), γ is the block effect (levels k : 1-3), ε is the error term by which treatment is evaluated, φ is dead basal area on the measured plot in 2014 (a surrogate for beetle severity), ρ is the plot effect (levels l : 1-120), τ is a measured tree covariate to account for size in 2001 (for tree m), and ω is the tree error term.

Model residuals were visually inspected for normality. Residuals from some of the height-based responses demonstrated slight departures from normality (long distributional tails) but could not be ameliorated by transformation; we note that model standard errors are therefore approximate. Overall model fit was evaluated with marginal and conditional R^2 values (Nakagawa and Schielzeth 2013). Marginal R^2 is here defined as the proportion of variance explained by the fixed effects (μ , α , β , φ , and τ) to all variance components in the model; conditional R^2 is the proportion of the summed fixed and random components (all except ω) to all variance components in the model.

Results

Treatment effects on tree growth

Treatment influenced ponderosa pine and Douglas-fir stem growth over the course of the study (Figure 2; Figure 3; Table 2). Of the ponderosa pine models, model fit was the best for volume, but the worst for height. The opposite rankings were true of the Douglas-fir models. The suite of models showed that thinning (thin-only and thin+burn treatments) positively influenced

dbh growth over unthinned treatments in both ponderosa pine and Douglas-fir, but volume growth was only greater for ponderosa pine. More specifically, ponderosa pine dbh growth was twice as great in thinned treatments (model prediction: 0.496 cm yr⁻¹) than unthinned treatments (model prediction: 0.243 cm yr⁻¹) regardless of initial tree size, which was not a significant covariate. Initial tree size was significant for the Douglas-fir dbh model and given initial data range of 25 cm to 61 cm dbh, our models predict dbh growth to be 0.453 cm yr⁻¹ and 0.557 cm yr⁻¹, respectively, in thinned treatments, but 0.254 cm yr⁻¹ and 0.358 cm yr⁻¹ in the unthinned treatment. Thus, Douglas-fir dbh growth was improved by thinning, but the effect (relative to unthinned) decreased with tree size from 78% greater growth in the smallest trees to only 56% more growth in the largest trees. Likewise, thinning caused 73% greater dbh growth on plots that had no beetle mortality (for median dbh, 31.9 cm), but only 47% greater growth on plots that had higher mortality (1.56 m² of basal area lost). Initial volume was significant for the ponderosa pine volume growth model, and growth after thinning was 336% and 28% greater than the unthinned treatment for the smallest and largest tree sizes, respectively (initial size range 0.24 m³ to 3.01 m³). Burning and the interaction between burning and thinning did not significantly affect stem growth.

Ponderosa pine and Douglas-fir crowns responded differently to treatments (Figure 2; Figure 3; Table 2). Although R² values for ponderosa pine were on average lower than for the stem growth models, thinning had a positive effect on crown length, width, and surface area growth relative to unthinned treatment; crown length also depended on initial size while crown width depended on initial size and beetle severity. Thinning caused trees with shortest crowns (6.6 m) to increase 81% more than trees in unthinned treatments, while trees with longest crowns (20.4 m) decreased, but the decrease was 72% lower in thinned than unthinned treatments (i.e.,

thinning minimizes crown length reduction). When compared to the tree height model, coefficients show that crown length growth was 100% of tree height growth for small trees and 86% for large trees in thinned treatments, but for unthinned treatments crown length growth was only 63% of tree height growth for small trees and -40% for large trees. Likewise, thinning increased crown width growth by 111% in trees with narrowest crowns (2.3 m); widest crowns (12.6 m) still grew at least 3 cm year⁻¹ in thinned treatments while trees in unthinned treatments reduced in width. The effect of thinning on crown width was moderated by beetle severity, as thinning caused the median tree (5.0 m) to grow 187% more than unthinned treatments where beetles did not kill trees, but only 50% more than unthinned treatments where beetle severity was greatest (0.82 m² basal area lost). Thinning caused ponderosa pine crown surface areas to grow an additional 159% irrespective of tree starting size. Burning and the interaction of burning and thinning, however, did not have a significant effect on ponderosa pine growth. Our models show marginal evidence that thinning increased Douglas-fir crown length growth compared to unthinned treatments but this response varied with initial tree size (49% increases for small crown lengths [6.3 m] and 297% for large lengths [16.5 m]). However, thinning and burning did not affect Douglas-fir crown width or surface area growth.

Treatment effects on tree attributes

Tree attributes varied by diameter class (Tables 3 and 4) and treatment had differential effects on ponderosa pine and Douglas-fir attributes. Model fit was best for the height:diameter model in both species. Initial tree size (dbh) had a significant effect for all variables in both species. For ponderosa pine, there was no evidence that thinning affected height:diameter, but slight evidence that burning reduced height:diameter. Burning was associated with 7% to 12% lower height:diameter ratios than the unburned treatment as initial dbh increased. This reversed

for ponderosa pine growth efficiency, where the model showed that thinning improved growth efficiency but burning had no effect. Growth efficiency after thinning was 53% greater for the smallest diameter trees and remained positive for large trees as growth efficiency in the unthinned units approached zero. The only treatment effects in Douglas-fir were on growth efficiency. Growth efficiency improved 25% to 44% due to thinning and 21% to 36% due to burning, based on small and large initial tree dbh, respectively. Whereas tree size improved treatment effects on growth efficiency, beetle severity dampened them: growth efficiency improved 27% to 14% due to thinning and 23% to 11% due to burning, as beetle severity increased. We observed no treatment effect on ponderosa pine bark thickness, Douglas-fir bark thickness, or Douglas-fir height:diameter; nor did we find any treatment interaction in any of the attributes.

Discussion

Burning versus thinning

Our models illustrate that thinning-based fuel reduction and restoration (thin-only and thin+burn treatments) have the broadest impacts on individual trees, and more so for ponderosa pine than Douglas-fir. Trees in thinned stands have very different morphological characteristics and growth patterns than those in the unthinned treatments. On the other hand, burning-based fuel reduction treatments had comparatively little impact on mid-term tree morphology and growth responses. We believe the lack of burning effect is primarily due to treatment severity and resultant competitive conditions. The prescribed burns in the FFS study had little impact on mature (dbh > 10.16 cm) stem density (Table 1; Metlen and Fiedler 2006; Schwilk et al. 2009) and only resulted in minimally perceptible change to residual overstory trees. Although burning improves nutrient availability (Gundale et al. 2006; Ganzlin et al. 2016), water limitation or

competition may be inhibiting full utilization of higher nutrient loads. Low-severity burns are actually common when reintroducing fire (as in Skinner 2005; Schwilk et al. 2009) for fear of widespread overstory mortality or runaway crown fire that threatens nearby natural resources, structures, or lives. This study provides evidence that single-entry low-severity burning is largely ineffective at changing individual overstory tree growth trends and easy-to-measure tree attributes that may confer resistance (save for Douglas-fir growth efficiency). Moderate-severity prescribed burns or repeated application of low-severity burning is necessary if landowners want to see significant physical change in overstory tree characteristics.

It should be noted that a number of studies have shown that thinning alone insufficiently reduces crown fire potential, though it is the primary objective of fuel reduction treatments (e.g., Stephens and Moghaddas 2005; Schwilk et al. 2009; Stephens et al. 2009; Fiedler et al. 2010). This is because thinning alone does not treat dead surface fuels and can even increase loading, may not treat mid-story ladder fuels, does not increase crown base heights as well as burning, and increases in-stand wind speeds, depending on burn prescription. Furthermore, although a one-time low-severity fire may not impact the overstory tree characteristics examined in this study, it may confer increased resistance to disturbances in alternative ways (e.g., Hood et al. 2016). We do not negate these findings, but seek to inform multiple-resource managers of the temporal effects of treatments on individual tree growth and attributes.

Implications of post-treatment growth

Crowns are fundamentally important tree attributes. The tree crown is the photosynthetic machinery that assimilates carbon for cellular respiration, growth, storage, and extractives. Larger crowns have a greater capacity to produce more photosynthate and meet tree demands. Furthermore, crown dimensions are excellent predictors of tree growth potential (e.g., Dunning

1922; Keen 1943), and they can be more easily measured than tree leaf area. Since thinning-based fuel reduction increases tree carbohydrate source, it subsequently prepares trees for more rapid growth and helps realize potential ecologic or economic gains.

The primary motivation for these treatments was to reduce crown fire potential. Prescribed fire can accomplish this by scorching and killing lower branches, increasing crown base height. Yet, perhaps because burn prescription was conservative and we only considered trees larger than 25.4 cm dbh, we found no significant effect of fire on crown length. Rather, our models show that thinning-based fuel reduction increased crown length development, especially by arresting crown recession of the smaller overstory trees (crown length growth for a small tree in thinned treatment is equivalent to tree height growth). This has long been known with respect to commercial thinning (e.g., Kramer 1966; Siemon et al. 1976), but is rarely discussed in the fuel management literature (but see Jain et al. 2012). Although crown growth should improve overall tree growth, it can be detrimental to tree and stand fire hazard if the gap between crown and surface fuel strata is reduced as crown recession is arrested or slowed. In fact, crown length reduction (“lifting canopy base height”) is one tenet of fuel treatments (Agee and Skinner 2005). This is because low hanging foliage is more likely to ignite from surface fires and nearby fuel ladders, and because fuller crowns (and higher bulk densities) provide more fuel for crown-to-crown fire transfer. An important consideration is that the gap between surface and overstory fuel strata may be short-lived due to combined slowed recession from above, as this study demonstrates in the thinned treatments, and growth from the understory below. Although trees in both the thin-only and the thin+burn treatments had slowed crown recession, the gap between overstory crown bases and understory fuels is larger in thin+burn because prescribed fire killed understory shrubs and advance regeneration (pers. obs.).

Additional crown growth is an ecological advantage of thinning-based treatments. Individual trees with wide crowns and persistent crown bases develop large diameter branches to support the added structure. Large diameter branches are key foundational features that support lichen community development by increasing substrate area and duration for colonization (Esseen et al. 1996). A healthy lichen community is particularly valuable for managers seeking to improve floristic diversity, arthropod habitat, or herbivore fodder. Deep crowns with large branches also provide better roosting habitat for wildlife such as the turkey, northern goshawk, northern flying squirrel, and fisher (Boeker and Scott 1969; Hagar 2007). Also, large branches are ecologically important because they eventually add to a suite of forest floor processes once the branches are shed (Harmon et al. 1986). These branches become coarse woody debris that persist exponentially longer than fine branch material, providing heterogeneous structure for plant and invertebrate detritivores that drive nutrient cycling (Franklin et al. 2002). Although these stands have a long way to go to emulate the open-canopied uneven-aged structure of fire-maintained old-growth, branch development is here accelerated by thinning-based fuel treatment and restoration (similar to Keyes 2011) in a manner that transitions these stands into a position to provide for the ecological processes and habitat needs for complex structures in older forests.

These treatments were not intended to be isolated entries, but rather the first of a multi-entry, treatment regime management strategy, as advocated by Reinhardt et al. (2008). Treatment regimes are a necessary reality (whether or not they are planned for) in dry, fire-prone forests where wildfire is continually excluded. However, treatment regimes require financial remuneration, which in turn is directly affected by how treatments cause tree dimensions to vary. Typically, thinning improves diameter growth, increases the amount of extractable volume per tree, and concentrates stand volume on fewer, more valuable trees than in the unthinned

treatments. But thinning for fuel reduction is often severe. As our study suggests, severe thinning improves diameter growth, but increases crown length and width development, extends lower limb retention, and will increase knot presence and size in potential boards (Maguire et al. 1991; Nyland 2016, p. 439). So although thinning-based fuel reduction and restoration treatments increase the extractable product per tree, the quality of extracted timber could potentially detract from final value.

It is interesting to note that starting size did not significantly influence pine dbh or crown surface area growth. This may mean that the treatment had such a strong effect on this population that the average tree in any given size class grew the maximum average physical limit (“free growth”). That these trees are free-to-grow is supported by traditional understanding of density-dependent competition measures as interpreted by density management metrics. Long and Shaw (2005) identify a free-to-grow developmental period when relative density is less than 25% of a species’ maximum (cf 15% in Drew and Flewelling 1979). In this study, the average thin-only stand had a relative density of 20.5% in 2001 and has reached 26.6% as of 2014; thin + burn stands began at 15.9% and have grown to 20.0% of maximum relative density using Reineke’s Stand Density Index (Reineke 1933). In contrast, all of the unthinned stands started the measurement period with relative densities between 40% and 50%. Particularly where treatments create homogeneous structure, planning fuel reduction and restoration treatments can be improved by considering growing stock levels and stand development stages using density management diagrams.

Fuel reduction and tree resistance

Bark thickness and resistance to cambial kill is dependent on both species and tree diameter (Ryan and Reinhardt 1988; Jones et al. 2006). Fuel reduction and restoration treatments

are specifically designed to retain individual trees that have improved resistance (i.e., thick bark) to fire. Both our ponderosa pine and Douglas-fir bark thickness models show that thickness increases with initial tree size. However, after controlling for differences in initial tree size, we found no additional effect of thinning or burning on bark thickness. This model analysis masks that tree size increased more rapidly in thinning-based treatments. Our study supports that thinning improves tree growth and that larger trees are associated with thicker bark. Thicker bark confers improved resistance to surface fire because it insulates stem cambium (Pausas 2015), therefore this study indirectly indicates that thinning-based fuel reduction treatment improves surface fire resistance. Public land management agencies are constantly looking for metrics by which to monitor and evaluate tree and stand resistance to future fire. High average tree bark thickness is one metric that managers can use that is not only meaningful, but attainable with thinning-based fuel treatments via their positive effects on diameter distributions and tree growth.

Previous research has identified a height:diameter threshold ratio of approximately 80:1 above which individual tree damage is most common (Cremer et al. 1982; Wonn and O'Hara 2001). Additionally, tree diameter itself is a powerful predictor of resistance to breakage, with resistance proportional to the cube of dbh (Peltola 2006). Since diameter growth is influenced by stand density but often times height is not, height:diameter ratios should vary with treatment and have direct ramifications for tree resistance to snow and wind breakage. Our models showed that the study's trees have low susceptibility to breakage (ratio less than 80), but that burning further increased resistance to breakage in ponderosa pine. This was due to a non-significant decrease in tree height growth that, when paired with diameter growth, caused the height:diameter ratio to be marginally influenced by burning. In other words, tree resistance to snow and wind breakage was

increased by burning because burning more positively impacted dbh than height. Our results are difficult to corroborate because most prescribed burning studies do not assess the effects of burning on height, particularly in the West. In Oregon, one study that assessed height growth found a negative effect of burning on height (Landsberg 1992), however, Busse et al. (2000) show reduced tree basal area increment but no impact on height. Boyer (1987) amassed a number of sources from the Southeast that supported his finding that frequent burning diminished height growth in southern pine plantations, yet he found no mechanistic explanation. Clearly the holistic effects of burning on tree growth and attributes need to be further studied.

Although growth efficiency is not a direct resistance metric, Waring (1983) identified that it is a “sensitive indicator to environmental stresses” and that increased growth efficiency is associated with decreased tree stress and increased resistance to disease and insect attack. Fuel reduction and restoration treatments do not typically report values for tree growth efficiency as a treatment response, but we might expect that trees released to wide spacing become inefficient because of the lack of competitive pressure (O’Hara 1988). However, our models corroborate that thinning, even as a fuel reduction treatment, results in greater growth efficiency in ponderosa pine (Oren et al. 1987; Fajardo et al. 2007; but see McDowell et al. 2007). Thinning may improve ponderosa pine growth efficiency because it is a shade-intolerant species that thrives in full sun, which the thinning treatments provide by overstory removal. Furthermore, in water-limited ponderosa pine systems, thinning treatments permit trees to invest more in secondary growth, carbon storage, or resins because there is less belowground competition for water (Breda et al. 1995; Kolb et al. 1998). We also found that burning was associated with improved growth efficiency in Douglas-fir. Burning would improve efficiency where crown scorch caused the tree to compensate for foliage loss (Wallin et al. 2003). Alternatively, burning may improve

efficiency by mobilizing nitrogen on the forest floor or simply by removing competition. This effect of burning has not been adequately explored in the literature and merits further research.

Comment on beetle-induced mortality

These data demonstrate that fuel reduction treatments have lasting effects on residual tree growth and attributes. These comparisons were only made possible after removing model variance attributable to factors apart from the experimental design: namely, initial tree size of the respective attribute and local bark beetle-induced mortality, as approximated by dead basal area. On one hand, we limited inference about these elements because it is not within our treatment-focused scope. On the other hand, however, we have largely ignored them because this analysis is insufficient to fully explore their role in the growth of tree components. For instance, tree size often has a non-linear influence on growth, but our models only attributed a simple linear effect to initial size, masking the more nuanced detail. As for bark beetle influence, we were unable to fully attribute tree death to bark beetles, because mortality agent was not recorded in this study (but see Hood et al. 2016). Therefore we have focused interpretation of our results on the role that thinning and burning played in moderating tree morphology.

Conclusion

Combined fuel reduction and restoration treatments are common across the western United States because of limited proactive management budgets. Despite being principally engineered to improve stand-level resistance to future surface fire and avoidance of crown fire, treated areas are almost always multiple-use forests that have a variety of objectives. It is important to consider how these treatments influence objectives other than crown fire hazard reduction. Large trees, in particular, are important structural components to many management

objectives. Treatment influence on large trees will subsequently impact stand development and ecology, wildlife use, and potential for economic returns.

Overall we found that tree morphology varied by fuel reduction type. Specifically, thinning-based fuel reduction caused tree stems to grow broader (not taller), and caused ponderosa pine crowns to increase in size altogether. Burning, however, had no effect on measured tree growth. These results do not validate the effectiveness of fuel reduction treatments to reduce crown fire hazard, but they do show the dominant effect of severe thinning-based treatments on growth. Differences in morphological growth rates may have practical impacts on fuel, economic, or ecological objectives that may guide managers' choice in restorative fuel treatment type. Furthermore, these trends may cause unexpected results as we scale up from the tree to consider stand-level growth metrics.

Tree attributes that may confer resistance also varied by fuel reduction treatment, and were influenced by both thinning and burning. Thinning-based fuel reduction indirectly improves bark thickness via increased dbh growth, which should improve tree resistance to surface fire. Thinning increases growth efficiency, which should help trees resist biotic disturbance agents. Broadcast burning had differential effects on tree attributes. It reduced ponderosa pine height:diameter, which likely improves resistance to wind and snow breakage. Burning also improved Douglas-fir growth efficiency, which should further improve resistance to biotic disturbances. These results highlight that fuel reduction treatments have a positive impact on metrics that confer tree resistance to at least three types of disturbances, portending greater potential for long-term persistence and success in a suite of management goals.

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Table 1. Live stand summary statistics for Lubrecht's Fire and Fire Surrogate Study across measurement years. Data presented are aggregated means of experimental units and 1 standard error. Note that 2001 date is post-harvest but pre-burn, and that insect outbreak occurred between the 2005 and 2014 measurement.

Attribute	Treatment	2001	2005	2014
Density (trees ha ⁻¹)	Control	432 (46)	426 (48)	293 (58)
	Burn-only	411 (10)	385 (7)	265 (40)
	Thin-only	170 (19)	170 (19)	168 (21)
	Thin+Burn	109 (12)	106 (10)	95 (9)
Basal area (m ² ha ⁻¹)	Control	22.3	23.2	16.4
		(4.6)	(4.7)	(4.8)
	Burn-only	19.1	19.1	15.7
		(1.8)	(1.1)	(3.2)
		9.9 (0.3)	11.0	13.6
Thin-only	(0.3)	(0.3)	(0.3)	
Thin+Burn	8.0 (1.1)	8.5 (1.3)	9.9 (1.5)	
Quadratic mean diameter (cm)	Control	26.5	27.3	26.9
		(2.4)	(2.3)	(2.2)
	Burn-only	24.7	25.5	27.3
		(0.9)	(0.9)	(2.5)
		28.7	30.3	34.1
	Thin-only	(1.6)	(1.7)	(2.0)
Thin+Burn	27.8	29.3	34.2	
	(2.1)	(2.0)	(0.6)	
Reineke's (1933) Stand Density Index (metric units)	Control	431 (79)	444 (81)	311 (88)
	Burn-only	377 (29)	373 (14)	293 (56)
	Thin-only	185 (6)	202 (6)	240 (8)
	Thin+Burn	142 (18)	149 (21)	179 (31)

*Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638.

Table 2. Linear mixed-effects model coefficients for individual tree (DBH > 25.4 cm) growth. Annual growth refers to surviving tree growth from 2001 to 2014. P-values less than 0.100 are in boldface. “(Intercept)” coefficient refers to the Control treatment.

Species	Coefficient	Annual stem change responses						Annual crown change responses					
		DBH		Height		Volume		Length		Width		Surface Area	
		Estimate	p value	Estimate	p value	Estimate	p value	Estimate	p value	Estimate	p value	Estimate	p value
Pinus ponderosa	(Intercept)	0.243	<0.001	0.288	<0.001	-0.001	0.740	0.205	0.003	0.062	0.026	1.322	0.233
	Beetle severity	0.001	0.907	0.016	0.034	0.001	0.125	0.003	0.773	0.009	0.059	0.311	0.190
	Initial size	-0.001	0.771	-0.002	0.008	0.001	<0.001	-0.003	0.004	-0.002	0.048	<0.001	0.360
	Thinned	0.253	0.002	0.076	0.130	0.019	0.006	0.154	0.014	0.054	0.064	3.418	0.019
	Burned	0.031	0.560	-0.068	0.163	-0.003	0.529	-0.052	0.290	-0.014	0.568	-1.209	0.305
	ThinnedxBurned	-0.032	0.651	0.062	0.323	<0.001	0.993	-0.001	0.992	-0.010	0.772	-0.611	0.678
	<i>Marginal R²</i>	0.39		0.23		0.57		0.29		0.15		0.24	
	<i>Conditional R²</i>	0.63		0.54		0.79		0.48		0.30		0.46	
Pseudotsuga menziesii	(Intercept)	0.181	<0.001	0.528	<0.001	0.010	0.006	0.284	0.004	0.059	0.254	1.552	0.288
	Beetle severity	0.009	0.006	0.004	0.478	0.001	0.072	-0.021	0.291	-0.014	0.126	-0.542	0.211
	Initial size	0.007	0.001	-0.006	<0.001	0.000	<0.001	-0.005	0.023	-0.002	0.386	<0.001	0.505
	Thinned	0.199	0.005	-0.057	0.534	0.005	0.374	0.093	0.096	0.019	0.634	1.697	0.193
	Burned	0.024	0.415	-0.074	0.309	-0.003	0.411	-0.047	0.371	0.022	0.546	-0.444	0.709
	ThinnedxBurned	-0.047	0.393	0.144	0.277	0.007	0.359	-0.058	0.407	-0.022	0.693	-1.466	0.404
	<i>Marginal R²</i>	0.44		0.25		0.34		0.30		0.08		0.17	
	<i>Conditional R²</i>	0.60		0.63		0.53		0.35		0.36		0.52	

Table 3. Average tree resistance attributes by treatment. Mean and 1 standard error shown.

Species	Attribute	Treatment	All size classes	Only dbh > 25.4 cm
Pinus ponderosa	Height:diameter (m m ⁻¹)	Control	67.5 (3.7)	58.8 (6.0)
		Burn-only	67.3 (1.2)	51.5 (3.2)
		Thin-only	56.5 (2.7)	52.9 (1.9)
		Thin+Burn	57.2 (1.7)	54.1 (1.7)
	Bark thickness (cm)	Control	1.68 (0.07)	2.89 (0.14)
		Burn-only	1.87 (0.14)	2.86 (0.08)
		Thin-only	1.99 (0.09)	2.76 (0.20)
		Thin+Burn	2.34 (0.2)	2.80 (0.30)
	Growth efficiency (cm ² cm ⁻²)	Control	0.52 (0.01)	0.19 (0.01)
		Burn-only	0.46 (0.04)	0.22 (0.01)
		Thin-only	0.48 (0.09)	0.30 (0.01)
		Thin+Burn	0.58 (0.21)	0.37 (0.03)
Pseudotsuga menziesii	Height:diameter (m m ⁻¹)	Control	64.9 (1.2)	58.1 (2.4)
		Burn-only	61.9 (3.2)	54.8 (1.3)
		Thin-only	59.1 (0.6)	53.7 (0.8)
		Thin+Burn	55.3 (2.5)	49.9 (4.5)
	Bark thickness (cm)	Control	1.64 (0.04)	2.00 (0.04)
		Burn-only	1.71 (0.19)	2.19 (0.23)
		Thin-only	1.38 (0.22)	1.69 (0.24)
		Thin+Burn	2.24 (0.27)	2.58 (0.29)
	Growth efficiency (cm ² cm ⁻²)	Control	0.66 (0.07)	0.58 (0.07)
		Burn-only	0.75 (0.01)	0.62 (0.04)
		Thin-only	0.8 (0.13)	0.55 (0.06)
		Thin+Burn	0.83 (0.04)	0.72 (0.08)

Table 4. Linear mixed-effects model coefficients for individual tree (DBH > 25.4 cm) disturbance resistance metrics (height:diameter, bark thickness, and growth efficiency). “(Intercept)” coefficient refers to the Control treatment.

Species	Coefficient	Height:dbh (m m ⁻¹)		Bark thickness (cm)		Growth efficiency (cm ² cm ⁻²)	
		Estimate	p value	Estimate	p value	Estimate	p value
Pinus ponderosa							
	(Intercept)	79.416	<0.001	1.738	<0.001	0.407	<0.001
	Beetle severity	0.242	0.520	0.062	0.056	0.006	0.257
	Initial dbh	-1.657	<0.001	0.063	<0.001	-0.015	<0.001
	Thinned	-1.642	0.514	-0.118	0.691	0.135	0.003
	Burned	-4.529	0.099	-0.066	0.821	0.021	0.488
	Thinned×Burned	2.877	0.398	0.134	0.743	-0.023	0.563
	<i>Marginal R²</i>	0.49		0.20		0.41	
	<i>Conditional R²</i>	0.68		0.54		0.48	
Pseudotsuga menziesii							
	(Intercept)	83.245	<0.001	0.587	0.020	0.751	<0.001
	Beetle severity	-0.021	0.937	0.000	0.974	0.031	<0.001
	Initial dbh	-2.260	<0.001	0.093	<0.001	-0.017	0.004
	Thinned	-8.103	0.124	-0.170	0.572	0.144	0.070
	Burned	-2.732	0.442	0.132	0.560	0.120	0.051
	Thinned×Burned	6.858	0.296	0.583	0.199	0.015	0.877
	<i>Marginal R²</i>	0.47		0.35		0.24	
	<i>Conditional R²</i>	0.78		0.50		0.31	

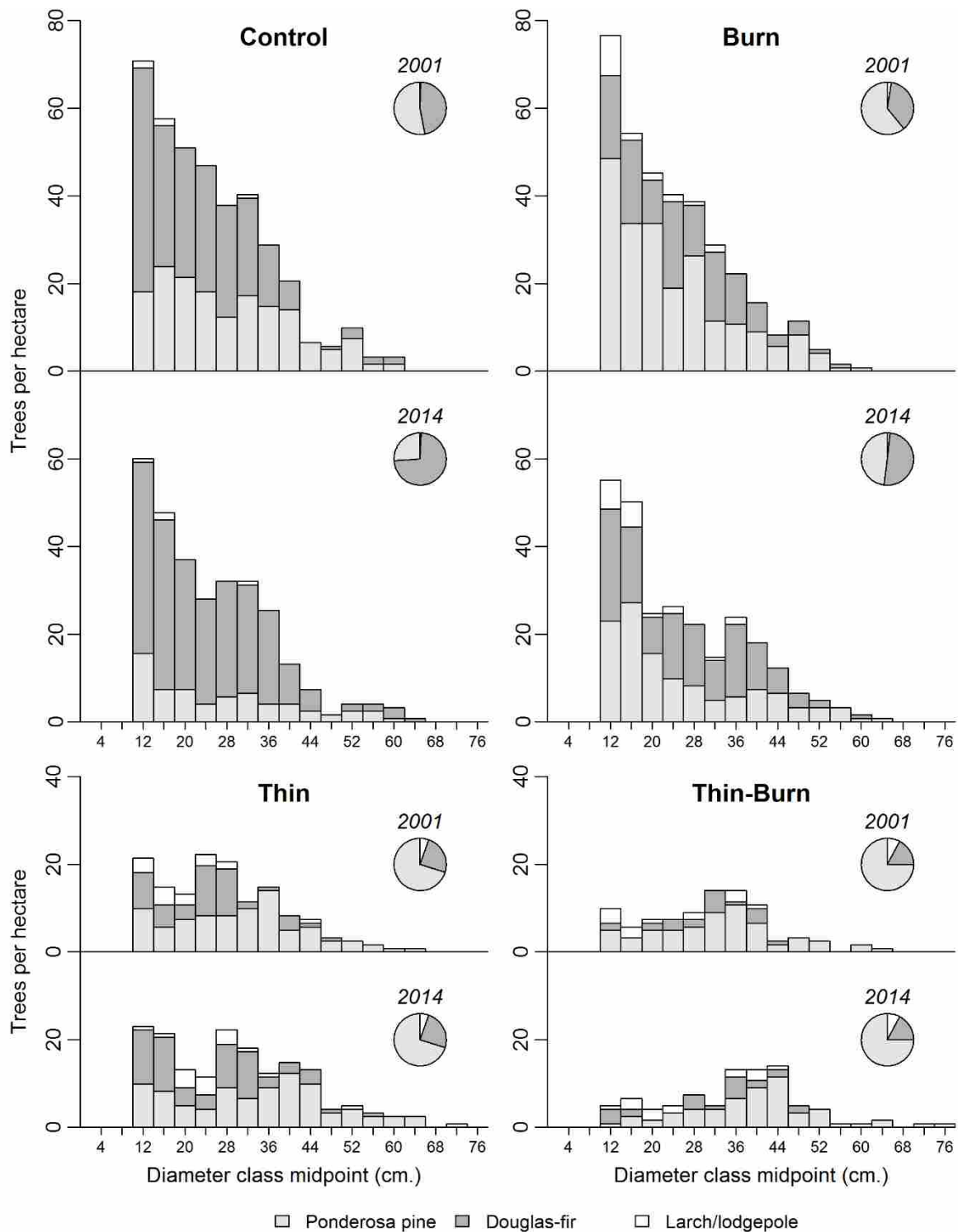


Figure 1. 2001 and 2014 live tree diameter distributions by treatment, year, and species. Stacked bars show stem density by 4 cm classes (blocks pooled). Inset pie charts represent proportional basal area by species. Understory trees (less than 10 cm dbh) are not shown.

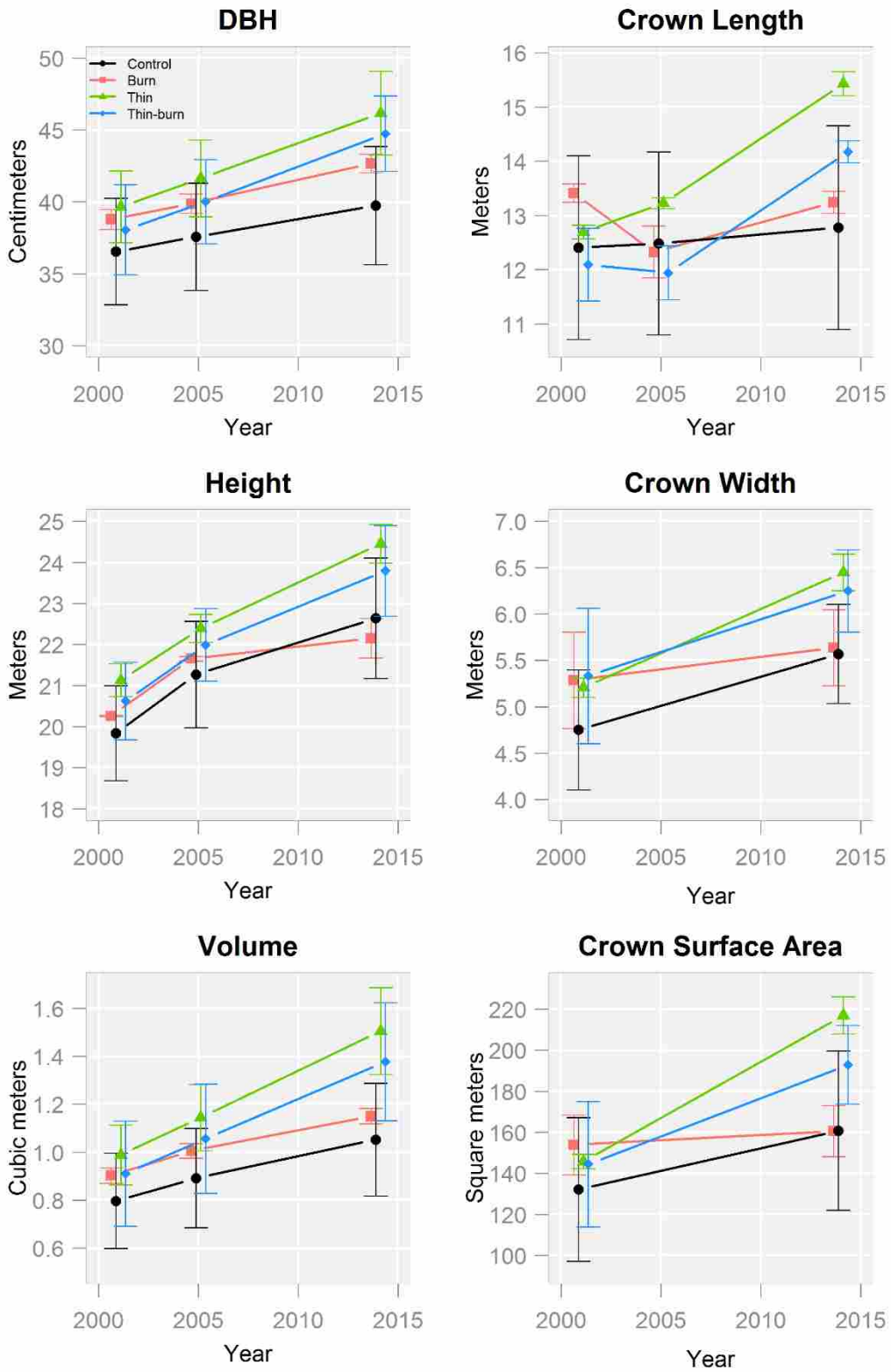


Figure 2. Stem and crown dimensions by treatment and year for ponderosa pine greater than 25.4 cm dbh.

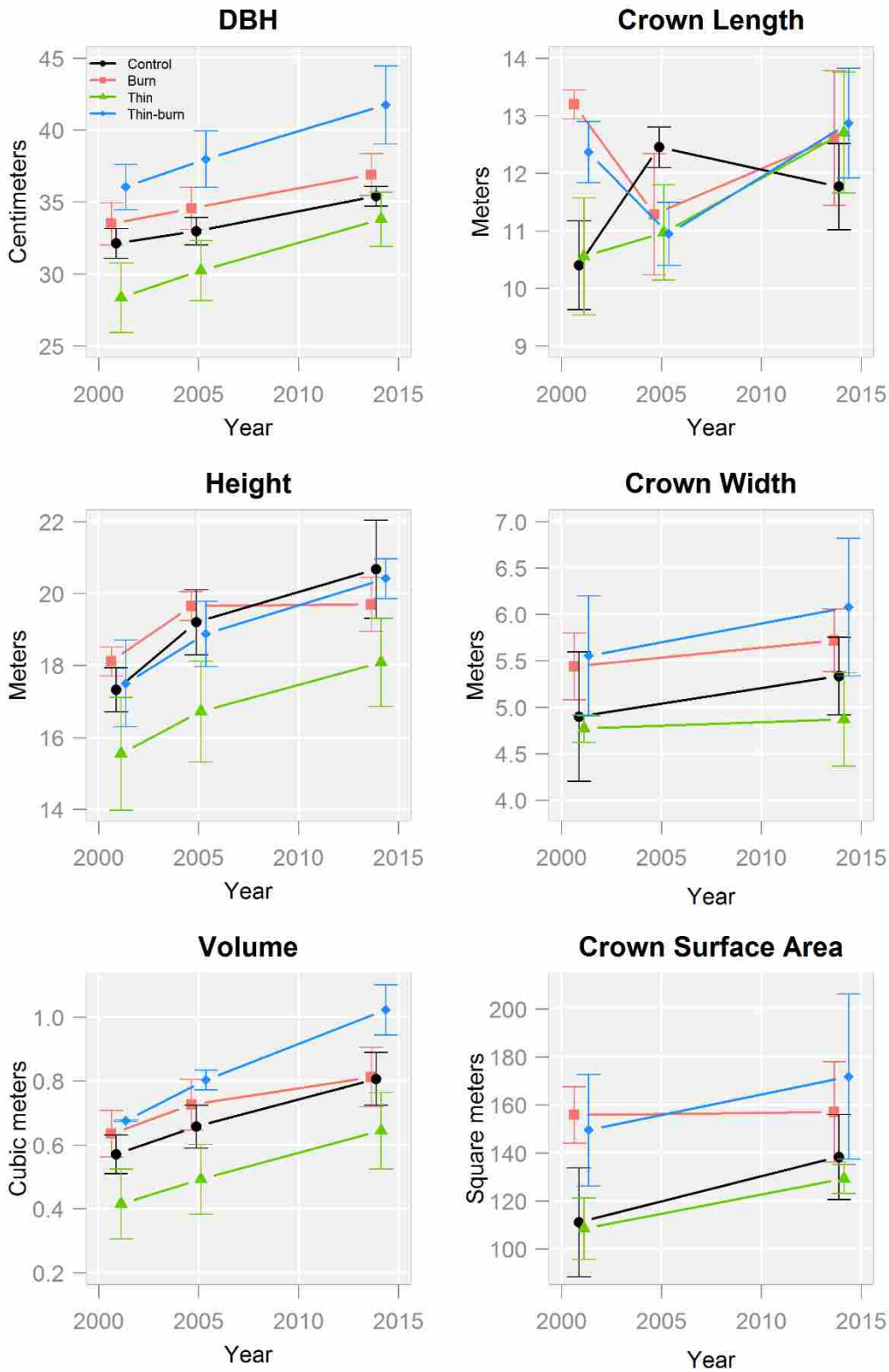


Figure 3. Stem and crown dimensions by treatment and year for Douglas-fir greater than 25.4 cm dbh.

Chapter 3: Forest fuels and crown fire hazard after combined fuel reduction treatments and bark-beetle outbreak

Abstract

Fuel reduction treatments have been widely implemented across the Western U.S. in recent decades for fire protection and restoration purposes. Although research has demonstrated that combined thinning and burning effectively reduces crown fire hazard in the few years immediately following treatment, very little research has identified the mid-term effectiveness of thinning and burning treatments. Furthermore, it is also unclear how post-treatment disturbances in treated areas, such as widespread bark beetle outbreak, affect fuel treatment effectiveness. We used an experiment to test the differences in fuel loads and crown fire hazard between fuel reduction treatments (no-action Control, Burn-only, Thin-only, Thin+Burn) that were affected by mountain pine beetle outbreak approximately five years after implementation. Stands were measured in 2002 (immediately following fuel treatment) and 2016 (14 years after treatments and at least 4 years following beetle outbreak). We found that beetle-altered thinned treatments (Thin-only and Thin+Burn) had overall less fuel and lower crown fire hazard than corresponding unthinned treatments. The post-beetle effects of burning (Burn-only and Thin+Burn) were initially milder than those of thinning, but burning still reduced crown fire hazard over unburned stands 14 years after treatment. Additionally, we used mediation analysis to determine the relative impacts of silviculture and beetle outbreak on treatment differences for those metrics. Beetle kill inflated differences between Controls and thinned units for surface fuel loads and probability of torching, but diminished differences between these treatments for canopy fuel

loads, bulk density, and crowning index. Despite a muting effect that beetle outbreak and time had on some fuel and crown fire hazard metrics, our study suggests that the effects of silvicultural treatment on mitigating crown fire hazard persist even after stand-transforming insect outbreaks, especially when thinning and burning are combined.

Introduction

Forest managers use fuel reduction treatments to regulate potential wildfire behavior, especially to reduce the probability of crown fire. Many restoration efforts in fire-prone ecosystems include restorative fuel reduction strategies to reverse the effects that fire exclusion has had on forest fuels, structure, and composition (Brown et al. 2004; Fulé et al. 2012). However, forest structural development in the years following treatment may compromise the effectiveness of treatment to resist crown fire (Keyes and Varner 2006; Affleck et al. 2012; Tinkham et al. 2016). Furthermore, forests are exposed to multiple disturbances and stressors (Bebi et al. 2003; Bigler et al. 2005), and despite specific management objectives to improve stand resistance to fire, treated stands are subject to various disturbance agents besides fire. Understanding how treated stands develop with time and in response to disturbance such as beetle outbreak has important implications for fuel treatment effectiveness and longevity in light of original management objectives.

Fuel reduction treatments are designed to reduce crown fire hazard and increase resistance to that disturbance. Fire exclusion and unchecked ingrowth over the past century have elevated surface and canopy fuel loads in the Western U.S. (Parsons and DeBenedetti 1979; Covington and Moore 1994; Keeling et al. 2006). Increased fuel loads in conjunction with warmer and drier climate have caused wildfires to increase in size and contiguity, and cost to

protect resources have grown accordingly (Westerling et al. 2006; Flannigan et al. 2009; Miller et al. 2009). Crown fire threatens human safety and property, and, in forest types where crown fire is uncharacteristic, it also threatens ecological resilience. Fuel reduction is a proactive treatment that alters potential fire behavior by removing and modifying forest fuels to encourage low-severity (low overstory mortality) surface fire instead of crown fire (high overstory mortality). Fuel treatments reduce surface fuel loads, reduce canopy density, increase height to canopy base, and retain large, fire resistant trees (Agee and Skinner 2005; Hessburg et al. 2015). Although these goals can be attained with various silvicultural techniques, thinning and burning are the most typical means of fuel reduction. The relative effectiveness of thinning and burning to reduce crown fire hazard have been thoroughly studied immediately after treatment (Stephens and Moghaddas 2005; Harrington et al. 2007; Stephens et al. 2009; Fulé et al. 2012; McIver et al. 2012a), generally highlighting that burning reduces surface fuels, thinning improves forest structure, and the combination of the two best reduces crown fire hazard.

However, fuel reduction treatments are only temporarily effective (Reinhardt et al. 2008). As fuel treatments age, regeneration, ingrowth, and residual trees grow into open space and increase fuel load and crown fire hazard (Keyes and O'Hara 2002; Keyes and Varner 2006; Affleck et al. 2012). Although stimulated growth and regeneration are expected to follow treatment, it is still unclear how long treatments remain effective (though see Finney et al. 2005; Fernandes 2009; Jain et al. 2012; Stephens et al. 2012; Tinkham et al. 2016). Understanding of treatment longevity is especially important where logistics and economics limit successive treatment.

Fire suppression, past management, and warming climate have increased crown fire hazard in the West, but they have also been attributed to abetting recent insect outbreaks (Raffa

et al. 2008; Bentz et al. 2010). Recent bark beetle episodes in the late 1990s to 2012 have profoundly affected a suite of forest types., killing 5.6% of the forested area in the Western U.S. (Hicke et al. 2016). After trees are selectively killed by bark beetles, fire is one of the primary concerns for managers because mortality alters fuel profiles. Canopy and surface fuel profiles change immediately after and in the few years following tree death (British Columbia Ministry of Forests 2004), as foliage transitions from green to red to gray phases on the tree, then progressively falls to the forest floor with accompanying limbs and stems. The impact of beetle outbreak on potential fire in unmanaged forest landscapes has been a controversial topic, requiring nuanced assessment of fire behavior, hazard, and effects (Jenkins et al. 2008, 2014; Simard et al. 2011; Harvey et al. 2013; Hart et al. 2015; Kane et al. 2017).

Where bark beetle outbreaks are widespread, they can also directly impact stands previously managed for crown fire resistance with fuel reduction treatments. The relationship between fuel reduction treatments and beetle outbreaks remains largely uncharacterized. A few studies have identified that fuel treatments may moderate beetle-caused mortality by reducing vegetative competition (Fettig et al. 2010; Jenkins et al. 2014; Hood et al. 2016). Conversely, beetle-caused mortality may moderate fuel treatments by altering fuel loads and vegetative competition, depending on foliage phase. In unmanaged stands, gray-phase mortality may reduce active crown-to-crown fire transfer and torching probability by reducing crown fuel load (Simard et al. 2011), similar to a fuel treatment. But beetle-caused mortality can increase surface flame lengths, spotting, and residence times, exacerbating fire severity and residual crown fire hazard (Moran and Cochrane 2012; Jenkins et al. 2014). In treated stands, which densify and become more prone to crown fire over time, beetle outbreak may likewise maintain fuel treatment effectiveness by reducing crown fire hazard, or it may render treatments useless to their original

objective by increasing crown fire hazard. Knowledge of fuels and crown fire hazard throughout the forest is valuable for safety assessment, inventory, and planning, but differences between treated and untreated stands are especially valuable for determining resilience of active management objectives to subsequent disturbance.

The purpose of this study is to understand how silvicultural fuel reduction and subsequent bark-beetle outbreak influence fuel and potential for crown fire. We utilize the *Pinus ponderosa/Pseudotsuga menziesii* forest of the northern Rocky Mountains' Fire and Fire Surrogate Study (McIver and Weatherspoon 2010) as a balanced experimental design to contrast fuel reduction treatments (no-action, burn-only, thin-only, thin+burn). Our sites were fully treated by 2002, approximately five years before a widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak that overlapped all experimental units. We analyze data from 14 years after silvicultural treatment and at least 4 years after beetle outbreak with the specific objectives to determine: (1) the combined silviculture and beetle outbreak effects on fuel loads over time; (2) the combined silviculture and beetle outbreak effects on a suite of crown fire hazard metrics over time; and (3) the relative effects of silviculture and beetle-caused mortality on treatment differences in fuel load and crown fire hazard. This study uniquely showcases the impact that time and beetle outbreak have on restorative fuel treatments, demonstrating how beetle-caused mortality interacts with the development of potential fire hazard in treated versus untreated stands.

Methods

Study site

This study was conducted at the University of Montana's Lubrecht Experimental Forest (46°53'N, 113°26'W), an 11,300 ha forest in western Montana's Blackfoot River drainage of the

Garnet Range. Study sites range in elevation from 1,230 to 1,388 m ASL, and are comprised of *Pseudotsuga menziesii/Vaccinium caespitosum* and *Pseudotsuga menziesii/Spiraea betulifolia* habitat types (Pfister et al. 1977). This forest is generally composed of second-growth ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), with western larch (*Larix occidentalis* Nutt.) regenerated from heavy cutting in the early 20th century. Soils are fine or clayey-skeletal, mixed, Typic Eutroboralfs, as well as loamy-skeletal, mixed, frigid, Udic Ustochrepts (Nimlos 1986).

Climate in this study area is maritime-continental. Annual precipitation is approximately 460 mm (PRISM Climate Group, 4 km resolution), nearly half of which falls as snow. Mean temperatures range from -6°C in December and January to 17°C in July and August. Average plant growing season is between 60 and 90 days. Historic fire frequency at Lubrecht prior to the 20th century ranged from 2 to 14 years, with a mean composite fire return interval of 7 years (Grissino-Mayer et al. 2006).

Silvicultural activities and beetle “treatment”

The Lubrecht Experimental Forest was selected as a site for the Fire and Fire Surrogate Study, a multidisciplinary research project that aimed to quantify the short-term effects of restorative fuel reduction treatments in frequent-fire forests across the US (Weatherspoon 2000; McIver and Weatherspoon 2010). The study provides a framework to examine the effects of common fuel treatments on treatment longevity, fuel development, and potential fire behavior. Treatments were implemented in each of three blocks using a randomized factorial design: two levels of thinning (thinned and unthinned) by two levels of prescribed burning (burned and unburned), for a total of four treatment levels (no-action control, thin-only, burn-only,

thin+burn). Prescription intensity was designed to maintain 80% overstory tree survival given a wildfire in 80th percentile weather conditions (Weatherspoon 2000). Stands were cut in 2001 and burned in 2002, creating twelve 9 ha experimental units. The cutting prescription was a combined low thinning and improvement cut to a residual basal area of 11.5 m² ha⁻¹, favoring retention of ponderosa pine and western larch over Douglas-fir (Metlen and Fiedler 2006). Burning treatments were spring burns with windspeeds less than 13 km hr⁻¹. Burns were generally low severity, with pockets of high severity in two of the thin+burn treatments. Fiedler et al. (2010) analyzed treatment effect on stand structure and short-term growth, and Stephens et al. (2009) summarized short-term woody fuel and potential fire behavior responses to treatment across western Fire and Fire Surrogate sites.

Not long after measurements of short-term treatment responses were completed, beetle populations (primarily MPB) rose to outbreak levels in Montana (Gannon and Sontag 2010). Beetle-caused overstory mortality levels were high in Control and Burn-only units over the course of 2006 to 2012 (Hood et al. 2016), leading to similar live ponderosa pine basal area across all treatments. After the outbreak, therefore, changes in fuel loads, fire hazard, productivity and stand dynamics are no longer a pure effect of fuel reduction treatments, but rather of the combination of fuel reduction treatments and beetle-caused mortality. This beetle outbreak grants the opportunity to assess a novel but increasingly common condition in the West: fuel reduction treatment followed by MPB outbreak. Therefore, the meaning of “treatment” in this study changes with measurement year. Before beetle outbreak, “treatment” refers to the silvicultural fuel reduction treatment. Afterwards and unless otherwise noted, “treatment” refers to fuel reduction followed by MPB outbreak.

Field Methods

Live trees were measured twice on permanently monumented plots in the Fire and Fire Surrogate Study. Trees were initially measured the year after treatment (measured in 1999 for Control, 2001 for Thin-only, 2002 for Burn-only and Thin+Burn) on 0.10 ha rectangular modified-Whittaker plots (Shmida 1984; Metlen and Fiedler 2006). These were 10 randomly selected plot locations from 36 systematically located grid points within each treatment unit, making for a total of 120 plots. For each mature tree (diameter at breast height [dbh; 1.37 m] greater than 10.16 cm), species, dbh, total height, and height to the base of live crown were recorded. Height to the base of live crown was the estimated average branch height of the compacted lower limit of the crown (US Forest Service 2005). Trees smaller than 10.16 cm dbh but taller than 1.37 m were measured on five, 100 m² subplots; trees between 0.10 and 1.37 m tall were measured on twenty, 1 m² subplots. In 2014 we sampled mature trees according to measurement protocol above, but restricted the sample to 0.04 ha circular plots overlaid on the Whittaker plot centers, measuring a subset of trees from each of the study's 120 plots. Trees smaller than 10.16 cm dbh were measured in 2016 using the original Whittaker subplot protocol outlined above.

Dead surface fuels were first measured the year after treatment (same years as above) using a mixture of planar intercept and destructive sampling. A modified Brown's (1974) protocol was used to quantify 1-hr (material < 0.64 cm diameter), 10-hr (0.64 cm ≤ diameter < 2.54 cm), 100-hr (2.54 cm ≤ diameter < 7.62 cm), and 1000-hr+ (diameter ≥ 7.62 cm) timelag classes. On each of the 36 grid points, two 15.2 m transects were established; 1-hr and 10-hr fuels were tallied for 1.8 m of the length, 100-hr fuels were tallied for 3.7 m, and 1000-hr+ fuel diameters were recorded along the entire transect lengths. Duff and litter depths were measured

at two points along transects. In the Thin-only and Thin+Burn treatments, 1-hr, 10-hr, litter, and duff materials were not measured along transects but destructively sampled on two, 1 m² quadrats. These materials were taken to the lab, oven dried, and weighed to determine load by fuel type. In 2016, we remeasured dead surface fuels using the original modified Brown's transects for all 36 grid points in all of the treatment units.

For simplicity's sake, the above datasets will be referred to by the last year of measurement. Namely, "2002" for the collective immediate post-treatment dataset, and "2016" for the post-beetle-outbreak dataset. By the time of final measurement, stands were in the post-epidemic, leaf-off, gray phase of the MPB rotation (Jenkins et al. 2008).

In addition to the 2002 and 2016 datasets, we supplemented our dataset with data measured and analyzed by Hood et al. (2016). Using the same Whittaker plot tree measurement protocol described above, they measured MPB-caused mortality to the overstory between 2006 and 2012. We appended our dataset with their measure of plot-scale beetle outbreak severity (overstory stems ha⁻¹).

Analytical and statistical methods

We calculated dead surface fuel loads according to Brown (1974), but used site specific depth-to-load regressions to calculate duff load (M. Harrington, *unpublished data*). Dead and downed debris were segregated into three pools for analysis: fine woody debris comprised fuel less than 7.62 cm diameter (1-hr, 10-hr, and 100-hr); coarse woody debris comprised sound fuel greater than or equal to 7.62 cm diameter (1000-hr); and forest floor comprised litter and duff layers. Fuels data and tree lists were input into the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS; Dixon, 2002; Rebas, 2010) to calculate plot-scale forest conditions and potential fire hazard metrics for our two measurement years. We estimated fire

behavior using the standard FFE-FVS method, whereby measured dead fuel loads are compared to Albini's (1976) 13 original fire behavior fuel models, and the algorithm selects and weights predicted fire behavior from one to two most similar models (Rebain 2010). Potential fire behavior and crown fire hazard metrics were based on FFE-FVS's default "severe" fire weather scenario (4% 10-hr fuel moisture, 21.1° C ambient temperature, and 32.2 km hr⁻¹ windspeed at 6.1 m) instead of percentile (e.g., 80th or 95th) fire weather conditions to provide standardized analysis. Output gathered from FFE-FVS included canopy fuel load (live and dead foliage and branchwood), potential fire behavior (fire type and surface flame length), and crown fire hazard (canopy base height, canopy bulk density, probability of torching, and crowning index) calculations.

We used nested ANOVA to investigate if treatment (and treatment) influences fuel loads and crown fire hazard states in 2002 and 2016. In this study, plot is nested within experimental unit which is nested within a block. We performed this analysis using the `anova.lme` function in R's `nlme` package (Pinheiro et al. 2016; R Core Team 2016). ANOVA models had the form:

$$\hat{y}_{ijkl} = \mu + \alpha_i + \beta_j \times \gamma_k + \varepsilon_{ijk} + \delta_{ijkl}$$

where \hat{y} is the plot-scale response variable (2002 and 2016 fine woody debris, coarse woody debris, forest floor, canopy fuel, canopy base height, canopy bulk density, probability of torching, and crowning index), μ is the grand mean, α_i is the block effect (levels 1-3), β_j is the prescribed burn effect (levels not burned and burned), γ_k is the thinning effect (levels not thinned and thinned), ε_{ijk} is the experimental unit error term, and δ_{ijkl} is the residual error term associated with plots. Although the block effect would ideally be treated as a random effect, we considered it a fixed effect in this model because there were only three factor levels, therefore, only experimental unit was treated as a random effect.

Next, we used linear mixed effects regression to determine the effect that treatment has on the development of fuel loads and crown fire hazard over time. This was done using the `lme` function in `nlme`. Regression models had the same structure as the nested ANOVA model, except that \hat{y} is the change in plot-scale response variable (fine woody debris, coarse woody debris, forest floor, canopy fuel, canopy base height, canopy bulk density, probability of torching, and crowning index) from 2002 to 2016.

Finally, we conducted mediation analyses to parse out the effects of silvicultural manipulation and beetle outbreak on those fuel and crown fire hazard metrics. In mediation analysis, the goal is to characterize the direct effect of X on Y , the indirect effect of X on Y as mediated by M , and the total effect of X on Y given mediation (Figure 1; Baron and Kenny 1986; MacKinnon et al. 2007). We note that direct effect does not refer to X without M on Y , but X on Y not explained by the indirect pathway through M . Coefficients are derived by fitting two statistical models: $Y = f(X, M)$, and $M = f(X)$. The direct effect is quantified as the regression coefficient of the relationship between X and Y (leg c of Figure 1), the indirect effect is quantified as the product of the relationships between X and M (leg a) and M and Y (leg b), while the total effect is the sum of direct and indirect effects. In this study, we are particularly interested in the role that silvicultural treatment (X) has on the eight different 2016 fuel and crown fire hazard metrics (Y), acknowledging that silvicultural treatment affects beetle-caused mortality (M) which in turn drives 2016 crown fire hazard metrics (Figure 1). We determined the relationships a , b , and c using linear mixed effects regression and given the same nesting structure characterized in our ANOVA models. Since we wanted to determine the effect that treatment had on mediation, we contrasted each of the active treatment effects with the Control (i.e., Burn-only vs. Control, Thin-only vs. Control, Thin+Burn vs. Control). All variables were

standardized for interpretation of effect size across fuel and crown fire hazard metrics. The bottom panel of Figure 1 illustrates standardized coefficients for canopy base height as an example. We utilized a non-parametric bootstrap resampling routine (N=1000 replications) to determine if direct, indirect, and total effects were significantly different from zero.

In all analyses, treatment effects were considered to have strong evidence of significance at the 95% confidence level, and marginal evidence of significance at the 90% level. We inspected residuals from nested ANOVA and linear mixed effects regression models of response state and change for constant variance across treatments using Levene's test of homoscedasticity. Where residuals were heteroscedastic we applied treatment level variance functions using R's `varIdent` function. Furthermore, we applied square root transform on responses that showed increasing residual variance with predicted values.

Where expedient for summarizing broad patterns and concise interpretation we grouped treatments according to the crossed factorial design nomenclature. Thinned or thinning refers to Thin-only and Thin+Burn treatments, while unthinned refers to Control and Burn-only. Burned or burning refers to Burn-only and Thin+Burn treatments, while unburned refers to Control and Thin-only.

Results

We summarized stand structure by treatment in 2002 and 2016 (Table 1). Thinned stands had 67% lower stem densities than unthinned stands in 2002 (79% and 60% lower by basal area and stand density index, respectively), but all density metrics were more similar across treatments by 2016. Although differences between thinned and unthinned stands in stem density, basal area, and stand density index abated over time by 33%, 63%, and 54%, respectively, the

contrast between thinned and unthinned quadratic mean diameters increased by 161% over the measurement period as large trees in the unthinned units were killed by MPB.

Fuel loads

Treatment effect on fine woody debris (FWD) in 2002 (the year following silvicultural treatment) followed an expected pattern (Figure 2). Burning, thinning, and their interaction all had significant effects on FWD (Table 2; $P \leq 0.0243$). Burning reduced FWD loads by 63% (compared to unburned) and thinning increased FWD loads by 250% (compared to unthinned). In 2016 (at least 4 years following beetle-caused mortality), only thinning had a significant effect on FWD load (Table 2; $P = 0.0275$). Overall, thinned treatment FWD loads in 2016 were 34% less than unthinned treatments. Whereas in 2002, Thin+Burn and Control loads were no different, in 2016 these two were the only individual treatments that were statistically distinct (Figure 2). Unthinned units significantly accumulated fuel between 2002 and 2016 (Table 3; $P \leq 0.0073$), but FWD in the Thin-only treatment decreased ($P = 0.0095$), and did not change in the Thin+Burn treatment ($P = 0.4904$).

Coarse woody debris (CWD) was similar across treatments in 2002 (Figure 2; Table 2). By 2016, CWD loads were lower in thinned than unthinned treatments (Table 2; $P = 0.0020$). Variability among Control stands (i.e., standard deviation) was 15 times greater than treated stands because of one stand with particularly high CWD load. Overall, thinned treatment CWD loads were 83% less than the unthinned treatments. Similar to trends observed in FWD dynamics, unthinned treatments accumulated CWD from 2002 to 2016 (Table 3; $P \leq 0.0565$), whereas CWD in the Thin-only treatment reduced over time (Table 3; $P = 0.0152$) and the Thin+Burn treatment did not change ($P = 0.6007$).

Forest floor (FF) loads varied by treatment in 2002 (Figure 2; Table 2). Loads were 59% lower in burned treatments than unburned treatments ($P = 0.007$). Although ANOVA results indicated a significant burning and thinning interaction ($P = 0.0382$), pairwise comparisons show FF loads assemble into two main treatment groups: burned and unburned. In 2016, FF loads did not vary by treatment (Table 2). Burned treatments significantly accumulated FF loads between 2002 and 2016 (Table 3; $P < 0.0055$), but FF in unburned treatments either decreased (Control; $P = 0.0832$) or did not change ($P = 0.9288$).

Canopy fuel (CF) differed by thinning in 2002 (Figure 2; Table 2). The immediate effect of thinning was a 58% reduction in CF versus the unthinned treatments ($P = 0.0005$). In 2016 there was slight evidence of both thinning and burning effects (Table 2; P of 0.0959 and 0.0604, respectively). These effects were relatively minor on their own, but when combined, caused the Thin+Burn treatment to have 43% less CF than the Control. Thinned treatment CF loads increased between 2002 and 2016 ($P \leq 0.0177$), but unthinned treatment loads decreased ($P \leq 0.0488$).

Crown fire hazard

We used FFE-FVS to assign fire behavior fuel models and predict potential fire behavior for our 2002 and 2016 data (Table 4). In 2002, fuel model 8 (“closed timber litter”) was the most commonly assigned model across treatments. Fuel model 8 was still the most assigned model in thinned’ treatments in 2016, but the unthinned’ treatments were better characterized by fuel model 10 (“timber [litter and understory]”), with occasional assignments of fuel model 12 (“medium logging slash”). Predicted surface fire flame length was greatest in the thin-only treatment and lowest in the burn-only treatment in 2002, but the thin-only treatment had the lowest predicted flame lengths in 2016. In 2002, crown fire (passive type) was only predicted for

the burned treatments (13% of plots). Passive crown fire was predicted for all treatment' types in 2016. However, the Control' had the greatest propensity by far for crown fire, whether active, passive, or conditional.

Canopy base height (CBH) in 2002 varied due to thinning (Figure 3; Table 5), where mean CBHs were 130% taller in thinned treatments than unthinned ($P = 0.0002$). By 2016, CBH varied by both burning and thinning (Table 5). Burned treatments were associated with 105% greater CBHs than unburned ($P = 0.0082$), and thinned treatments had 79% greater CBHs than unthinned treatments ($P = 0.0075$). There was slight evidence that interaction amplified these effects ($P = 0.0938$) such that the Thin+Burn treatment was 3.2 greater than the Control. CBH dropped significantly in the Thin-only treatment from 2002 to 2016 (Table 6; $P = 0.0028$) as ladder fuel ingrowth densified the canopy from below, but CBH did not change in the remaining treatments ($P \geq 0.3498$).

Immediately after treatment, canopy bulk density (CBD) in thinned treatments was 55% less than in unthinned treatments (Figure 3; Table 5; $P = 0.0003$). In 2016, CBDs were more similar among treatments than in 2002, but still varied significantly by treatment (Table 5). Burned treatments had 33% lower CBDs than unburned treatments ($P = 0.0314$) and thinned treatments had 46% lower CBDs than unthinned treatments ($P = 0.0041$). Although change in CBD between 2002 and 2016 appears to vary by thinning (reduction in unthinned due to beetle kill and accumulation in thinned due to ingrowth), reduction was only significant for the Burn-only treatment (Table 6; $P = 0.0404$) and accumulation for the Thin-only treatment ($P = 0.0080$).

Probability of torching (PT) in 2002 depended on both burning and thinning treatments (Figure 3; Table 5). Burning reduced PT by 64% ($P = 0.0031$) and thinning reduced it by 34% ($P = 0.0073$). Probability of torching in 2016 was only dependent on thinning (Table 6). In this

case, unthinned treatment PT was 111% greater than thinned treatments probabilities ($P = 0.0049$). Between 2002 and 2016, PT in unthinned treatments significantly increased with inputs to the surface fuel load (Table 6; $P \leq 0.0361$), but PT did not significantly change in thinned treatments ($P \geq 0.1237$).

Crowning index (CI) differed by thinning in 2002 (Figure 3; Table 5), which was expected because thinning reduced CBDs. More specifically, thinning resulted in 95% greater CIs than the unthinned treatments. By 2016 CI differed by both burning and thinning (Table 5). Burned stands had 37% greater CI than unburned stands ($P = 0.0369$) and thinned stands had 42% greater CI than unthinned stands ($P = 0.0251$). Although the ANOVA interaction term was not significant, pairwise differences revealed that the Thin+Burn treatment had 48% to 89% greater CI than the remaining treatments. CIs remained relatively constant between 2002 and 2016 except for in the Thin-only treatment, where it dropped significantly as ingrowth densified the canopy (Table 6; $P = 0.0193$).

Crown fire hazard mediation

We fit models for mediation analysis of four fuel classes and four crown fire hazard metrics to segregate the direct (silvicultural treatment) and indirect (treatment via beetle outbreak) effects that contribute to total differences between the Control and remaining treatments in 2016. In this analysis, total effects were consistent with the fuel and crown fire hazard metrics reported above by treatment, except this analysis presents differences between individual treatments and the Control.

Differences in fuel loads between Control and thinning treatments depended on beetle outbreak, but not differences between Control and Burn-only (Figure 4). The Thin-only and Thin+Burn indirect effects were significantly non-zero for FWD, CWD, and CF responses,

demonstrating that beetle outbreak mediated differences between Control and thinned treatments for three of our four fuel metrics. Substantial (standardized effect size > 0.05) indirect effects were consistent with total effect direction for all responses except for CF, meaning that beetle outbreak generally increased contrasts between Control and treatments, but decreased CF differences between Control and thinned treatments.

Just as with fuel loads, differences in crown fire hazard metrics between Control and thinning treatments depended on beetle outbreak, but not differences between Control and Burn-only (Figure 4). Thin-only indirect effects were significantly non-zero for CBD, PT, and CI, while Thin+Burn indirect effects were only significant for CBD and PT. Thus beetle outbreak did not affect CBH differences between Control and treatments, nor did it affect any response differences between Control and Burn-only. Indirect effects were consistent with total effect directions only for PT; they were inconsistent with total effects for CBH, CBD, and CI. The magnitude and direction of indirect effects on PT illustrate that most of the difference between the Control and thinned treatments was due to beetle outbreak. Conversely, beetle outbreak obscured differences in CBH, CBD, and CI between Control and thinned treatments.

Discussion

The 2002 fuels and potential crown fire metrics that we report corroborate findings from earlier fuel reduction treatment studies (Stephens and Moghaddas 2005; Fulé et al. 2012; McIver et al. 2012b). Overall, surface fuels were reduced by burning, canopy fuels were reduced by thinning, and potential for crown fire was lowest in the combined thinned and burned treatments.

This study characterized fuel development and crown fire hazard dynamics 14 years after initial treatment and at least 4 years following MPB outbreak. In general, we observed that fuel

loads were elevated after outbreak and ingrowth, and potential for crown fire was greatest in the untreated Control, intermediate in Burn-only and Thin-only, and lowest in Thin+Burn (Table 7).

Despite the subsequent biotic disturbance, the management objective in these treated stands is still to resist crown fire. Interaction between disturbances such as beetle outbreak and potential fire has been a growing concern (Bebi et al. 2003; Schoennagel et al. 2012; Jenkins et al. 2014; Kane et al. 2017), but other studies have not specifically considered this interaction within treated areas. To more satisfactorily address the drivers and outcomes of combined treatment and beetle mortality effects, we discuss the mediation analysis prior to the assessment of load and fire hazard dynamics.

Mediation analysis: treatment differences driven by silviculture or beetles?

In order to effectively interpret treatment outcomes we must begin with the relationship between the two components of treatment in 2016: silvicultural fuel reduction and beetle-caused mortality. Studies have shown endemic (non-outbreak) beetle populations become more active in response to burning treatments, and tend to kill injured or less vigorous trees (e.g., Larsson et al. 1983; Negrón and Popp 2004; Fettig et al. 2010). On our sites, Six and Skov (2009) identified that by 2008 three bark beetle species (Douglas-fir beetle [*Dendroctonus pseudotsugae*], pine engraver [*Ips pini*], and western pine beetle [*Dendroctonus brevicomis*]) increased in abundance because of burning treatments. Mountain pine beetle population size was not found to respond to treatment, but successful MPB attacks were more prevalent in unthinned treatments. By 2012, MPB-caused overstory mortality was high in control and burn-only units (Hood et al. 2016), leading to similar live ponderosa pine basal areas across all treatments.

We applied these beetle-kill data to our mediation analysis, confirming that fuel reduction treatment and beetle-caused mortality were inextricably linked: the number of overstory trees killed had a strong negative association with thinning and a slight positive association with burning. In addition to characterizing the combined effects of these “treatments,” our analysis ascertains the relative effects of silviculture and beetles on forest fuels and crown fire hazard, including treatment-outbreak agreement or antagonism (Table 7).

A number of studies have shown that in unmanaged stands, beetle-caused mortality alters forest fuel profiles (summarized in Jenkins et al. 2012, but see Simard et al. 2011). Our mediation analysis illustrates that CF loads were significantly less in Thin+Burn than Control stands despite beetle kill, and FWD loads were less in Thin+Burn stands because of beetle kill. Additionally, beetle kill inflated differences between thinned and Control stands in FWD and CWD pools, but reduced existing differences in the CF pool. These linked fuel loads demonstrate that beetles caused fuel transfer from overstory to surface pools, and that although beetle kill partially masked or diminished differences between thinned and unthinned canopies, unthinned canopy fuels translocated to the ground inflated surface fuel loads beyond thinned treatments. The nature of these differences is also manifested in the divergence of assigned fire behavior fuel models by treatments. FFE-FVS assigned slash group fire behavior fuel models (“medium logging slash” and “heavy logging slash”) to characterize unthinned surface fuel profiles, which is expected to make potential fire behavior more volatile, increasing soil heating and belowground severity.

Though beetle kill inflated surface fuel differences between thinned and Control stands, our analysis of fire hazard indicated beetles only inflated differences in probability of torching between those treatments. Studies have shown that MPB outbreak can exacerbate fire behavior,

depending on time since disturbance and metrics analyzed (synthesized in Jenkins et al. 2014; but see Harvey et al. 2013). But beyond beetle-caused inputs to surface fuels, beetles actually thin out forest canopies and eventually moderate potential crown fire spread akin to the silviculturist's crown fire hazard reduction treatments. Our analysis shows that beetle kill – which was greater in unthinned stands – offsets the initial positive effect of thinning on canopy-based crown fire hazard metrics (CBD and CI). However, since this offset effect is minor (indirect effect magnitude smaller than direct effect magnitude), it demonstrates that “natural thinning” by beetles neither reduces fire hazard like active management nor hinders the effective longevity of thinning. Probability of torching, on the other hand, incorporates potential surface fire behavior where the canopy-based metrics do not. Silviculture and beetle effects had consistent influence on the thinning versus Control contrast for this metric because silvicultural thinning reduces probability of torching but beetle kill increases it by compounding ladder fuels with heavy surface loads, inflating the difference (in fuel loads and longevity) between thinned and unthinned stands.

We found no fuel or crown fire hazard differences (treatment or beetle caused) between Burn-only and Control treatments. This is likely because the prescribed burning treatment was mostly kept to low fire intensities to limit overstory mortality. Fire effects were also limited because many trees, including successional species, had grown to fire tolerant sizes in the fire-excluded 20th century. Burning effect may have been more muddled by beetles if the treatment were more severe and had more strongly influenced successful beetle attacks (Wallin et al. 2003) or reduced overstory density as much as thinning treatments. When combined with thinning in the form of the Thin+Burn treatment, however, we did observe a minor interaction between beetles and burning: beetle effects in the Thin+Burn treatments were always slightly less than in

the Thin-only treatment. This is because treatment more poorly differentiated beetle kill between Thin+Burn and Control than between Thin-only and Control (leg *a* of Figure 1). Thus, beetles influenced fuel and crown fire hazard responses in both the Thin+Burn and the Control similarly, but differences were mostly due to silvicultural treatment.

Combined effects: the state of treatment in 2016

Bifurcating the silviculture and beetle effects on fuel reduction treatments in 2016 is useful for understanding the relative importance of these factors on the fuel development process and on change in crown fire hazard, but land managers may be more concerned with the state of treatment fuel loads and crown fire hazard. In this sense, treatment effectiveness at maintaining low crown fire hazard may be a more practically important matter than effect mediation.

We found thinned stands had less fuel and all-around lower crown fire hazard than unthinned stands in 2016. One major difference between 2002 and 2016 thinning effects was the radical increase of surface fuel (FWD and CWD) in unthinned stands, which likely would not have happened without beetle outbreak. These surface fuels are directly tied to increased surface fire behavior and potential for torching. Although thinning was a statistically significant predictor of torching probability in both 2002 and 2016, 2016 probabilities were undesirably higher in unthinned (50%) than thinned stands and therefore more significant in practical terms. This condition is typical of unmanaged second-growth ponderosa pine-Douglas fir forests impacted by beetles throughout the interior West and reflects that torching and crowning fire behavior may be commonplace in many unmaintained, post-outbreak stands (Jain et al. 2012).

We also found that burned stands had less canopy fuel and lower probabilities of sustaining crown fire than unburned stands in 2016. Interestingly, we observed delayed effects of burning on canopy fuel and canopy-based crown fire hazard metrics (CBH, CBD, CI) that were

not present in 2002. This delay is likely due to secondary fire-induced mortality, namely, pre-outbreak beetle attacks on trees weakened by prescribed fire, as documented by Six and Skov (2009). Despite these two beetle episodes (pre-outbreak then outbreak) in the Burn-only treatment, and that the Control was only slightly different from the Burn-only in all of the 2016 fuel and crown fire hazard facets, FFE-FVS predicted “surface” type fire only 40% of the time in the Control versus at least 70% in other treatments. Fire, and fire modeling, is very sensitive to thresholds in fuels, weather, and topography. Although the potential fire behavior and crown fire hazard metrics that this study presents are more valuable for comparative analysis than absolute characterization, they illustrate that prescribed fire may only have mild effects on measured vegetation and fuels structure, but still reduce potential fire behavior below important crowning thresholds (Van Wagner 1977).

The combination of burning and thinning is clearly the most effective for sustained crown fire hazard reduction in light of post-treatment growth and subsequent disturbance. The 2016 Thin+Burn was superior to the Burn-only and Thin-only treatments for three main reasons. First, it reduced surface and canopy fuels. Combined thinning and burning most effectively reduces fuels because thinning removes substantial tree and canopy biomass, while burning consumes surface fuels that have built up prior to thinning in addition to activity fuels (Stephens and Moghaddas 2005). Second, the Thin+Burn reduced beetle-caused mortality relative to Control and Burn-only. Although thinning during outbreak-level disturbances may be ineffective (Six et al. 2014), thinning prior to outbreak has been shown to moderate mortality (Fettig et al. 2014; Jenkins et al. 2014; Hood et al. 2016). Third, the Thin+Burn dampened development of ladder fuels by killing regeneration and potential ingrowth. Keyes and O’Hara (2002) suggested that fuel treatments stimulate forest regeneration, and in turn negate fuel reduction objectives.

Although Thin+Burn stands are in fact regenerating, the combination of these treatments consumed advance regeneration and reset an understory development phase, lengthening the duration of treatment effectiveness. The recent divergence from the Thin-only emphasizes that treating the understory is imperative for extending the duration of treatment longevity. Although stand densities in both the Thin-only and the Thin+Burn were most similar to stand densities in local historical stands with intact frequent fire regimes (e.g., per Clyatt et al. 2016), without re-entry or burning, the Thin-only treatment may not be able to resist crown fire like the Thin+Burn or historical, open ponderosa pine stands (Arno et al. 2008). Fuel treatments in ponderosa pine forest types that include both thinning and burning best establish forest structure that is able to resist beetles and crown fire well into the second decade. This timeframe is especially important for ponderosa pine forests in the inland Northwest, where fire return intervals may range up to half a century (Arno et al. 1995) and managers may be financially or logistically unable to keep up fuel reduction treatments.

Summary

Fuel reduction treatments have been widely implemented to reduce crown fire potential in fire-prone forests. However, recent bark beetle outbreaks have impacted millions of acres of unmanaged and managed forests throughout the West. This study shows that fuel reduction treatments followed by MPB outbreak generate their own unique responses that most likely differ from original treatment responses. Overall, thinned then MPB-attacked stands had less fuel and lower crown fire potential than unthinned attacked stands. Burned then attacked stands had less canopy fuel and also had lower crown fire potential than unburned attacked stands for three of our four metrics. Combined thinning and burning best improved fuel reduction treatment

longevity – even after beetle outbreak this treatment exhibited little change in fuel profile and crown fire hazard.

Bark beetle outbreaks reduce live stem densities and canopy fuels. However, outbreaks and fuel reduction treatments retain a different suite of forest structures than beetle outbreak, and these differences can have profound impacts on potential fire behavior. Beetle outbreak had a complex effect on fuels and crown fire hazard in treated versus untreated stands, amplifying some differences and reducing others. High levels of beetle outbreak in Control stands and ladder fuel ingrowth in Thin-only stands made fuel and potential fire behavior in these two treatments more similar in a number of ways. Although beetles killed more trees in Thin+Burn than Thin-only stands, beetle outbreak had less impact on the differences between Thin+Burn and Control than Thin-only and Control, again emphasizing that combined thinning and burning establishes crown fire-resistant forest structure that is better able to resist change due to time and beetle outbreak.

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Table 1. Stand structure metrics by treatment following the Fire and Fire Surrogate Study's fuel reduction treatments in 2002 (immediately after treatment) and in 2016 (following 2005 to 2012 regional beetle outbreak).

Year	Treatment	Density	Basal area	Stand density Index ^a	Quadratic mean diameter
		<i>stems ha⁻¹</i>	<i>m² ha⁻¹</i>	<i>(metric)</i>	<i>cm</i>
2002	Control	322 (60)	23.1 (5.7)	420 (99)	31.1 (1.5)
2002	Burn-only	304 (53)	20.8 (2.7)	384 (51)	31.2 (1.0)
2002	Thin-only	111 (11)	9.7 (0.4)	170 (8)	33.4 (0.5)
2002	Thin+Burn	94 (12)	8.8 (1.2)	151 (22)	33.4 (0.9)
2016	Control	323 (60)	17.8 (5.1)	339 (91)	26.7 (1.9)
2016	Burn-only	291 (43)	17.5 (2.9)	328 (49)	28.0 (2.4)
2016	Thin-only	188 (27)	14.9 (0.4)	265 (11)	33.4 (2.1)
2016	Thin+Burn	99 (13)	10.9 (0.8)	181 (15)	33.0 (1.5)

^aReineke LH (1933) Perfecting a stand-density index for even-aged forests. *J Agric Res* 46:627–638.

Table 2. Nested ANOVA of forest fuels by treatment following the Fire and Fire Surrogate Study's fuel reduction treatments in 2002 (immediately after treatment) and in 2016 (following 2005 to 2012 regional beetle outbreak).

Response	Source	numDF	denDF	2002		2016	
				<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
FWD ^a (Mg ha ⁻¹)	Intercept	1	108	108.85	<0.0001	714.80	<0.0001
	Block	2	6	5.93	0.0380	1.33	0.3320
	Burning	1	6	24.83	0.0025	1.28	0.3018
	Thinning	1	6	32.56	0.0013	8.38	0.0275
	Thinning × Burning	1	6	8.94	0.0243	0.11	0.7527
CWD ^b (Mg ha ⁻¹)	Intercept	1	108	71.79	<0.0001	90.25	<0.0001
	Block	2	6	0.80	0.4914	0.54	0.6077
	Burning	1	6	2.95	0.1369	0.18	0.6890
	Thinning	1	6	1.44	0.2758	26.93	0.0020
	Thinning × Burning	1	6	1.17	0.3203	2.31	0.1792
FF ^c (Mg ha ⁻¹)	Intercept	1	108	306.12	<0.0001	1916.24	<0.0001
	Block	2	6	0.77	0.5028	0.74	0.5160
	Burning	1	6	39.95	0.0007	0.12	0.7420
	Thinning	1	6	3.93	0.0949	0.20	0.6674
	Thinning × Burning	1	6	7.00	0.0382	0.22	0.6538
CF ^d (Mg ha ⁻¹)	Intercept	1	108	276.03	<0.0001	284.01	<0.0001
	Block	2	6	1.07	0.3999	2.04	0.2109
	Burning	1	6	1.69	0.2409	5.33	0.0604
	Thinning	1	6	46.79	0.0005	3.89	0.0959
	Thinning × Burning	1	6	0.01	0.9356	1.16	0.3225

^aFine woody debris (surface wood < 7.62 cm diameter)

^bCoarse woody debris (sound surface wood ≥ 7.62 cm diameter)

^cForest floor (litter and duff layers)

^dCanopy fuels (foliage and materials < 7.62 cm diameter)

Table 3. Fuel load change by treatment between 2002 (immediately following treatment) and 2016 (following 2005 to 2012 regional beetle outbreak) at the Fire and Fire Surrogate Study. Estimates were derived and tested against zero using linear mixed effects models.

Response	Treatment	Estimate	Std. Err.	<i>P</i>
FWD ^a (Mg ha ⁻¹)	Control	5.17	1.30	0.0073
	Burn-only	7.32	1.35	0.0016
	Thin-only	-11.39	3.04	0.0095
	Thin+Burn	-1.02	1.39	0.4904
CWD ^b (Mg ha ⁻¹)	Control	16.96	7.20	0.0565
	Burn-only	12.02	2.99	0.0070
	Thin-only	-4.34	1.29	0.0152
	Thin+Burn	-0.71	1.29	0.6007
FF ^c (Mg ha ⁻¹)	Control	-8.59	4.14	0.0832
	Burn-only	13.14	2.28	0.0012
	Thin-only	-0.25	2.66	0.9288
	Thin+Burn	9.82	2.32	0.0055
CF ^d (Mg ha ⁻¹)	Control	-7.61	3.09	0.0488
	Burn-only	-7.06	2.02	0.0128
	Thin-only	9.47	0.76	<0.0001
	Thin+Burn	3.58	1.11	0.0177

^aFine woody debris (surface wood < 7.62 cm diameter)

^bCoarse woody debris (sound surface wood ≥ 7.62 cm diameter)

^cForest floor (litter and duff layers)

^dCanopy fuels (foliage and materials < 7.62 cm diameter)

Table 4. Dominant fuel models and potential fire behavior by treatment following the Fire and Fire Surrogate Study’s fuel reduction treatments in 2002 (immediately after treatment) and in 2016 (following 2005 to 2012 regional beetle outbreak). Fuel models and fire behavior were determined using the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS). Predicted fire behavior is based on standard severe fire weather conditions (FFE-FVS “severe” category: 4% 10-hr fuel moisture, 21.1° C, and 32.2 kph 6.1 m windspeed).

Year	Treatment	Primary fuel model ^a				Surface flame length <i>m</i>	Predicted fire type ^b			
		8%.....	10%.....	12%.....	13%.....		Surface%.....	Cond'l%.....	Passive%.....	Active%.....
2002	Control	67 (3)	27 (7)	7 (3)	0 (0)	0.83 (0.01)	63 (13)	23 (12)	13 (3)	0 (0)
2002	Burn-only	93 (3)	7 (3)	0 (0)	0 (0)	0.43 (0.06)	80 (10)	20 (10)	0 (0)	0 (0)
2002	Thin-only	53 (3)	30 (0)	17 (3)	0 (0)	1.54 (0.03)	87 (3)	0 (0)	13 (3)	0 (0)
2002	Thin+Burn	93 (3)	3 (3)	3 (3)	0 (0)	0.71 (0.13)	100 (0)	0 (0)	0 (0)	0 (0)
2016	Control	33 (20)	40 (15)	23 (19)	3 (3)	1.56 (0.32)	40 (15)	17 (12)	40 (15)	3 (3)
2016	Burn-only	37 (9)	50 (10)	13 (3)	0 (0)	1.50 (0.13)	70 (12)	7 (7)	23 (7)	0 (0)
2016	Thin-only	70 (6)	30 (6)	0 (0)	0 (0)	1.11 (0.03)	83 (3)	0 (0)	17 (3)	0 (0)
2016	Thin+Burn	60 (0)	40 (0)	0 (0)	0 (0)	1.47 (0.11)	90 (6)	0 (0)	10 (6)	0 (0)

^aAlbini, FA (1976). Estimating wildfire behavior and effects. Gen. Tech. Rep. INT-30. Odgen, UT. USDA Forest Service Intermountain Forest and Range Experiment Station. 92 p.

^bScott, JH and ED Reinhardt (2001). Assessing crown fire potential by linking models of surface and crown fire behavior. Res. Pap. RMRS-RP-29. Fort Collins, CO. USDA Forest Service Rocky Mountain Research Station. 59 p.

Table 5. Nested ANOVA of crown fire hazard metrics by treatment following the Fire and Fire Surrogate Study's fuel reduction treatments in 2002 (immediately after treatment) and in 2016 (following 2005 to 2012 regional beetle outbreak).

Response	Source	numDF	denDF	2002		2016	
				<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
CBH ^a (m)	Intercept	1	105	345.60	<0.0001	258.37	<0.0001
	Block	2	6	0.99	0.4251	3.73	0.0884
	Burning	1	6	3.03	0.1323	15.03	0.0082
	Thinning	1	6	60.38	0.0002	15.67	0.0075
	Thinning × Burning	1	6	1.83	0.2247	3.96	0.0938
CBD ^b (kg m ⁻³)	Intercept	1	105	315.84	<0.0001	1674.82	<0.0001
	Block	2	6	0.44	0.6636	3.23	0.1118
	Burning	1	6	0.82	0.4012	7.81	0.0314
	Thinning	1	6	52.78	0.0003	20.16	0.0041
	Thinning × Burning	1	6	0.02	0.9003	0.00	0.9467
p(Torch) ^c (%)	Intercept	1	105	38.18	<0.0001	151.13	<0.0001
	Block	2	6	0.13	0.8768	4.32	0.0688
	Burning	1	6	22.85	0.0031	0.85	0.392
	Thinning	1	6	15.81	0.0073	18.73	0.0049
	Thinning × Burning	1	6	0.57	0.4775	0.40	0.5510
CI ^d (km hr ⁻¹)	Intercept	1	105	704.41	<0.0001	306.23	<0.0001
	Block	2	6	2.45	0.1670	1.49	0.2990
	Burning	1	6	1.80	0.2288	7.14	0.0369
	Thinning	1	6	54.16	0.0003	8.79	0.0251
	Thinning × Burning	1	6	0.01	0.9294	1.44	0.2754

^aCanopy base height (lowest height where canopy bulk density exceeds 0.011 kg m⁻³)

^bCanopy bulk density (maximum canopy fuel mass per volume given 4.5 m running mean)

^cProbability of torching (probability of surface fire ascending into crowns given Monte Carlo simulation)

^dCrowning index (6.1 m windspeed required to cause active crown fire)

Table 6. Crown fire hazard metric change by treatment between 2002 (immediately following treatment) and 2016 (following 2005 to 2012 regional beetle outbreak) at the Fire and Fire Surrogate Study. Estimates were derived and tested against zero using linear mixed effects models.

Response	Treatment	Estimate	Std. Err.	<i>P</i>
CBH (m)	Control	-0.34	0.53	0.5479
	Burn-only	0.53	0.52	0.3498
	Thin-only	-2.54	0.52	0.0028
	Thin+Burn	-0.31	0.55	0.5941
CBD (kg m ⁻³)	Control	-0.006	0.007	0.4431
	Burn-only	-0.017	0.007	0.0404
	Thin-only	0.015	0.004	0.0080
	Thin+Burn	0.005	0.004	0.2406
p(Torch) (%)	Control	20.46	7.61	0.0361
	Burn-only	32.97	7.50	0.0046
	Thin-only	4.22	7.50	0.5938
	Thin+Burn	14.02	7.83	0.1237
CI (km hr ⁻¹)	Control	5.84	8.33	0.5096
	Burn-only	11.41	8.19	0.2130
	Thin-only	-25.95	8.19	0.0193
	Thin+Burn	0.77	8.63	0.9318

^aCanopy base height (lowest height where canopy bulk density exceeds 0.011 kg m⁻³)

^bCanopy bulk density (maximum canopy fuel mass per volume given 4.5 m running mean)

^cProbability of torching (probability of surface fire ascending into crowns given Monte Carlo simulation)

^dCrowning index (6.1 m windspeed required to cause active crown fire)

Table 7. Summary of fuel load and crown fire hazard differences by treatment at the Fire and Fire Surrogate Study. Fuel load and crown fire hazard attributes: FWD=fine woody debris, CWD=coarse woody debris, FF=forest floor, CF=canopy fuel, CBH=canopy base height, CBD=canopy bulk density, PT=probability of torching, CI=crowing index.

Treatment	2002 to 2016 change ^a								Beetle outbreak impact (vs Control) ^b								2016 Tukey-Kramer rank ^c							
	FWD	CWD	FF	CF	CBH	CBD	PT	CI	FWD	CWD	FF	CF	CBH	CBD	PT	CI	FWD	CWD	FF	CF	CBH	CBD	PT	CI
Control	↑	↑	↓	↓			↑										B	B		B	A	C	B	A
Burn-only	↑	↑	↑	↓		↓	↑										AB	B		AB	B	BC	B	A
Thin-only	↓		↓	↑	↓	↑		↓	↔	↔		→←		→←	↔	→←	AB	A		AB	AB	AB	AB	A
Thin+Burn			↑	↑					↔	↔		→←		→←	↔		A	A		A	C	A	A	B

^aStatistically significant differences ($\alpha=0.10$) between 2002 and 2016 values. ↑=values increased, ↓=values decreased, blank=no change.

^bStatistically significant effect ($\alpha=0.10$) of beetle outbreak on treatment effect over Control. ↔=Treatment and Control differences inflated, →←=treatment and Control differences diminished, blank=no effect.

^cStatistically significant pairwise differences ($\alpha=0.05$) at 2016 measurement. Shared letters indicate no difference. A=lowest value, blank=no difference.

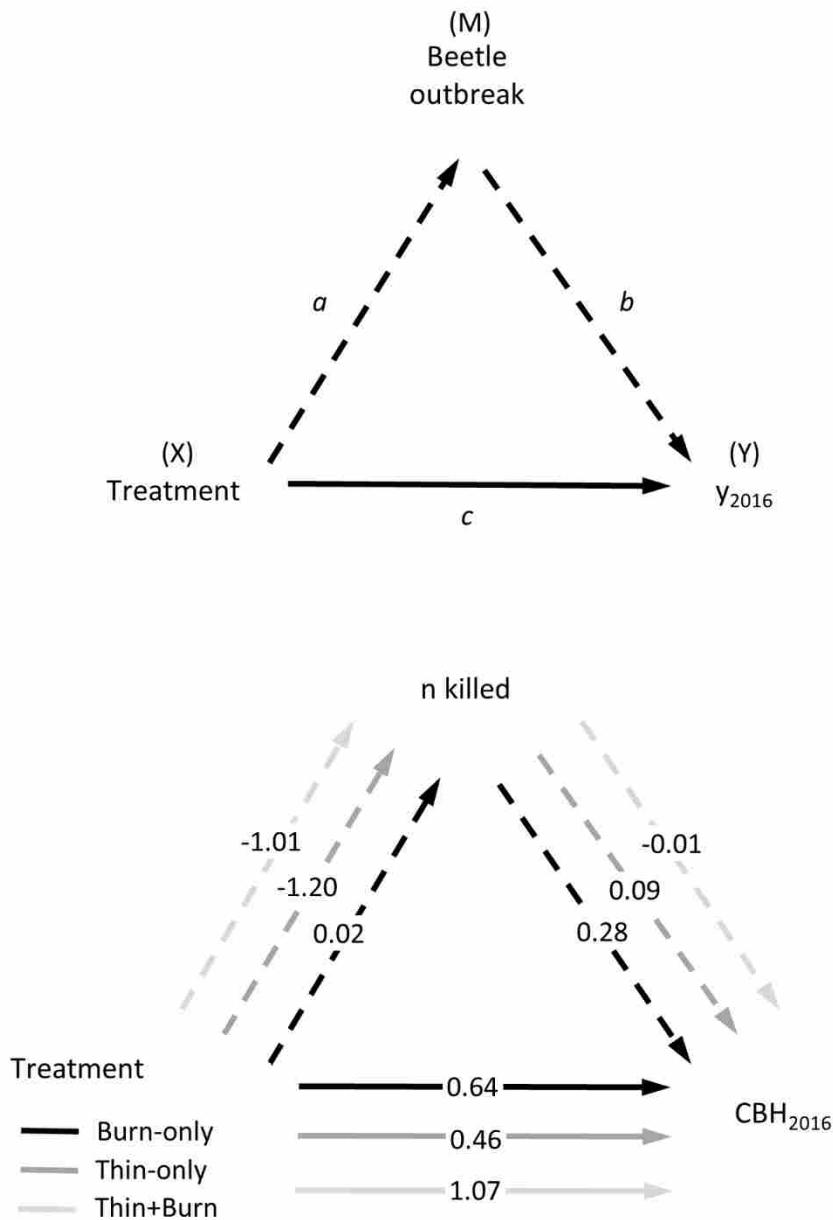


Figure 1. Conceptual diagram of mediation analysis testing the effect of fuel reduction treatment (versus Control) on fuel and crown fire hazard as mediated by bark beetle outbreak. Upper panel illustrates overall conceptual framework, with the direct effect as the solid arrow and the indirect effect represented by the dashed arrow pathway. As an example, the lower panel illustrates regression coefficients linking treatment (“Burn-only”, “Thin-only”, “Thin+Burn”) to canopy base height (“CBH₂₀₁₆”) with the number of trees killed by bark beetles (“n killed”) representing outbreak severity.

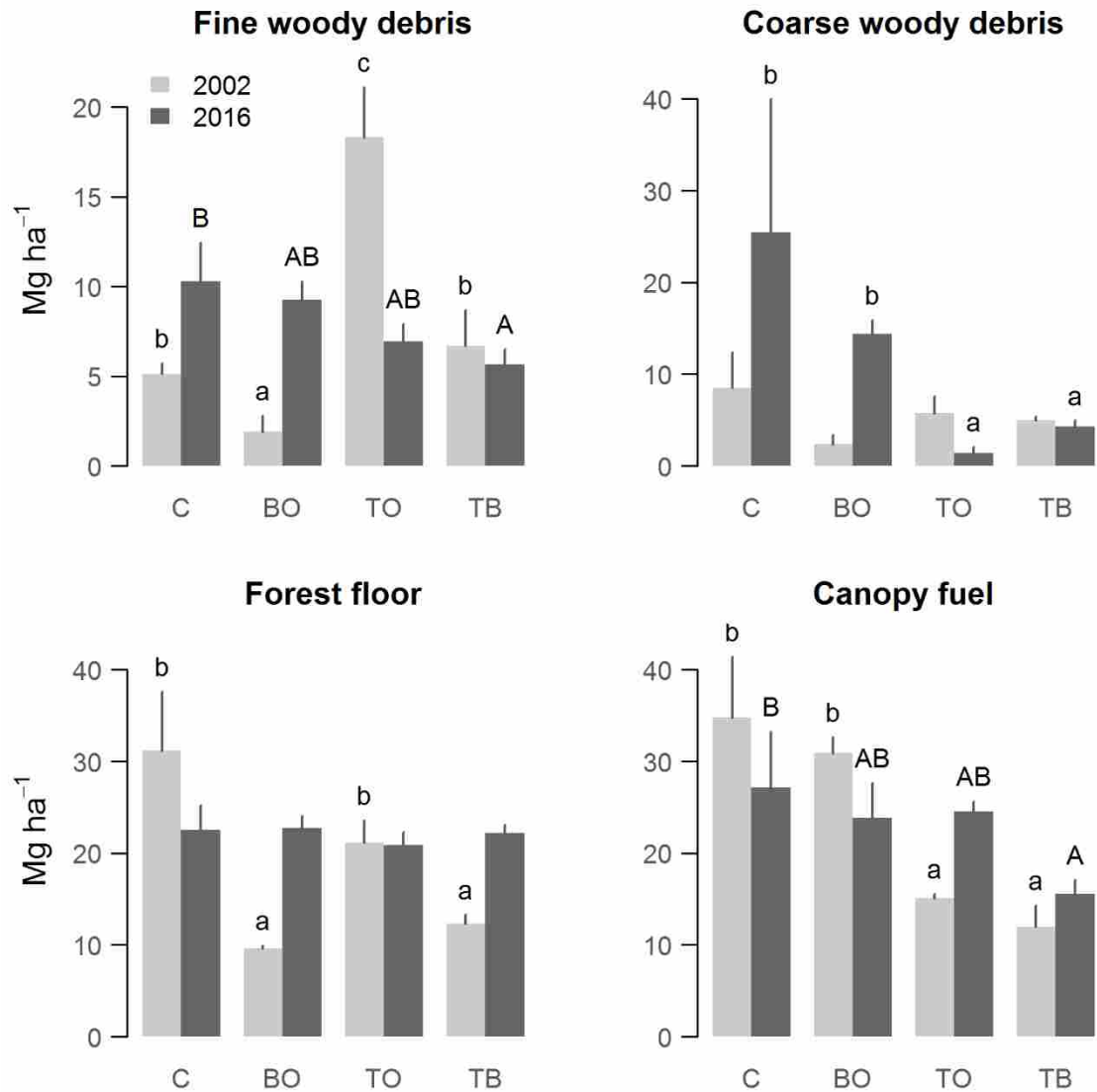


Figure 2. Forest fuels (mean and standard error) by treatment following the Fire and Fire Surrogate Study's fuel reduction treatments in 2002 (immediately after treatment) and in 2016 (following 2005 to 2012 regional beetle outbreak). C=Control, BO=Burn-only, TO=Thin-only, TB=Thin+Burn. Fine woody debris includes surface wood < 7.62 cm diameter; coarse woody debris includes sound surface wood ≥ 7.62 cm diameter; forest floor includes litter and duff layers; canopy fuels include foliage and materials < 7.62 cm diameter. Letters above bars denote pairwise differences between treatments (lowercase=2002 differences, uppercase=2016 differences); letters not shown where ANOVA tests not significant.

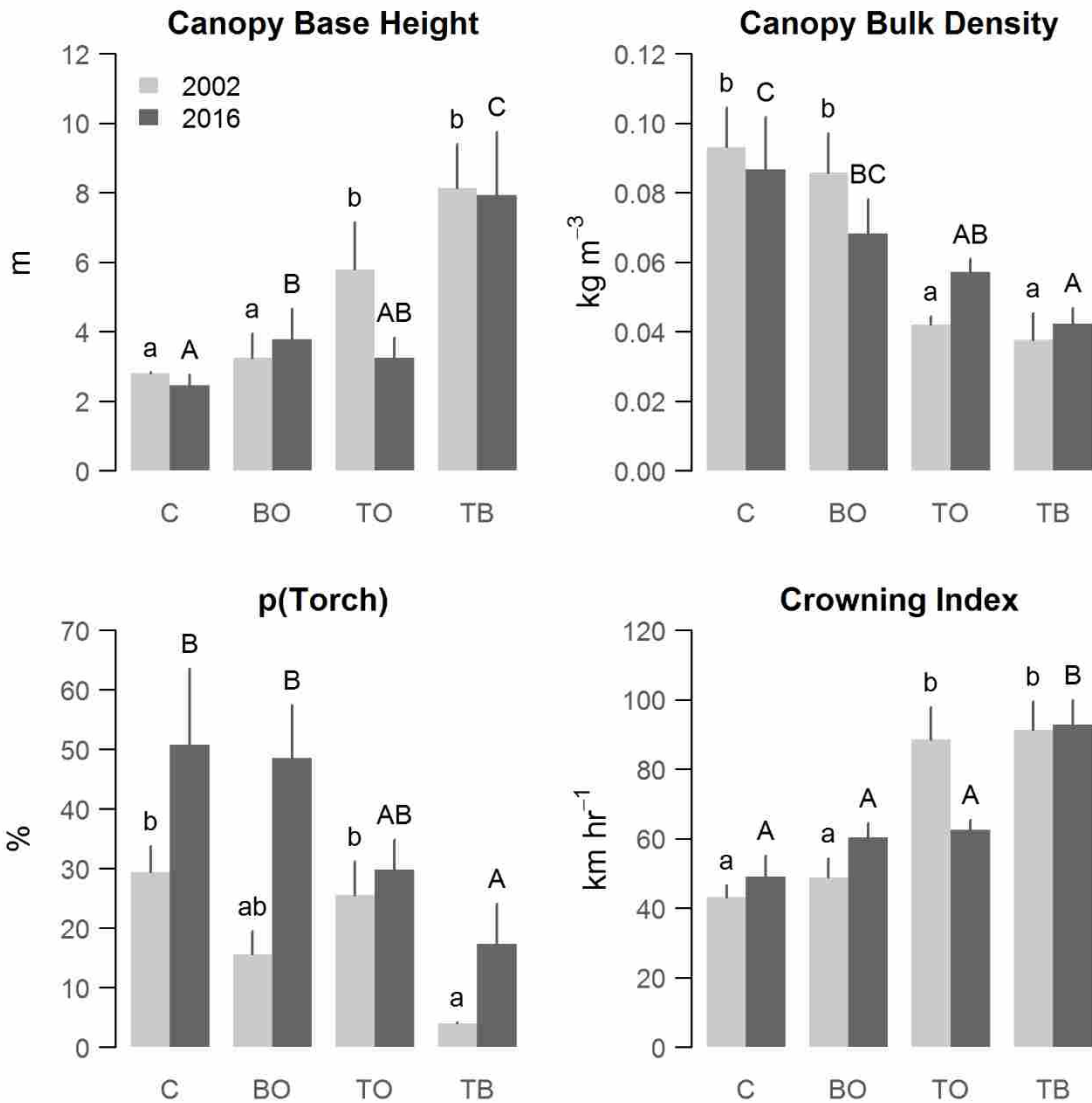


Figure 3. Crown fire hazard (mean and standard error) by treatment following the Fire and Fire Surrogate Study's fuel reduction treatments (completed in 2001) and regional beetle outbreak (2005 to 2012). C=Control, BO=Burn-only, TO=Thin-only, TB=Thin+Burn. Canopy base height is the lowest height where canopy bulk density exceeds 0.011 kg m^{-3} ; canopy bulk density is the maximum canopy fuel mass per volume given 4.5 m running mean; p(Torch) or probability of torching is the probability of surface fire ascending into crowns given Monte Carlo simulation; crowning index is the 6.1 m windspeed required to cause active crown fire. Letters above bars denote pairwise differences between treatments (lowercase=2002 differences, uppercase=2016 differences); letters not shown where ANOVA tests not significant.

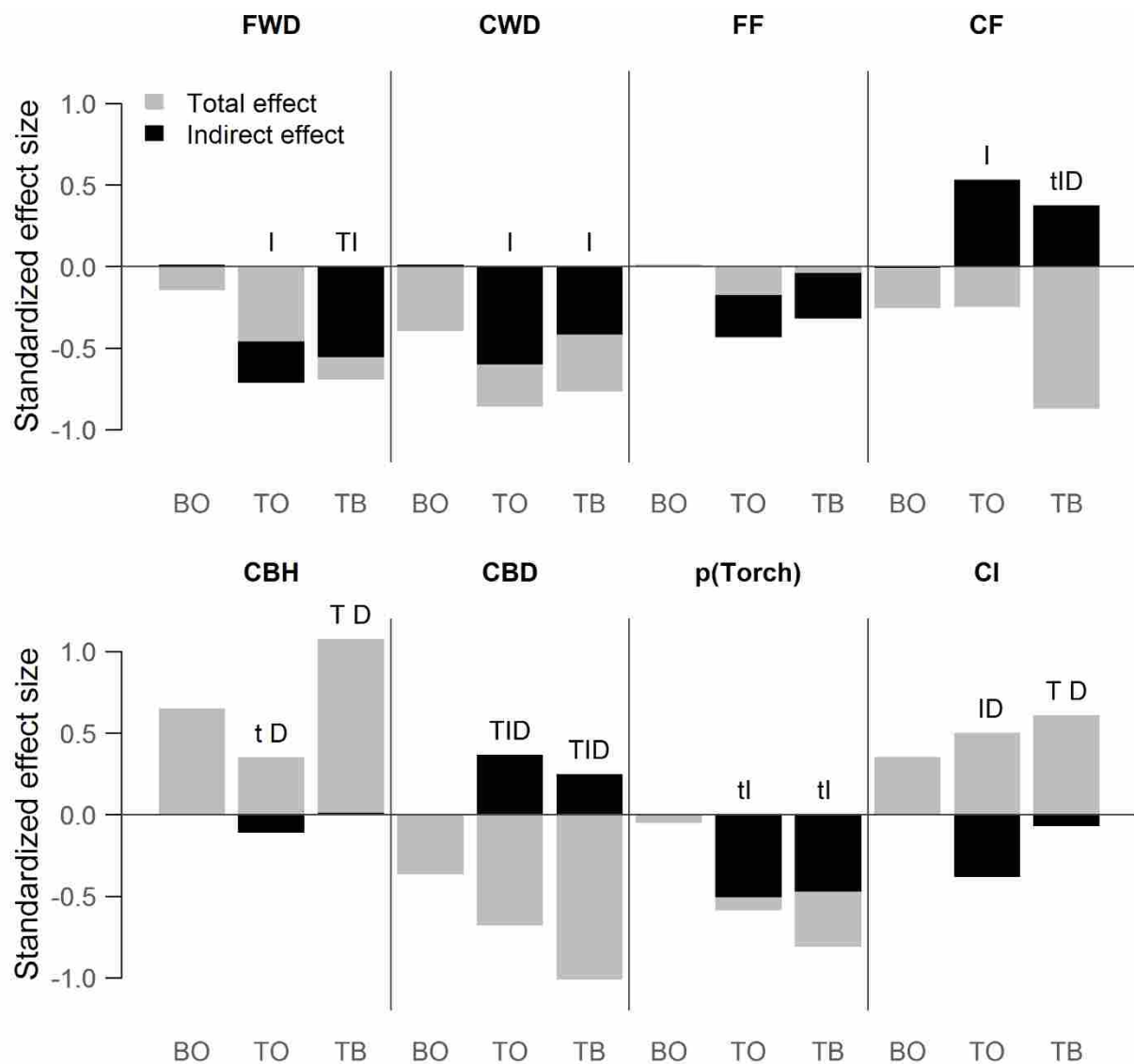


Figure 4. Mediation analysis treatment effect sizes (vs. Control) on 2016 fuel (top panel) and potential crown fire hazard (bottom panel). BO=Burn-only, TO=Thin-only, TB=Thin+Burn. Total effect represents observed or calculated treatment effect, indirect effect represents influence of treatment mediated by beetle outbreak on total effect, and direct effect (total minus indirect) represents standalone treatment effect. Effect significance at 95% confidence level is shown by capital letter above bars (T=total, I=indirect, D=direct); lowercase letters signify significance at 90% confidence.

Chapter 4: Stand dynamics 11 years after retention harvest in a lodgepole pine forest

Abstract

Structurally diverse forests provide resilience to an array of disturbances and are a mainstay of multiple-resource management. Silviculture based on natural disturbance can increase structural heterogeneity while providing other ecological and economic benefits. One useful silvicultural tool for promoting structural heterogeneity is retention harvesting, whereby a proportion of forest stands are left unlogged, transitioning even-aged stands to multi-aged. This technique is useful in stands with historically moderate- (20% to 70% mortality) and mixed-severity (complex of low, moderate, and high mortality) fire regimes as managers can retain live stems to emulate the variable structures and patterns that would have persisted after a dynamic fire. We report stand and tree dynamics 11 years after retention harvest (8-9 years after burning) in a central Montana Rocky Mountain lodgepole pine forest with evidence these fire regimes. Treatments were implemented on 16 experimental units with two 50% overstory basal area retention patterns (Aggregated and Dispersed) and two levels of prescribed fire use (Burned and Unburned). The aim of this study was to identify (1) how retention harvest spatial pattern affects stand dynamics, (2) whether growth, mortality, and regeneration processes were better described by treatment-scale retention pattern factors or fine-scale predicting covariates, and (3) how stem and basal area heterogeneity varied over the measurement period. We found that retention pattern affected overstory density, growth, mortality, and regeneration density and stocking. After including fine-scale tree size and competition covariates, the processes of overstory mortality, regeneration stocking, and regeneration height growth did not vary by treatment-scale

factors. Fine-scale covariates also explained overstory basal area growth, but growth was still greater in Dispersed treatments despite these predictors. Finally, we identified that structural heterogeneity degraded more rapidly in treatments with the Dispersed spatial pattern than Aggregated. This study evaluates novel silvicultural treatments in a lodgepole pine forest and highlights the tradeoffs between retention patterns combined with broadcast burning on forest change.

Introduction

A number of recent studies show that forest structural heterogeneity is associated with resilience to exogenous disturbances, including climate change, fire, and bark beetles (Drever et al., 2006; Johnson et al., 2014; Lydersen and North, 2012; Reynolds et al., 2013). Forest structural heterogeneity is also shown to improve elements of ecological function, including productivity and biodiversity (Huston, 1979; Seidl et al., 2014; Shugart et al., 2010; Tews et al., 2004). Furthermore, altering forest structure appears to be the primary means to actively bolster ecological resilience and function. Forest managers can improve ecological resilience and function by manipulating forest structure at a variety of scales, from tree neighborhood scales up to forest landscapes.

One of the ways that managers increase ecological resistance or resilience to disturbances is by making forest structure resemble that which follows a historically typical disturbance event, i.e., natural disturbance-based management (Attiwill, 1994; Drever et al., 2006; Long, 2009). This is often well-received because of the back-to-nature sentiment and aesthetic, but it also has the benefit of retaining trees on site that are more apt to survive future disturbance, increasing biodiversity, and/or modifying the physical environment to change the character of future

disturbances, all while providing timber for local economies (Bergeron et al., 1999; Churchill et al., 2013; Fiedler et al., 2001; Franklin et al., 2002; Mitchell et al., 2006). Retention harvesting (RH) is one such transformative silvicultural cutting option for creating structural heterogeneity and maintaining biological legacies that emulate the structure after natural disturbance (Franklin et al., 1997; O'Hara, 2001). This technique is primarily advocated as an alternative to clearcutting and traditional even-aged management, because various structural elements (e.g., green trees, snags, or riparian areas) are retained to provide biological continuity in forest structures and ecological processes over time. Thus, RH is a means to increase forest complexity (structural, functional, and compositional), aesthetic value, and habitat diversity while providing opportunity for timber product extraction (McCaughey et al., 2006; Mitchell and Beese, 2002).

In RH, residual stand structures vary to accommodate any number of spatial patterns and densities. Spatial retention patterns associated with RH are “aggregated” (attributes are retained in clumps), “dispersed” (retained attributes are spatially scattered and widespread), or a combination of the two, making RH a flexible management option with a multitude of structural outcomes (Beese et al., 2003; Halpern et al., 1999). While investigations have characterized forest change due to RH in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red pine (*Pinus resinosa* Aiton), effects of RH strategies on stand dynamics in lodgepole pine systems have not been documented to-date. Land managers need empirical understanding of stand development by retention pattern to assess whether RH prescriptions are viable to meet desired forest conditions.

Furthermore, it is unclear how tree growth, mortality, and regeneration processes vary within RH stands, or if spatial structure contributes to these processes after accounting for tree size and competition (Aubry et al., 2004). Stand-scale and tree neighborhood-scale structure

directly mediate stand development processes via competition (e.g., resource availability for growth and survival) and facilitation (e.g., seed source and microclimate moderation) (Oliver and Larson, 1996). This is dependent on distances between attributes of interest, differences in age, species, growth habit, and clumpiness. Thus, structure is fundamentally important for stand development, as well as resistance and resilience to exogenous disturbances (Crotteau et al., 2016; Larson and Churchill, 2012).

Although a useful tool for increasing structural heterogeneity in any forest type, RH is particularly appropriate in forests with historically moderate- (20% to 70% mortality) and mixed-severity (complex of low, moderate, and high mortality) disturbance regimes as these disturbances create stand heterogeneity. Though typically linked to high-severity disturbances and even aged stands from post-disturbance regeneration pulses (e.g., Turner et al., 2003), lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests are also associated with moderate or mixed-severity fire regimes (hereafter, just "mixed"; Agee, 1993; Barrett, 1993; Horton, 1956). Mixed-severity fires partially remove overstory and stimulate regeneration to form a multi-aged stand structure (Axelson et al., 2010) that may in turn be maintained by future mixed-severity fire or reset by stand replacing crown fire (Fischer and Clayton, 1983). Given the more conspicuous prevalence of stand replacing fires in lodgepole pine forests, typical active management using the clearcutting silvicultural system emulates the open-overstory conditions conducive to regenerating lodgepole pine, a shade intolerant species with prolific seed banks (Alexander et al., 1983). Yet, given the ecological precedent of a mixed-severity regime and associated multi-aged forest structure, RH is a silvicultural option that balances both practical (economic) and ecological (resilience) goals (Keyes et al., 2014) in such forest types. Since

lodgepole pine is a major commercial species with a vast range in North America, it is important to better understand the changes to forest structure under such alternative treatments.

One concern with natural disturbance-based management, such as RH to emulate mixed-severity disturbance, is that treatments do not fully approximate the disturbance modeled after (Nitschke, 2005; Perera et al., 2004). For example, post-disturbance spatial heterogeneity of live and dead vegetation, surface debris, nutrient cycling and water yield in natural versus managed stands may not align. One reason stands managed with RH may not adequately represent naturally perturbed stands is that we have little information on the spatial variability of these processes and stand structures (Long, 2009). In systems with low-severity disturbance regimes, spatial patterns have been successfully mapped and proven advantageous for emulating structure (Churchill et al., 2014; Sánchez Meador et al., 2011). However, mixed-severity disturbance regimes are especially variable and are occasionally reset by stand replacing fire, making it difficult to assess spatial characteristics of historical fires and subsequent in-stand patchiness (Collins and Stephens, 2010). Further research and monitoring of these disturbance regimes will inform clump size and spatial distributions within stands necessary to better emulate the natural process. As with a number of natural disturbance-based management options in fire dependent ecosystems, prescribed burning can be used as a subdued surrogate for natural fire (e.g., Larson and Churchill, 2012; Mitchell et al., 2006; Noss et al., 2006). Pairing RH with prescribed burning can improve site preparation for regeneration, fuel reduction, nutrient release, and environmental heterogeneity, more closely approximating the disturbance modeled after.

The goal of this study was to evaluate post-RH stand dynamics in lodgepole pine to inform future RH treatments. We examine forest structure 11 years after a replicated experimental RH treatment in a lodgepole pine forest in central Montana to determine the effects

of retention spatial pattern and subsequent prescribed fire on stand structure, growth, mortality, and regeneration (collectively referred to here as “stand dynamics”). Harvests retained 50% basal area in either aggregated or dispersed spatial patterns, and half of treated stands were burned with prescribed fire. Our first research question is: what are the 11 year stand dynamics after retention harvesting in lodgepole pine, and how do these dynamics differ with prescribed burning? We expected that stand dynamics would differ by RH pattern because of the starkly different retention approaches, and that prescribed fire after RH would stimulate regenerating cohort at the expense of the overstory. However, we also expected that these dynamics would vary within treated stands because of heterogeneous treatment structure, and that environmental and competitive conditions would drive dynamics. Therefore our second question is: are stand dynamics after RH treatments and subsequent prescribed fire simply attributable to tree size and competition, or does harvest pattern affect dynamics beyond those measures? We expected that RH and fire treatments may further explain variation in stand dynamics because environmental heterogeneity may be inadequately quantified with simple covariates. Our third research question is: does retention pattern perpetuate the variability in structure and growth that treatments establish? We predicted treatments would lead to greater stand variability and growth with time when retention pattern affects post-harvest growth and mortality. The results of this study apply most pertinently to lodgepole pine forests in the Rocky Mountains, but analytical methodology and overstory-understory dynamics will resonate with RH applications in conifer forests throughout the world.

Methods

Study Site

The United States Forest Service's Tenderfoot Creek Experimental Forest is a 3,693 ha watershed in the Little Belt Mountains, within the Lewis and Clark National Forest in central Montana. Elevation ranges from 1,840 m to 2,421 m. The forest is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson), forming nearly pure even-aged and multi-aged stands. Associated overstory species are subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and whitebark pine (*Pinus albicaulis* Engelm.). Associated shrub species are grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville) and thinleaf huckleberry (*V. globulare* Douglas ex Torr.). Soils are typified by loamy skeletal, mixed Typic Cryochrepts, and clayey, mixed Aquic Cryoboralfs (Adams et al., 2008).

Climate in the experimental forest is generally continental, though is also influenced by the Pacific maritime climate extending beyond the Continental Divide. Annual precipitation is 880 mm, ranging from 594 mm to 1,050 mm across the elevation gradient (Adams et al., 2008). The majority of the precipitation occurs in the form of snow from November to May. Typical mean temperatures range from -9°C in January to 17°C in July, with freezing temperatures possible throughout the year. The average plant growing season is estimated to be between 30 and 75 days.

Reconstructed fire history revealed a characteristic mixed-severity fire regime in the study area (Barrett, 1993). For the period of 1580 to 1992, mean fire return interval was 38 years, with large, severe fires occurring less frequently, and low- to mixed-severity fires occurring between large, severe fire events. Treated stands were multi-aged, ranging from 80 to 274 years old just prior to treatment implementation.

Experimental Design and Sampling

Two-aged silvicultural treatments were installed in 16 units, split among two sub-watersheds of Tenderfoot Creek on the Experimental Forest (McCaughey et al., 2006). Units in two adjacent sub-watersheds were established as untreated reserves (hereafter, ‘controls’). The harvest prescription called for 50% (range: 40% to 60%) basal area retention and created two spatial patterns: aggregated and dispersed. The aggregated spatial pattern was characterized by 4 to 27 large (0.1 to 0.6 ha) clumps or reserves distributed throughout each stand in irregular shapes. In the dispersed spatial pattern, residual overstory was primarily distributed at an even spacing wide enough for harvesting machinery to navigate. Following harvest, half of the treatment units were broadcast burned in the fall with low-intensity fire (though severity was greater than anticipated; see Hood et al. 2012). Thus, there were a total of 16 treatment units: two RH treatments (Aggregated and Dispersed) \times two fire treatments (Burned and Unburned) \times two replicates per subwatershed \times two subwatersheds. Harvesting took place in 1999 and 2000; stands selected to be treated with prescribed fire were burned in 2002 or 2003. Pre- and post-treatment (to 2004) stand conditions have been documented in detail (Hood et al., 2012).

We report data from two overstory and regeneration sampling events. We measured overstory and regeneration on 180 nested points/plots (5 to 17 per unit) approximately 11 years after harvest, and combine our measurements with a post-treatment dataset from the same plots to evaluate stand dynamics. Plots were located on a grid, independent of treatment structural attributes. Pretreatment overstory trees were measured using either 4.59 m²ha⁻¹ or 9.18 m²ha⁻¹ basal area factor prisms (measurement year range: 1997-2000; 2000-2001 for controls). Overstory trees were revisited one year post-harvest (prior to prescribed burn) and cut trees were noted; harvested trees were removed for a “post-harvest” dataset, our “initial” measurement.

Another follow-up visit was made one year after burning (2003-2004) to record fire damage on overstory trees. In 2011, we remeasured overstory trees in the treatment units using 0.040 ha circular fixed-area plots; transition to fixed-area plots was designed to facilitate simple a simple future remeasurement. In both overstory measurements (post-harvest and 2011), species and diameter were recorded for all stems ≥ 10.16 cm diameter at breast height (1.37 m; DBH).

Seedlings (height < 1.37 m) were tallied by species in 2004 and 2011 for regeneration density and composition. These were measured on 0.001 ha circular fixed-area plots which overlaid each of the overstory plot locations. Crop seedlings (tallest lodgepole pine regeneration) were measured in 2011 on four 0.010 ha quadrants of the 0.040 ha overstory plots for stocking and height growth. Quadrants were considered stocked at 100 trees ha⁻¹ if crop seedling was present; plot stocking was the average of stocked quadrats, ranging from 0 to 100% stocking. Although stocking at 100 trees ha⁻¹ is insufficient for post-clearcut reforestation in the region, we considered it to represent the low end of acceptable stocking in a heterogeneous multi-aged stand. Recent crop seedling periodic annual height growth was the average annual height growth over the period 2006 to 2010, measured retrospectively by distance between whorls.

Analysis

We addressed our research questions by analyzing post-harvest changes in the overstory and natural regeneration attributes over the entire period since treatment. We examined species composition and density for the overstory and regenerating cohort by averaging data by treatment (n=4 unit replicates per treatment) but refrain from statistically testing these given the change in sampling methods (switched from point sample to areal plot sample) over the measurements.

Specific stand dynamics processes (overstory tree basal area growth, overstory tree mortality, crop regeneration (“crop seedling stocking”), and crop seedling height growth) were assessed and tested with general and generalized linear mixed-effects models, with measured plots nested within experimental units. We developed four statistical models for each of the four response variables to address our research questions: (1) a Null model (only watershed block-unit-plot nesting structure included), (2) a Treatment model (RH × fire treatment interaction included), (3) a Predictive model (best selected model given full suite of immediately post-harvest size, structure, and environmental covariates, including fire treatment but excluding RH treatment and interaction), and (4) a Saturated model (Predictive model plus interaction between RH × fire treatment, and RH × Fire × covariates interactions). These models were fitted to explain processes and highlight differences by treatment, not necessarily for prediction. We used AIC (Burnham and Anderson, 2002) for model selection and comparison; models were considered to be a better fit if AIC was at least two points lower. Coefficient P-values were used to parse out effects in selected models assuming an α of 0.05 means strong statistical evidence and 0.10 means marginal statistical evidence. For each model, we report AIC, marginal (fixed-effects only) and saturated (including plot and tree random effects) R^2 (Nakagawa and Schielzeth, 2013), and for binomial models, a dispersion parameter (model residual deviance per degrees of freedom). We noted covariate explanatory power using marginal R^2 and a leave-one-out analysis.

Selected covariates for the linear models were: percent live crown, “basal area greater”, percent basal charring, height:DBH ratio, overstory stand density index (SDI), and seedling height. Each of these covariates were initial (post-harvest) measurement values from the beginning of our measurement period (except seedling height, which was retrospectively

measured to 2006). Percent live crown was the compacted length of live crown divided by total tree height. Basal area greater was the summed basal area of trees with greater DBH than the tree of interest on the 0.04 ha plot. Percent basal charring was the percent of total tree basal circumference covered in char from prescribed fire. Height:DBH was the ratio of total tree height to DBH in the same units. Stand density index was the metric conversion of the relative density measure developed by Reineke (1933). Seedling height was the height of the 2006 whorl of crop lodgepole pine regeneration.

The basal area growth models predict the basal area periodic annual increment for overstory trees visited in both the post-harvest and 2011 measurements (n=122; 93% lodgepole pine). Basal area growth was considered to have a Gaussian error structure and was modeled using `lme` in R (Pinheiro et al., 2016; R Core Team, 2016). The predicted basal area growth rate under the Saturated model had the form:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \varepsilon_1 + \varepsilon_2 \quad [1]$$

where y is periodic annual basal area growth, β_0 through β_6 are estimated coefficients, x_1 is the watershed block (0=North facing, 1=South facing), x_2 is the prescribed fire effect (0=burned, 1=unburned), x_3 is the retention pattern effect (0=aggregated, 1=dispersed), x_4 is percent live crown, x_5 is basal area greater, ε_1 is the error term associated with the stand (experimental unit), and ε_2 is the error term associated with plots nested within the stand.

The mortality models predict tree death between the two overstory measurements (n=177; 93% lodgepole pine). This response (live or dead) had a binomial error structure and was modeled using `glmer` in R (Bates et al., 2015). The predicted mortality rate under the Saturated model had the form:

$$y = \frac{e^{\rho}}{1+e^{\rho}} \quad [2]$$

where

$$\rho = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \beta_7 x_6 + \beta_8 x_7 + \beta_9 x_8 + \varepsilon_1 + \varepsilon_2 \quad [3]$$

where y is tree mortality (0=live, 1=dead), β_0 through β_6 are estimated coefficients, x_1 is the watershed block (0=North facing, 1=South facing), x_2 is the prescribed fire effect (0=burned, 1=unburned), x_3 is the retention pattern effect (0=aggregated, 1=dispersed), x_4 is DBH, x_5 is total height, x_6 is height to diameter ratio, x_7 is percent basal char, x_8 is percent live crown, ε_1 is the error term associated with the stand (experimental unit), and ε_2 is the error term associated with plots nested within the stand.

The stocking models predict lodgepole pine regeneration stocking at 100 trees ha⁻¹ in 2011, at the plot scale (n=129). Since the response was a proportion bounded by 0 and 1, this error structure was modeled as binomial using `glm` in R. The predicted stocking rate under the Saturated model had the same form as Eqn. [2], but y is plot stocking (0=0% stocked, 1=100% stocked), and

$$\rho = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \varepsilon_1 \quad [4]$$

where β_0 through β_6 are estimated coefficients, x_1 is the watershed block (0=North facing, 1=South facing), x_2 is the prescribed fire effect (0=burned, 1=unburned), x_3 is the retention pattern effect (0=aggregated, 1=dispersed), x_4 is post-harvest overstory stand density index (SDI; Reineke, 1933), and ε_1 is the error term associated with the stand (experimental unit).

The height growth models predict recent periodic annual height growth of crop regeneration seedlings, based on up to four years of growth ending in 2010 (n=333). Height growth had a Gaussian error structure and was modeled using `lme` in R. The predicted height growth rate under the Saturated model had the form:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_2 x_3 + \beta_5 x_4 + \beta_6 x_5 + \beta_7 x_6 + \varepsilon_1 + \varepsilon_2 \quad [5]$$

where y is periodic annual height growth, β_0 through β_6 are estimated coefficients, x_1 is the watershed block (0=North facing, 1=South facing), x_2 is the prescribed fire effect (0=burned, 1=unburned), x_3 is the retention pattern effect (0=aggregated, 1=dispersed), x_4 is post-harvest overstory SDI, x_5 is initial (retrospective) seedling height at the beginning of measurement, dating back as far as 2006, ε_1 is the error term associated with the stand (experimental unit), and ε_2 is the error term associated with plots nested within the stand.

Results

Overstory

SPECIES COMPOSITION

Lodgepole pine dominated overstory species composition throughout the duration of this study, followed by subalpine fir and Engelmann spruce. Immediately after harvest, overstory lodgepole pine composition by basal area was lowest in the Aggregated treatments (83.3% [1 SE: 16.7%] in Unburned and 84.4% [10.0%] in Burned), and slightly greater in the Dispersed treatments (86.2% [8.0%] in Burned and 98.2% [1.8%] in Unburned). By the 2011 measurement, Aggregated treatments still had lower lodgepole pine composition (80.5% [11.3%] in Unburned and 86.8% [7.3%] in Burned) than Dispersed treatments (88.2% [8.4%] in Unburned and 95.4% [4.1%] in Burned).

STAND DENSITY

Mean post-harvest basal area densities in treated plots ranged from 10.4 m²ha⁻¹ to 28.0 m²ha⁻¹, roughly 40% to 60% of pre-harvest densities (Table 1). Immediately after harvest (prior to burning), plots in the Aggregated Burned treatment had the highest basal area densities, which differed from its Unburned counterpart despite having the same aggregated harvest prescription. Aggregated RHs had low minima and high maxima, reflecting fully cleared stand openings juxtaposed with dense retention clumps. Mean densities in the Aggregated RH treatment

encompassed those of the Dispersed RH treatment. Similar to the Aggregated treatments, stands assigned to the Burn treatment in the Dispersed RH treatment had greater densities than the stands assigned to the Unburned treatment.

By 2011 (approximately 11 years after harvest and 8 years after prescribed fire), mean basal area densities in the Aggregated RH treatments became more similar following a 35% reduction in the Burned treatment basal area and a slight increase in the Unburned treatment (Table 1). In Aggregated RH treatments, basal area densities remained higher in the Burned treatment relative to the Unburned treatment throughout distribution quartiles, but in the Dispersed RH treatment basal area in the Unburned treatment became slightly greater than in the Burned treatment, where basal area dropped in response to fire. The average range of values decreased 40 to 55% in the Dispersed treatment compared to only a 25% reduction in the Aggregated treatments. Furthermore, variability throughout the Dispersed treatments' distributions (i.e., by quartile) declined substantially (by an average of 48% and 70% for the Unburned and Burned, respectively) but standard errors increased or only slightly decreased in the Aggregated treatments (+40% in Burned or -8% in Unburned). Altogether, this indicates that the Dispersed RH pattern moderated structural heterogeneity over time relative to the aggregated.

OVERSTORY TREE GROWTH

When tree growth was evaluated by treatment alone (Treatment model), there was marginal statistical evidence of the RH \times fire treatment interaction ($P=0.0624$; Table 2). Overstory tree annual basal area growth in Aggregated treatments averaged 4.01 cm² (Burned) and 3.09 cm² (Unburned), and Dispersed treatments averaged 4.97 cm² (Burned) and 6.93 cm²

(Unburned). Levene's test of homogeneity among treatments, ignoring the nested data structure, indicated that variance of growth was no different across treatments (P-value=0.3436).

The annual basal area growth Predictive model had lower AIC and higher marginal R^2 than the Treatment model, indicating that post-harvest structural attributes better account for growth than treatment factor levels (Table 2). Annual basal area growth was best predicted by the combination of post-harvest percent live crown, post-harvest overstory SDI, and post-harvest basal area of local trees larger than the response tree. These covariates had opposite effects, showing that basal area growth increased with relative crown size but diminished with competition. Crown ratio and basal area greater comprised 27% and 19%, respectively, of the explanatory power of the model.

After adding treatment factors to the Predictive model to form the Saturated annual basal area growth model (Table 2), the overstory SDI covariate no longer improved the model and it was removed. The Saturated growth model had significantly lower AIC and higher R^2 than the Predictive model, indicating that treatment factors were still important even after accounting for predictive covariates (Figure 1).

OVERSTORY TREE MORTALITY

Like overstory tree growth, our overstory tree mortality Treatment model showed marginal statistical evidence that mortality was influenced by the interaction of retention pattern and prescribed fire (P=0.0545; Table 3). Over the entire period, mortality rates in the Aggregated treatments were 25.4% (Burned) and 23.6% (Unburned), and 50.4% (Burned) and 7.1% (Unburned) in the Dispersed treatments. Among Burned treatments, tree mortality in the Dispersed retention was especially high because fire spread throughout each unit, while fire in the Aggregated treatment generally did not enter into retention clumps. Levene's test of

homogeneity among treatments, ignoring the nested data structure, suggested that variability of mortality differed by treatment (P-value=0.0095). In this analysis, trees in the Burned Dispersed RH treatment had the most variable mortality rate whereas trees in the Unburned Dispersed RH varied least.

Our Predictive model AIC and R^2 illustrate that it fit the data much better than the Treatment model (Table 3). Mortality was best predicted by the combination of post-harvest tree DBH, height, taper (Ht:DBH), percent live crown, and percent basal char. These covariates indicate that probability of mortality increased with percent basal char, Ht:DBH, DBH, and percent live crown, but decreased with tree height (Figure 2). Percent basal char was the most influential covariate in this model, comprising 73% of the marginal R^2 ; Ht:DBH comprised 22% of the explanatory power.

The Saturated overstory tree mortality model's AIC indicated it was no better than the Predictive model (Table 3).

Regeneration

ABUNDANCE AND COMPOSITION

Natural regeneration was abundant in all the treated stands in 2004 and 2011 with lowest average abundance over 5,000 seedlings ha^{-1} (Table 4). In 2004, Aggregated treatments had 50% more seedlings than Dispersed treatments, and Burned treatments had 31% more than Unburned. By 2011, seedling density decreased by 26%, except in the Dispersed Unburned, which increased 54%. Burned treatments had 79% greater in-stand seedling density variability than Unburned in 2004, but by 2011 variability decreased by 46%, except in Dispersed Unburned, which increased 50%. In-stand variability was only substantially less than the mean (coefficient of variation < 1) in 2011's Aggregated Unburned treatment. Lodgepole pine comprised 51% of seedlings across

treatments in 2004, while the remainder was predominantly subalpine fir. Between 2004 and 2011, lodgepole pine seedling composition decreased by 44% and was eclipsed primarily by large caches of subalpine fir. Combined Engelmann spruce and whitebark pine seedling composition was never greater than 5.5% in the 2004 measurement, and not more than 13.3% in 2011 (both in Dis:B).

CROP SEEDLING STOCKING

Lodgepole pine stocking was significantly impacted by retention pattern when only considering treatment factors ($P=0.0153$; Table 5 Treatment model). In 2011, stocking levels in the Aggregated treatments were 46.9% (Burned) and 57.5% (Unburned), and in Dispersed treatments were 95.8% and 78.4%, respectively. Levene's test of homogeneity among treatments, ignoring the nested data structure, indicated that variability in stocking differed by treatment ($P\text{-value}=0.0005$). Burning caused both high (in Aggregated) and low (in Dispersed) variability in stocking estimates.

The Predictive stocking model only had a slightly better R^2 than the Treatment model, but AIC was far superior. After accounting for the blocking factor and an intercept, stocking was best predicted by post-harvest overstory SDI alone. The SDI covariate indicates that the relative density of the overstory above the regeneration measurement negatively impacted crop seedling stocking (Figure 3).

In contrast to the Predictive model's improvement over the Treatment model, the Saturated model had a substantially better R^2 than the Predictive model, but AIC indicated that it was not superior to it (Table 5). Improvement in the R^2 is largely from the marginally significant retention pattern term ($P\text{-value}=0.0619$) and its interaction with prescribed burning.

CROP SEEDLING HEIGHT GROWTH

Crop seedling height growth did not vary by treatment when only considering treatment factors (Table 6 Treatment model). Recent periodic annual height growth at 2010 was 17.6 cm (Burned) and 17.8 cm (Unburned) in Aggregated treatments, and 16.7 cm (Burned) and 15.2 cm (Unburned) in Dispersed treatments. Levene's test of homogeneity among treatments, ignoring the nested data structure, suggested that variability in growth did not significantly differ across treatments (P-value=0.0946).

Like the crop seedling stocking Predictive model, the height growth Predictive model only slightly improved the R^2 , but better impacted AIC (Table 6). Height growth was best predicted by post-harvest overstory SDI, prescribed fire occurrence, the square root of the seedling height at the beginning of the recent period (as early as 2006), and the interaction between prescribed fire and tree height. These covariates indicate that overstory competition reduced height growth, that seedling height had a diminishing improvement effect on growth for Burned treatments, and that height growth was largely independent of seedling height in Unburned treatments (Figure 4).

The Saturated model for annual height growth had a slightly better R^2 than the Predictive model but did not improve AIC (Table 6).

Discussion

To summarize broad results by our initial research questions, we first found that overstory tree growth, overstory tree mortality, and regeneration stocking varied by retention pattern or its interaction with prescribed fire. All treatments had ample regeneration and high in-stand variability throughout the study period, although subalpine fir regeneration composition is disproportionately greater than its presence in the overstory. Second, we identified that although it

improved model prediction, spatial stand structure represented by retention pattern factors did not contribute to the mechanistic understanding of overstory tree mortality, regeneration stocking, and regeneration height growth; instead, combinations of overstory competition, tree size, and tree form better explained those processes. Third, Aggregated retention treatments maintained overstory spatial heterogeneity better than Dispersed retention treatments over the measurement period.

Stand dynamics by treatment

Eleven years after treatments, overstories were still dominated by lodgepole pine, but lodgepole pine regeneration composition had declined. Lodgepole pine overstory dominance was greater in Burned treatments likely because fire-induced mortality of subalpine fir, the second-most abundant species, has thin bark and greater sensitivity to fire than lodgepole pine (Hood et al., 2008; Lotan and Critchfield, 1990). Fischer and Clayton (1983) identified that low-intensity fires maintain lodgepole dominance (and self-succession) in unmanaged Douglas-fir, subalpine fir, and Engelmann spruce habitat types east of the Continental Divide by reducing stem density, fuels, and shade-tolerant species (see also Agee, 1993). Without shade-tolerant species removal by wildfire or silvicultural treatments, overstory composition will eventually transition to fir-spruce after RH, thus failing to perpetuate the multi-aged lodgepole pine structure associated with mixed-severity fire that the RH was modeled after. However, sites with edaphically limiting soils that preclude shade-tolerant species (e.g., Oregon [Stuart et al., 1989]) or sites conducive to successful lodgepole pine regeneration (e.g., British Columbia [Axelson et al., 2010]) have been found to perpetuate multi-aged lodgepole pine even in the absence of fire. Despite the decline in the lodgepole pine component in the Unburned treatments, lodgepole pine overstory dominance was still the defining and influential characteristic of each of these treatments in 2011.

It was surprising that lodgepole pine was a minority in 2011's total seedling species composition, 11 years after harvest. Since these treatments removed more than 50% of initial stand basal area, and residual overstory composition was over 80% lodgepole, we expected more regeneration from the shade-intolerant lodgepole pine (but see similar compositional shift in Day [1970]). This may be due to an asynchrony between cone production and treatment schedule, poor lodgepole pine cone release, or destruction of regeneration by treatment. However, lodgepole pine regeneration densities are sufficient to develop closed overstories, particularly in the Aggregated Burned and Dispersed Unburned treatments. Rocky Mountain lodgepole pine associated with mixed-severity fire has semi-serotinous cones (Lotan et al., 1985), but since we found no consistent trend by prescribed fire treatment it is also apparent that cone serotiny did not limit regeneration success. Furthermore, lodgepole pine's rapid early height growth will likely lead it to dominance and long-term height stratification despite the compositional minority (Cobb et al., 1993; Fahnestock, 1976). Traits that make lodgepole pine an adept colonizer after mixed-severity fire (i.e., prolific regeneration, cone serotiny, and rapid early height growth) may also stimulate thriving cohorts in stands managed with RH, though this study shows that lodgepole pine may not be dominant in the first decade after treatment.

Retention harvests created heterogeneous, non-normally distributed basal area distributions in treated units. In particular, stand conditions in the Aggregated treatment shifted from high to low densities (retention patch to opening) across very short distances. Although we advocate that RH can be used to emulate the patchy overstory structure created by mixed-severity fire, we have little basis for the size of the clumps (0.1 to 0.6 ha) in our Aggregated RH treatment units. We note that treatment basal area retention level and spatial distribution was only partially based on ecological data – existing data was low resolution and only identified

existence of multiple cohorts in the past centuries, not the patch size distribution within stands (Barrett, 1993). Furthermore, landscape analysis of lodgepole pine in these fire regimes indicate patch sizes larger than the retention clumps in this study's Aggregated treatments are necessary to emulate historical structure (Hardy et al., 2000; similarly, in Hessburg et al., 2015). Thus there was some historical ecological basis for treatment implementation, but it was infused with practical objectives for project feasibility, vigorous and widespread regeneration, ample overstory cover, windfirmness, and desired patchiness. Despite the motivational basis for the stand structure in these treatments, these residual overstory dynamics will help to inform similarly managed stands.

From the net loss in basal area (also in stems per acre and SDI; data not shown) in the majority of these stands, it is clear that mortality agents offset the increased resource availability for residual stems. Despite the site's low productivity (site index between 11.3 m and 16.8 m at 50 years) and short growth period (11 years), the net loss was unexpected (compare to Maguire et al., 2006; Palik et al., 2014) because extant mortality was not anticipated. However, sampling issues may have blurred these stand-scale effects. Some of the difference between Aggregated treatments (Burned vs. Unburned) is attributable to the plot layout, by which we sampled a higher proportion of group interiors in the Burned treatment than in the Unburned treatment owing to the manner in which the gridded plot network overlapped retention units. Also, estimates of overstory change over time (for all treatments) are not limited to ingrowth, growth, and mortality because differences in our sampling technique between overstory measurements adds methodological error to the density estimates. Namely, all trees had equal probability of inclusion in the fixed-area plot methodology in 2011, but larger trees had greater probability of inclusion than small trees in the post-harvest point sample, which is a probability proportional to

size sampling method. Thus change in densities reflect a composite of actual change and within-unit sampling error. Though multiple error sources may be disconcerting from a practical perspective (hence the reason we avoided statistical testing), Gregoire (1993) suggests the concern is of little statistical consequence.

Treatment models show retention pattern significantly impacted basal area growth and weakly moderated overstory tree mortality over the measurement period, but fire effects depended on RH treatment. In both the overstory growth and mortality models this effect was manifested by the interaction between retention pattern and prescribed fire, which showed that trees in the Unburned Dispersed treatment had greater growth and survival than expected from either treatment factor alone. Greater growth in residual trees after Dispersed RH has been documented in other studies. For instance, Douglas-fir dominated stands in the Demonstration of Ecosystem Management Options (DEMO) study showed greater volume growth with dispersed retention (Maguire et al., 2006; Urgenson et al., 2013a). This was accompanied with more overstory mortality, but the effect on Douglas-fir mortality was moderated by retention level. In Minnesota red pine, biomass growth was also slightly greater after dispersed retention, but mortality rates did not differ by treatment (Palik et al., 2014). However, these retention studies did not investigate the effects of prescribed fire, nor are studies of underburning in lodgepole pine forests common, so this study adds depth to both retention and lodgepole pine studies. Our results suggest why there are few experiments studying burning in this forest type: lodgepole pine survivorship is sensitive to even low-intensity fire if it chars more than half of the bole. These results are consistent with the argument by Lotan et al. (1985) who make the case that broadcast burning in lodgepole pine forests achieves multiple-use management objectives, but caution that burning should be implemented with special care to avoid mortality.

Notwithstanding the beneficial effect of burning on overstory composition (i.e. increased proportion of lodgepole pine), our data suggests that combining broadcast burning with a Dispersed pattern conflicts with retention objectives in lodgepole pine forests because of the substantial loss of overstory. In our study, median basal area densities in the Dispersed Burned treatment were a third of those in the Dispersed Unburned treatments in 2011, and mean basal area was only 13% of pre-treatment density. Whereas 10% to 15% overstory retention may be desirable for other forest types or objectives (e.g., Baker and Read, 2011; Mitchell and Beese, 2002), the recent accumulation of forest fuels (Crotteau et al., 2016) and live overstory losses in these burned stands did not resonate with this forest's original management intentions. More research is needed to evaluate the benefits that broadcast burning has on wildlife habitat, biodiversity, hydrology, disturbance resilience, and aesthetics in lodgepole pine forests to adequately consider management tolerance for diminished stand-scale growth and increased mortality in the Dispersed overstory.

Our Treatment models also indicate that crop seedling stocking was greatest in Dispersed treatments, but that crop seedling height growth was similar across all treatments. In the DEMO study, planted seedling mortality was greater in the Aggregated treatment for mid- and shade-tolerant species (Maguire et al., 2006), and though stocking was typically sufficient, it was occasionally low in the Aggregated treatment (Urgenson et al., 2013b). In contrast, planted seedling survival did not vary by treatment in a similar red pine experiment (Palik et al., 2014). In terms of height growth, the DEMO study resulted in greater height growth for shade intolerant species in the Aggregated treatment (Maguire et al., 2006). At the red pine experiment, seedling biomass growth was not statistically different by treatment, though it was greater in the openings of Aggregated treatments (Palik et al., 2014). In an alternative perspective, regeneration growth

was negatively impacted by levels of dispersed overstory retention in Alberta's Ecosystem Management Emulating Natural Disturbance (EMEND) experiment (Gradowski et al., 2008). In the end, regeneration growth was expected to be greater in Aggregated than Dispersed treatments because Dispersed treatments cast shade directly over regeneration (similar structure to a shelterwood harvest prior to the removal cut), which promotes even distribution of stocking but hinders regeneration growth as overstory retention does in. We may not have observed a treatment effect on regeneration height growth because overstory survival was so low in the Dispersed RH treatment, making regeneration conditions similar to the open environmental conditions present in the Aggregated RH treatment.

What drives differences in stand dynamics?

OVERSTORY

Basal area growth is important for overstory resistance to wind damage and continued function as two-storied stands. Basal area growth is also a measure of tree vigor, which may also improve resistance to successful bark beetle attack (Larsson et al., 1983). Our final basal area growth model indicated that both competition from above (basal area greater) and percent live crown were important predictors of overstory tree growth. These were expected results (e.g., per Hann and Larsen, 1990; Wykoff, 1990), but we were surprised that absolute measures of tree size such as basal area, height, and volume were excluded from the final Predictive model. The potential effects of those covariates may have been confounded by strictly linear predictors and our limited sample size, or it may be that the combined competition covariates (SDI and basal area greater) and relative crown length really are more influential than tree size for this range of data. Although basal area periodic annual increment is mechanistically explained by measures of crown size and competition, the Saturated model shows there was some unmeasured element that

contributed to variability in growth across the retention pattern and prescribed fire interaction. The prescribed fire and interaction terms may have replaced post-harvest overstory SDI as a significant predictor because mortality altered competition, and the competitive environment that predominantly influenced tree growth is better represented by treatment factors than post-harvest SDI.

The best overstory tree mortality model showed that mortality was linked to tree DBH, height, Ht:DBH, percent basal char, and percent live crown. The positive influence of DBH on mortality is counter-intuitive because large trees typically have the competitive edge over smaller neighbors. As such, our models suggest that competition has not been the primary driver of mortality during this measurement period, an idea confirmed by the absence of competition covariates in this model. The predominant mortality agent in this study was fire as shown by the predictive power of the basal char term. These results confirm that the impact fire has on near-term tree mortality (Hood et al., 2008) persists over a longer measurement period, and that fire damage is still a significant predictor of mortality even when multiple measures of tree size and competitive environment are accounted for. Our best model predicts 50% probability of mortality at 54% basal charring, which emphasizes that lodgepole pine tolerates fire poorly, and that patchy prescribed fire in this forest type can radically improve tree survival by retaining unburned patches. Additionally, the Ht:DBH model term suggests that wind was a significant mortality agent (as expected by Alexander, 1966) since high Ht:DBH values (slender trees) are associated with wind damage (Cremer et al., 1982; Wonn and O'Hara, 2001). This confirmed observations made by Hardy et al. (2006), who provide anecdotal evidence of wind-induced mortality shortly after initiating the Tenderfoot Project. According to this model, trees with Ht:DBH of 97 had a 50% probability of mortality. However, tree slenderness moderated

mortality less than we expected, as a Ht:DBH of 80 is recognized as a threshold for wind damage (Wonn and O'Hara, 2001). Finally, since the Saturated model was not better than the Predictive model, we identify that mortality was closely tied to tree size, shape, and charring, and not to competition or an unmeasured attribute of treatment-scale spatial structure.

REGENERATION

Stocking was moderated by post-harvest overstory density, which was greatest in the Burned treatment of the Aggregated retention pattern. The overstory density coefficient was expected to be significant because overstory competition inhibits successful regeneration of lodgepole pine, a shade-intolerant species (Lotan and Critchfield, 1990). Surprisingly, our best model predicts 50% stocking at an overstory SDI of 960, 55% of the maximum SDI for lodgepole pine and well beyond site occupancy where we would expect lodgepole regeneration to flourish (McCarter and Long, 1986). Although McCarter and Long (1986) found that post-harvest lodgepole pine regeneration stocking improved with overstory removal intensity, Alexander (1966) also found 53% stocking of advance regeneration in the uncut control, suggesting that stocking is less sensitive to residual overstory than regeneration abundance and growth. Overstory tree presence, as a seed source, may have had a positive impact on crop seedling stocking if retention level in these treatments was lower or more clumped (for instance, Cochran [1973] recommends openings less than two tree heights for optimum regeneration stocking). However, canopy openings in this study were small enough for adequate seed dispersal. The Saturated model shows that treatment levels add information to the fit beyond the effect of overstory density, but not enough to suggest causality of an unmeasured covariate that varies systematically by treatment. Therefore, 2011 crop seedling stocking in this study is primarily a function of post-harvest overstory density, but predictive capacity was improved by

treatment factors. This is important because seedling stocking increases stand resilience to beetles. Mountain pine beetle populations do not amplify to outbreak levels in cohorts less than 20 cm dbh or 80 years old (Axelson et al., 2010; Safranyik and Carroll, 2006), so regeneration secures stand resilience even if overstory is lost to outbreak.

Like the overstory tree growth model, the Predictive seedling height growth model supports our expectation that competition hinders height growth. We correctly anticipated that seedling size controls growth rate (Stage, 1975). The square root function effectively characterized the relationship between size and growth because increments in size improved height growth more for small trees than for larger trees in the regenerating cohort. Yet, we did not expect that the effect of starting height would benefit growth in the Burned treatment and not the Unburned treatment, the former having slightly greater average starting heights. This reflects that there is not a significant effect of prescribed fire on annual height growth until past height is accounted for because the smallest trees in the Burned treatments did not grow as much as the largest trees. This may be due to a post-burn nutrient pulse through the soil profile that only the initiated or larger regeneration was able to utilize (Vitousek and Matson, 1985). Giardina and Rhoades (2001) observed a positive seedling growth response to burned soils in the laboratory, but failed to find it in the coupled field study, partially supporting our results but also suggesting that growth response to burning is complex and variable. The Saturated model suggests that overstory density is paramount, and the retention tree spatial pattern (and its interaction with prescribed fire) does not significantly influence regeneration growth beyond its effect on post-harvest overstory density.

Treatment influence on spatial heterogeneity

Stand scale resistance and resilience to both beetle outbreak and crown fire may increase with spatial and structural heterogeneity (Crotteau et al., 2016; Johnson et al., 2014; Ziegler et al., 2017). Retention harvests created spatially heterogeneous conditions within stands in the Tenderfoot Project that are not fully characterized by the treatment mean and mean standard error. In some cases, the data range and distribution skewness is more informative than the mean for identifying structural differences between stands. We found that post-harvest variability in stand structure differed by retention pattern: although Dispersed treatment overstory density minima were similar to Aggregated treatment minima, Dispersed maxima were lower than the Aggregated treatments because Dispersed treatment prescription specifically prevented residual stand clumpiness. Furthermore, pattern-induced differences broadened over time. Our basal area data show that both within-treatment and within-stand variability dramatically decrease over time in the Dispersed units. Johnson and Fryer (1989) found that natural lodgepole pine-Engelmann spruce stands also became more homogeneous over time (lower coefficient of variation), and that increased mortality rates accelerated the transition from heterogeneity to homogeneity. Similarly, Kashian et al. (2005) identified that structural variability converged with undisturbed lodgepole pine stand age. Both retention patterns lose variability, but the accentuated loss in the Dispersed retention pattern is an undesirable side effect for managers that want to perpetuate structural heterogeneity within the stand and across the landscape. Managers can ameliorate the loss of variability in the Dispersed treatment while maintaining some of its benefits on residual tree growth and regeneration stocking by combining Aggregated and Dispersed retention patterns into a hybrid treatment.

Spatial variability in seedling density was greater in Burned treatments in both RH treatment patterns in 2004, but in 2011 the prescribed fire effect was only evident in the Aggregated retention pattern. It was surprising that 2011 in-stand variability in the Aggregated Unburned treatment was both the lowest of the treatments and the lowest relative to its mean, since the clumpy nature of gaps and retention patches in the Aggregated treatments should drive clumpy and thus highly variable regeneration. Seedling density will affect that cohort's subsequent patterns of canopy closure, crown recession, and competition-based stem mortality, and variability in the cohort's density will be important for crown class differentiation at the neighborhood scale and height mediation at the homogeneous patch scale (Oliver and Larson, 1996; Schaedel et al., 2017). Inconsistency in regeneration density is undesirable where well-distributed growing stock is a management goal, but the high variability in the Dispersed treatments and in the Aggregated Burn treatment provides a gradient of stand dynamics processes characteristic of a multiple use forest or mixed-severity fire regime (in crown differentiation, snag creation, woody debris deposition, understory reinitiation, precipitation interception, etc.; Puettmann et al., 2009). However, it is likewise possible that the within-stand variability is of no value in the long run if regeneration is so dense that stagnation of the new cohort is inevitable. For instance, Trappe and Harris (1958) recommend densities less than 1,980 seedlings ha⁻¹ to avoid negative crowding effects in lodgepole pine stands. Total regeneration densities were over 3 times this recommendation for most of our treatment units in 2011, suggesting that pre-commercial thinning may be necessary to foster ecological or timber objectives.

Variance of overstory mortality and regeneration stocking differed by treatment, but variance of overstory basal area growth and regeneration height growth did not. Thus, RH and

prescribed fire treatment influences variability in population dynamics and structure, but not growth. Explored further, we see that variability in mortality is driven more by prescribed fire than by retention pattern, but the opposite is true for regeneration stocking. This variance partition is useful because it suggests that managers can pick and choose treatment types (prescribed fire and/or retention pattern) based on the cohort (overstory or understory) in which post-treatment heterogeneity is desirable. Furthermore, since variability in growth is not impacted by treatment, growth can be forecasted with similar precision across treatments.

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Table 1. Distribution of post-harvest (~2000) and 2011 live basal area ($\text{m}^2 \text{ha}^{-1}$) by treatment. Each treatment value presented is an average of distribution statistics from four experimental units (stands). Standard errors are presented in parentheses.

Measurement	Retention Harvest Treatment	Fire Treatment	Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
Post-harvest	Control	Unburned	11.5 (2.3)	24.7 (2.4)	35.6 (3.4)	34.8 (2.5)	44.8 (3.8)	57.4 (4.4)
	Aggregated	Burned	0.0 (0.0)	9.8 (6.1)	28.7 (3.9)	28.0 (1.6)	45.9 (1.9)	59.7 (4.6)
	Aggregated	Unburned	0.0 (0.0)	0.0 (0.0)	3.4 (2.2)	10.4 (2.7)	16.6 (8.1)	41.3 (7.9)
	Dispersed	Burned	1.1 (1.1)	6.3 (2.2)	12.6 (5.1)	15.3 (5.0)	23.5 (8.3)	33.3 (10.5)
	Dispersed	Unburned	0.0 (0.0)	2.9 (2.2)	11.5 (2.3)	11.0 (2.2)	14.3 (3.8)	29.8 (5.8)
2011	Control	Unburned	20.9 (3.2)	31.2 (3.7)	35.7 (4.1)	36.0 (3.3)	41.8 (4.2)	49.9 (3.4)
	Aggregated	Burned	0.2 (0.2)	3.9 (2.6)	15.3 (5.7)	18.3 (3.3)	30.8 (3.8)	45.3 (4.9)
	Aggregated	Unburned	0.0 (0.0)	0.8 (0.7)	9.1 (2.3)	11.2 (2.9)	18.5 (7.5)	31.2 (5.2)
	Dispersed	Burned	0.3 (0.3)	1.4 (1.1)	2.8 (1.2)	4.8 (1.0)	6.9 (1.9)	14.6 (4.5)
	Dispersed	Unburned	1.1 (0.8)	5.1 (1.2)	8.3 (1.5)	8.9 (0.9)	12.2 (1.3)	19.3 (3.7)

Table 2. Model coefficients, P values, and fit statistics for four models of annual tree basal area growth (cm²) between post-harvest (~2000) measurement and 2011. Coefficients for random effects (Unit and Plot within Unit) are not shown.

Predictor	Null		Treatment		Predictive		Saturated	
	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	2.7261	0.0000	2.1503	0.0000	9.0778	0.0000	7.7714	0.0000
Watershed (Sun Creek)	2.0990	0.0226	1.8679	0.0156	1.6223	0.0481	1.5804	0.0267
RxFire (Unburned)			-0.9233	0.2838			-1.6829	0.0573
Retention Pattern (Dispersed)			0.9598	0.3364			0.6469	0.4847
RetPattern × RxFire (Disp:U)			2.8804	0.0624			3.6244	0.0189
Crown ratio (%)					-0.0595	0.0055	-0.0712	0.0003
SDI (metric)					-0.0021	0.0259		
BA greater (m ²)					-7.2333	0.0117	-8.3613	0.0025
Fit Stats								
Marginal R ²	0.07		0.20		0.24		0.31	
Conditional R ²	0.17		0.20		0.36		0.31	
AIC	-1004.5		-1014.7		-1019.7		-1029.5	

Table 3. Model coefficients, P values, and fit statistics for four models of overstory tree mortality between post-harvest (~2000) measurement and 2011. A predicted value of 1 indicates a 100% probability of mortality. Coefficients for random effects (Unit and Plot within Unit) are not shown. Note that with logistic regression expected value is calculated as $e^{\text{coefficients}}/(1+e^{\text{coefficients}})$.

Predictor	Null		Treatment		Predictive		Saturated	
	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	-0.7571	0.0870	-0.6641	0.2452	-20.9037	0.0007	-21.1316	0.0006
Watershed (Sun Creek)	-0.3393	0.5630	-0.4159	0.4762	-0.6106	0.4195	-0.5360	0.4632
RxFire (Unburned)			-0.0928	0.9061			1.7564	0.1151
Retention Pattern (Dispersed)			1.0996	0.1381			-0.0676	0.9421
RetPattern × RxFire (Disp:U)			-2.4926	0.0545			-1.0937	0.4649
DBH (cm)					0.4969	0.0016	0.4760	0.0020
Tree height (m)					-0.4481	0.0246	-0.4278	0.0316
Ht:DBH					0.1618	0.0019	0.1550	0.0024
Basal char (%)					0.0588	0.0003	0.0642	0.0001
Live crown (%)					-0.0334	0.1539	-0.0389	0.1034
Fit Stats								
Marginal R ²	0.01		0.10		0.52		0.54	
Conditional R ²	0.37		0.43		0.73		0.73	
AIC	216.4		214.1		163.9		164.2	
Deviance / resid df	1.20		1.18		0.87		0.86	

Table 4. Natural regeneration abundance mean, in-stand standard deviation, and composition in treated units in 2004 (1-2 years after burning) and in 2011. Values in parentheses are 1 standard errors.

Measurement	RetentionPattern	RxFire	Mean	In-stand st.dev.	Lodgepole pine	Subalpine fir
			<i>Stems ha⁻¹</i>	<i>Stems ha⁻¹</i>	%	%
2004	Aggregated	Burned	10,441 (4,026)	14,119 (3,184)	48.9 (26.2)	50.7 (25.9)
	Aggregated	Unburned	8,961 (2,243)	10,394 (2,589)	51.8 (22.5)	46.0 (21.8)
	Dispersed	Burned	7,906 (1,904)	13,711 (2,591)	46.8 (16.5)	47.6 (13.6)
	Dispersed	Unburned	5,017 (1,109)	5,160 (3,572)	57.4 (18.4)	39.8 (18.9)
2011	Aggregated	Burned	8,494 (2,890)	8,445 (6,486)	36.6 (26.2)	61.7 (25.6)
	Aggregated	Unburned	6,550 (3,500)	4,893 (1,922)	13.5 (11.0)	86.3 (11.2)
	Dispersed	Burned	5,414 (1,988)	7,548 (2,008)	22.7 (16.4)	64.0 (15.6)
	Dispersed	Unburned	7,714 (3,557)	7,758 (1,134)	42.8 (24.6)	51.4 (23.8)

Table 5. Model coefficients, P values, and fit statistics for four models of crop seedling stocking in 2011. A predicted value of 1 indicates 100% stocked with 40 regenerated lodgepole pine per acre. Coefficients for random effects (Unit and Plot within Unit) are not shown. Note that with logistic regression expected value is calculated as $e^{\text{coefficients}}/(1+e^{\text{coefficients}})$.

Predictor	Null		Treatment		Predictive		Saturated	
	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	0.9416	0.0676	-0.1232	0.8527	3.2091	0.0010	2.8168	0.0209
Watershed (Sun Creek)	1.2941	0.1147	1.3556	0.0652	1.0939	0.3540	1.3097	0.2143
RxFire (Unburned)			0.4266	0.6112			-1.2434	0.3363
Retention Pattern (Dispersed)			3.2577	0.0153			3.4439	0.0619
RetPattern × RxFire (Disp:U)			-2.2739	0.1510			-2.0817	0.3414
SDI (metric)					-0.0042	0.0000	-0.0042	0.0000
Fit Stats								
Marginal R ²	0.08		0.33		0.36		0.55	
Conditional R ²	0.35		0.45		0.68		0.71	
AIC	132.3		129.0		100.9		99.5	
Deviance / df	1.00		0.95		0.75		0.71	

Table 6. Model coefficients, P values, and fit statistics for four models of recent (up to 4 year) annual crop seedling height growth (cm) by 2010. Coefficients for random effects (Unit and Plot within Unit) are not shown.

Predictor	Null		Treatment		Predictive		Saturated	
	Coef	P value	Coef	P value	Coef	P value	Coef	P value
Intercept	16.7798	0.0000	17.6076	0.0000	13.3003	0.0000	13.9470	0.0000
Watershed (Sun Creek)	-1.1452	0.3011	-1.1662	0.2202	-1.5408	0.1797	-1.5615	0.1385
RxFire (Unburned)			0.2298	0.8643	2.5594	0.2413	3.1077	0.2064
Retention Pattern (Dispersed)			-0.8689	0.5089			-1.4197	0.3253
RetPattern × RxFire (Disp:U)			-1.7528	0.3430			-0.7399	0.7085
SDI (metric)					-0.0033	0.0031	-0.0031	0.0052
$\sqrt{\text{start height (cm)}}$					1.0242	0.0000	1.0357	0.0000
RxFire (Unburned) × $\sqrt{\text{start height}}$					-0.8051	0.0107	-0.8276	0.0088
Fit Stats								
Marginal R ²	0.01		0.05		0.11		0.15	
Conditional R ²	0.47		0.47		0.45		0.46	
AIC	-314.9		-313.8		-337.6		-337.1	

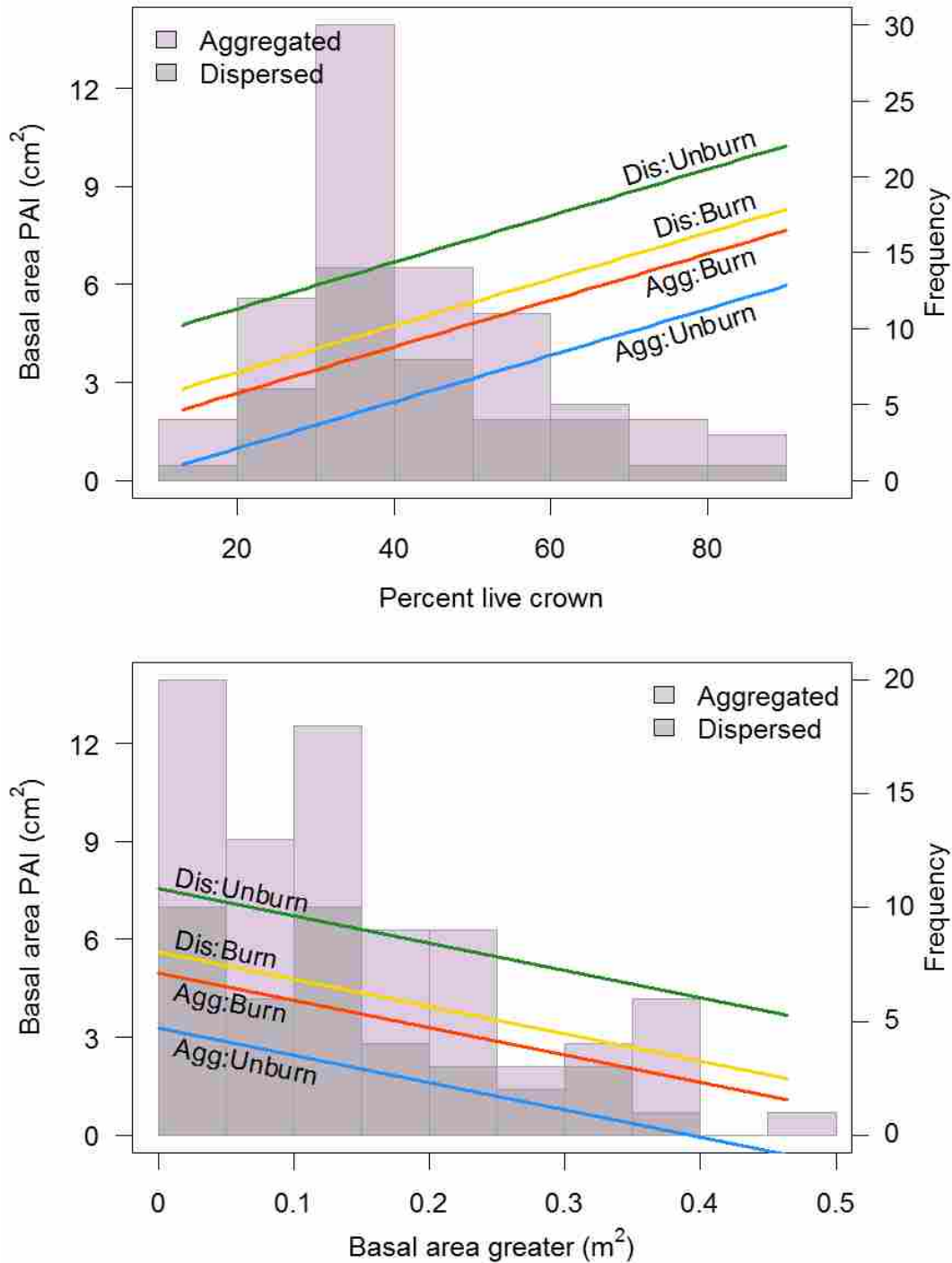


Figure 1. Treatment partial predictions (assuming median value of other covariate) of basal area periodic annual increment from the Saturated model as a function of percent live crown (top panel) and basal area greater (bottom panel). Overlaid histograms in background show frequency distribution of percent live crown and basal area greater (right y axis) in each retention harvest treatment.

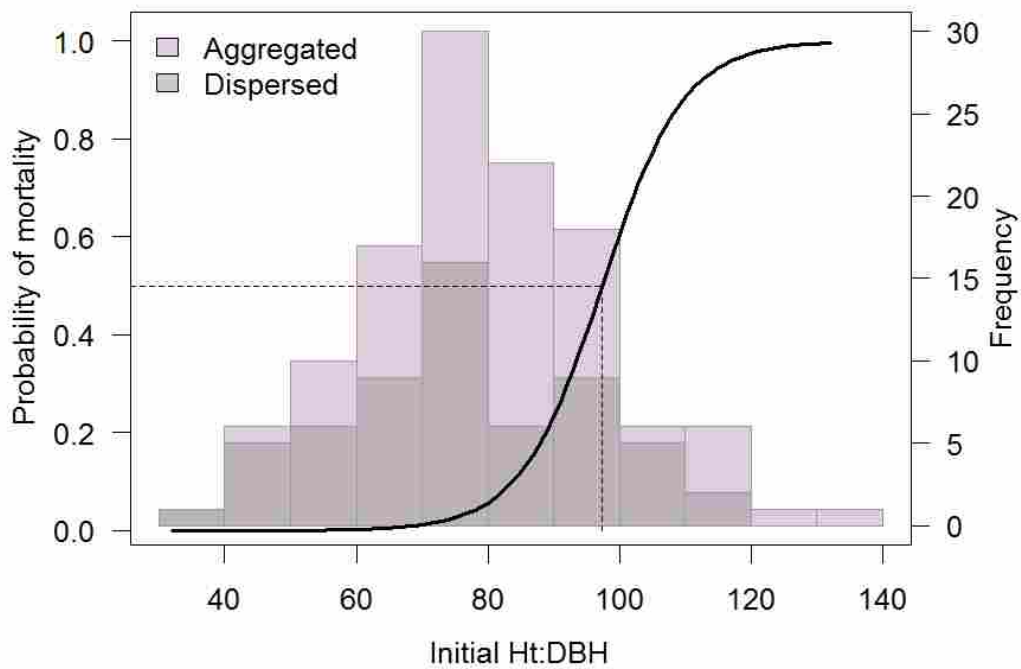
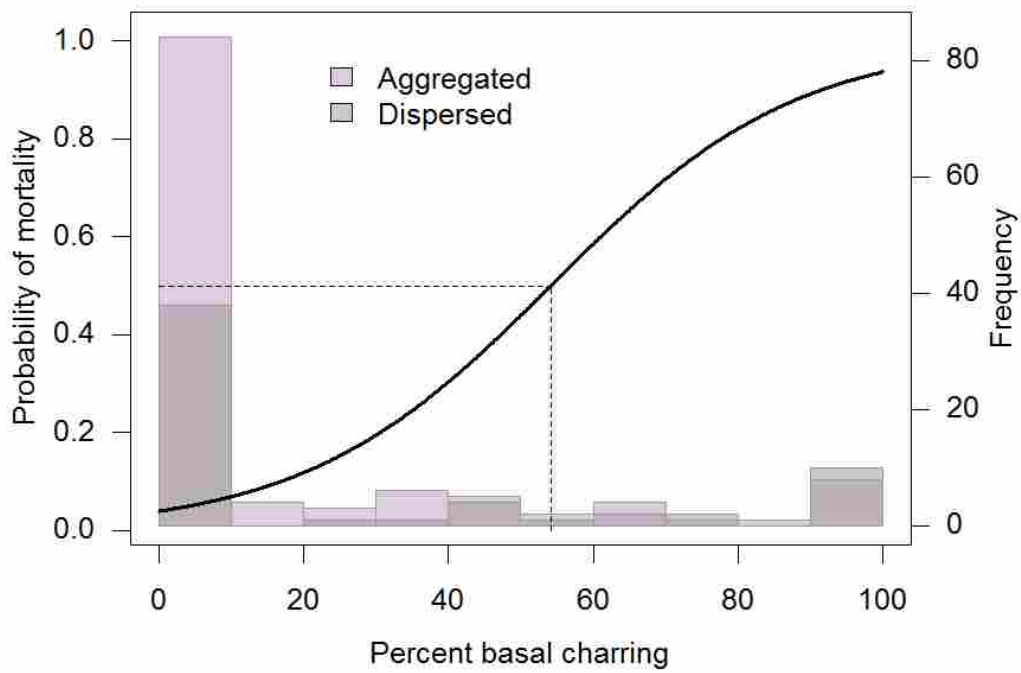


Figure 2. Treatment partial predictions (assuming median value of other covariates) of periodic stem mortality from the Predictive model as a function of percent basal charring (top) and post-harvest height:DBH (bottom). Overlaid histograms in background show frequency distribution of percent basal charring and height:DBH (right y axis) in each retention harvest treatment. Dashed line illustrates 50% probability of mortality.

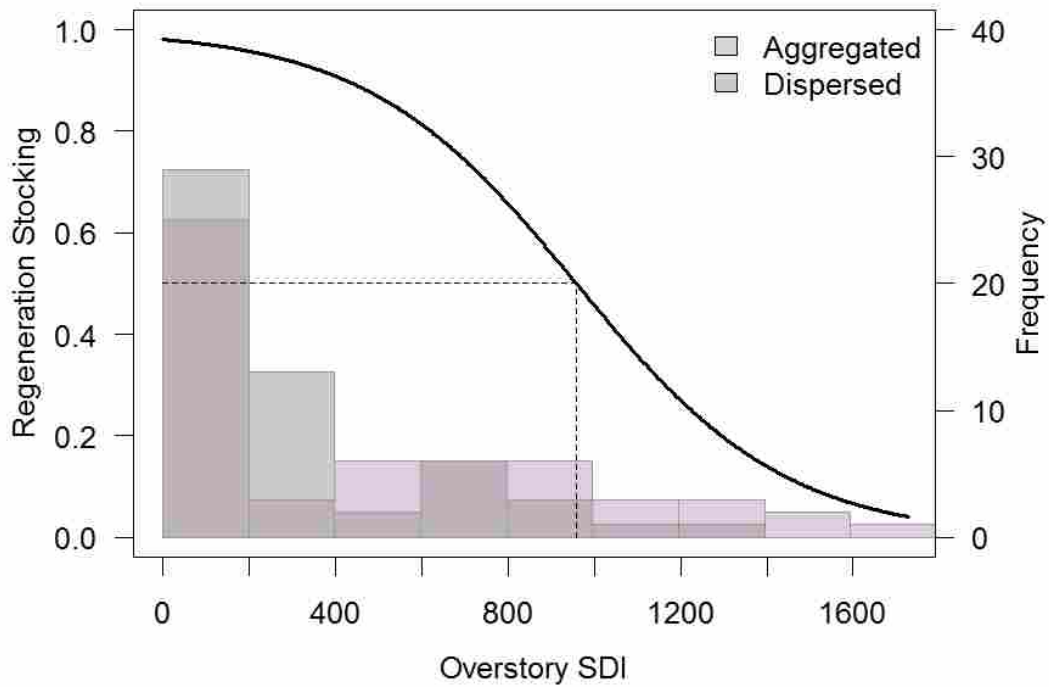


Figure 3. Predicted regeneration stocking from the Predictive model by post-harvest overstory SDI. Overlaid histograms in plot background (associated with y-axis on the right) show distribution of SDI by retention pattern. Dashed line illustrates 50% probability of stocking.

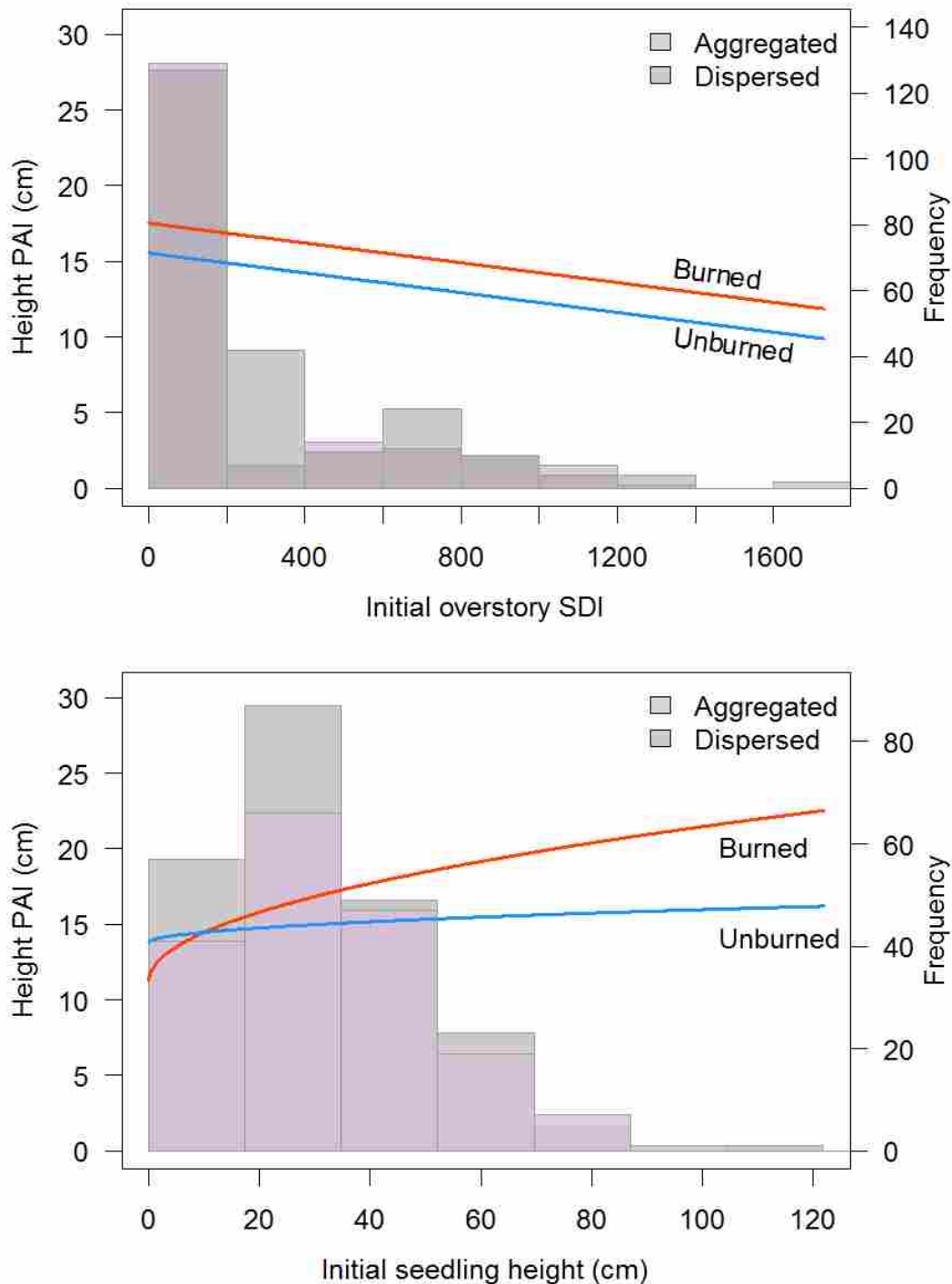


Figure 4. Treatment partial predictions (assuming median value of other covariates) of crop regeneration height periodic annual increment from the Predictive model as a function of post-harvest overstory SDI (top) and initial seedling height (bottom). Overlaid histograms in background show frequency distribution of overstory SDI and initial seedling height (right y axis) in each retention harvest treatment.

Chapter 5: Forest fuels and potential fire behavior twelve years after variable-retention harvest in lodgepole pine

Abstract

Variable-retention harvesting (VRH) in lodgepole pine offers an alternative to conventional, even-aged management. This harvesting technique promotes structural complexity and age-class diversity in residual stands and promotes resilience to disturbance. We examined fuel loads and potential fire behavior 12 years after two modes of VRH (dispersed and aggregated retention patterns) crossed by post-harvest prescribed fire (burned or unburned) in central Montana. Results characterize 12-year post-treatment fuel loads. We found greater fuel load reduction in treated than untreated stands, namely in the 10- and 100-hr classes ($p=0.002$ and $p=0.049$, respectively). Reductions in 1-hr ($p<0.001$), 10-hr ($p=0.008$), and 1000-hr ($p=0.014$) classes were greater in magnitude for unburned than burned treatments. Fire behavior modeling incorporated the regenerating seedling cohort into the surface fuel complex. Our analysis indicates greater surface fireline intensity in treated than untreated stands ($p<0.001$), and in unburned over burned stands ($p=0.001$) in dry, windy weather. Although potential fire behavior in treated stands is predicted to be more erratic, within-stand structural variability reduces probability of crown fire spread. Overall, results illustrate tradeoffs between potential fire attributes that should be acknowledged with VRH.

Introduction

Contemporary silviculturists and ecologists advocate that inter- and intra-stand structural diversity can promote long-term landscape and ecosystem resilience to a suite of disturbances (Drever et al. 2006; Puettmann et al. 2009; Keyes et al. 2014). This capacity for resilience is especially important because changes in climate are projected to alter the temperature and precipitation drivers that impact critical disturbances, including wildland fire and bark beetles (Chapman et al. 2012). Recent decades in public land management host numerous ecosystem stewardship treatments designed to increase forest resilience (e.g., Schultz et al. 2012). In the United States, the Forest Service aims to ‘restore, sustain, and enhance the Nation’s forests’ (US Department of Agriculture 2007); thus, management places an emphasis on ensuring critical ecological processes will persist following wildland fire, insect epidemics, or climate-related disturbances. Yet, silvicultural treatments designed to enhance resilience by promoting structural and age class diversity are rarely applied to lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. Ex S. Watson).

Lodgepole pine (LP) has the most extensive range of any conifer in western North America. It is the dominant forest cover over approximately 26 million hectares. LP is typically considered a shade-intolerant and fire-adapted pioneer species that often regenerates naturally as dense, even-aged stands (Lotan and Critchfield 1990). As such, traditional silvicultural systems in LP dominated forests aim to produce continuous canopied stands and are the epitome of even-aged management (Schmidt and Alexander 1985). Though even-aged management of LP mimics age distributions arising from one of its most common disturbance agents (i.e., stand-replacing fire), mixed-severity disturbances are also common and often result in multiaged LP stands (Arno 1980; Kollenberg and O’Hara 1999; Axelson et al. 2010). This indicates other silvicultural

alternatives can mimic live structures created by natural disturbances to enhance forest resilience.

Multiaged management of LP forests can improve both structural complexity and age-class diversity to a degree that supports variable light infiltration, cohort regeneration, wildlife forage, and tree vigor (Schmidt and Alexander 1985; O'Hara 2014). Furthermore, multiaged silviculture can complement spatially expansive even-aged regeneration systems such as clear cutting to promote heterogeneous stand and landscape conditions resilient to primary disturbances (i.e. bark beetle and wildland fire) (O'Hara 1998; Axelson et al. 2010; Johnson et al. 2014; Keyes et al. 2014).

One flexible silvicultural tool for multiaged management is the variable-retention harvest (VRH) (Franklin et al. 1997; Gustafsson et al. 2012). This tree harvesting approach enables managers to emulate the spatial, structural, and age complexity historically maintained in natural forests mosaicked by a suite of disturbances. However, little is known of the long-term effects of implementing these treatments, as VRHs are not currently part of a formal silvicultural management system (e.g., as outlined in Smith et al. 1997). Critical evaluation is required to determine the impacts of this multiaged management approach on post-treatment disturbance processes. In particular, we need to know if this relatively new strategy alters fuel conditions that drive the potential for stand-replacing wildfire. Treatments may exacerbate fire behavior by increasing near-surface windspeed due to reduced stem density, increasing dead surface fuel loads as treatments relocate crown fuels to the ground, and/or by promoting the ingrowth of natural regeneration and ladder fuels into the surface fuel complex (Keyes and Varner 2006).

In this study, we examined the effects of an experimental VRH in Rocky Mountain LP on surface woody debris accumulation and simulated fire behavior. This experiment was established

within the Tenderfoot Creek Experimental Forest (TCEF) in central Montana and was specifically designed to initiate two-aged stands. The VRH resulted in two forest structural patterns, according to spatially aggregated or dispersed overstory tree retention targets, and subsequently half of each of the harvested stands were burned.

Our first research question was: how do harvest pattern and use of prescribed fire influence downed woody debris (DWD) dynamics? We quantified post-treatment fuel loadings 2-4 years and 12 years post-harvest to address this query. Second, we asked if these treatments increase or decrease the potential for crown fire in residual overstories. We simulated potential fire using data-driven custom fire behavior models at multiple plots within stands to investigate the variability of potential fire behavior 12 years after VRH. The fire behavior predictions we present provide an integral assessment of this multiaged management strategy, and the relative findings are relevant where VRHs are implemented by forest managers in, but not exclusive to, LP forest types.

Methods

Study site

The TCEF is a 3,693 ha watershed in the Little Belt Mountains, within the Lewis and Clark National Forest in central Montana. Elevation ranges from 1,840 to 2,421 m ASL. The forest is dominated by LP, forming nearly pure even-aged and two-aged stands. Associated overstory species are Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Associated shrub species are grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville) and thinleaf huckleberry (*V. globulare* Douglas ex Torr.). Soils are typified by loamy skeletal, mixed Typic Cryochrepts, and clayey, mixed Aquic Cryoboralfs (Adams et al. 2008).

Climate in the study area is generally continental, though is also influenced by the Pacific maritime climate along the Continental Divide. Annual precipitation is 880 mm, ranging from 594-1,050 mm across the elevation gradient. The majority of the precipitation occurs in the form of snow from November to May. Typical mean temperatures range from -9°C in January to 17°C in July, with freezing temperatures possible throughout the year. The average plant growing season is estimated to be between 30 and 75 days (Adams et al. 2008).

Fire history reconstruction revealed a characteristic mixed-severity fire regime in the study area (Hardy et al. 2006). For the period of 1580 to 1992, mean fire return interval was 38 years, with large, severe fires occurring less frequently, and low- to mixed-severity fires occurring between large, severe fire events.

Experimental design and sampling

Treatments were installed in 16 units, split among two sub-watersheds of Tenderfoot Creek (McCaughey et al. 2006). Units in two adjacent sub-watersheds were established as untreated reserves (hereafter, 'controls'). The VRH prescription called for 50% basal area retention and created two stand structure types: aggregated, where residual overstory was distributed in a clumped spatial pattern; and dispersed, where residual overstory was primarily distributed at an even spacing (Figure 1). Half of the units were broadcast burned with low-intensity fire (though severity was greater than anticipated; see Hood et al. 2012). Burned treatments are labeled 'B' in tables and figures, whereas unburned treatments are labeled 'U'. Thus, there were a total of 16 treatment units: two replications of burn × harvest treatment per sub-watershed. Harvesting took place in 1999 and 2000; stands selected to be treated with prescribed fire were burned in 2002 or 2003. Pre- and post-harvest stand conditions have been documented in detail as a restoration guide (Hood et al. 2012).

Surface fuels and live tree characteristics were sampled after treatment. A planar-intercept sampling method (Brown 1974) was used to estimate DWD following treatment completion (2002 – 2004; as reported in Hardy et al. 2006), and then again in 2012. A total of 281 sample points were systematically located throughout stands, whereupon a set of two randomly oriented, perpendicular transects were established. To avoid trampling, transects were offset 3.28 m from sample points. On each transect, the following fuel characteristics were measured: 1000-hr fuels (diameter > 7.62 cm) on 19.8 m sections; 100-hr fuels (2.54 < diameter < 7.62 cm) on 3 m sections; and 1-hr (diameter < 0.64 cm) and 10-hr fuels (0.64 < diameter < 2.54 cm) on 1.8 m sections. Combined litter and duff depths were measured at two points along each transect.

We measured live tree characteristics at a subset (180 plots) of the surface fuel points using nested, fixed-area plots in 2011. Overstory trees were sampled using 0.04 ha circular plots, wherein we recorded diameter and species for all live stems greater than 10.16 cm diameter at breast height (dbh). Height was predicted from tree dbh using a local dbh-to-height regression equation (C. Keyes, *unpublished data*). Seedlings (dbh < 10.16 cm) were tallied on 0.001 ha circular subplots according to species and height.

Downed woody debris

Non-rotten woody loadings were calculated per time-lag size class (**Error! Reference source not found.**). Litter depth was assumed to be one-third of the total litter-duff depth measured; litter load was calculated at the rate of $4.41 \text{ t} \cdot \text{ha}^{-1} \cdot \text{cm}^{-1}$ (D. Lutes, pers. comm., Dec. 2013). Duff load calculation followed an equation developed for LP/subalpine fir forests of the Eastern Cascades (Woodard and Martin 1980). Estimates were averaged by sample point and

compared to reference conditions (Brown and Bevins 1986; Baker 2009; Fuel Characteristic Classification System [FCCS] - Ottmar et al. 2007).

As stated in our first objective, we contrasted the relative effects of treatments on DWD. Our four statistical null hypotheses were: (H1) there is no difference between treatment and control surface fuel loads; (H2) there is no difference between aggregated and dispersed retention surface fuel loads; (H3) there is no difference between burned and unburned surface fuel loads; and (H4) there is no treatment interaction (retention pattern \times burn status) effect on surface fuel loads. We modeled current fuel loads by fuel class to test these hypotheses as mutually orthogonal linear contrasts. Fitted linear mixed-effects models had the form:

$$y_{ijkl} = \mu + B_i + \varepsilon_{(1)i} + R_j + \varepsilon_{(2)ij} + T_k + \varepsilon_{(3)ijkl}$$

Where y_{ijkl} is the load in a given fuel class (i.e., 1-hr, 10-hr, 100-hr, sound 1000-hr, litter + duff load, or total dead surface fuel load) on plot l ; μ is the grand mean load in the fuel class; B_i is the random effect of the i^{th} sub-watershed block ($i=1,2$); R_j is the random effect of the j^{th} treatment replicate within a block ($j=1,2$); T_k is the fixed effect of the k^{th} treatment level ($k=1,2,3,4,5$; four treatments plus control); $\varepsilon_{(1)i} \sim N(0, \sigma_{\varepsilon(1)}^2)$, $\varepsilon_{(2)ij} \sim N(0, \sigma_{\varepsilon(2)}^2)$, and $\varepsilon_{(3)ijkl} \sim N(0, \sigma_{\varepsilon(3)}^2)$ are independent. Models were fitted using R statistical software (R Core Team 2013) and package nlme (Pinheiro et al. 2013) using a constant variance function structure to account for treatment heteroscedasticity where appropriate. We examined normal quantile plots and correlations between predicted and observed values for model validation.

To better understand fuel dynamics resulting from harvesting and burning treatments, we calculated the change in loadings by fuel class between measurements. Net load was linearly annualized to account for slight differences in inter-measurement period length. We modeled net annual fuel load (ΔAFL) by fuel class to determine the effect of treatment on load accumulation.

Δ AFL responses were modeled and linear contrasts were analyzed using the procedure described above.

Potential fire behavior

A noteworthy problem with typical application of fire behavior models is a reliance on default fire behavior fuel models (FMs), which often vary substantially from *in situ* fuel conditions. Customized model inputs are more appropriate where data are available (Varner and Keyes 2009). Furthermore, if silviculturists are interested in creating and managing for complex structural attributes, it is not appropriate to focus solely on stand-level mean values or coarsely averaged fuel loading to characterize potential fire behavior (Agee and Lolley 2006). In the same fashion, default FMs that do not adequately represent highly variable fuel characteristics in the field may lead to fire behavior simulations that are insufficient to accurately contrast heterogeneous stand conditions.

We used BehavePlus (V. 5.0.5; Andrews et al. 2008) and FOFEM (V. 6.0; Reinhardt et al. 1997) to characterize potential fire behavior resulting from the applied harvest and burning treatment combinations. We created customized FMs for each measured plot, electing to use unvalidated but data-driven FMs over default FMs that poorly matched plot-level characteristics. Surface fire was modeled using BehavePlus, fire intensity was adjusted based on parallel FOFEM modeling, and then potential for crown fire was modeled using BehavePlus. We used this model routine to better account for the wide array of DWD present in these novel fuelbeds.

This study's FMs were informed by DWD loadings, biomass of observed regeneration, live fuel loads derived from the Fire and Fuels Extension of the Forest Vegetation Simulator (FVS-FFE; Beukema et al. 1997), and the most similar standard FMs (Anderson 1982; Scott and Burgan 2005). Table 1 shows the inputs used to develop FMs. Since the FMs were not field-

validated, we focused our interpretation of simulated fire behavior on relative differences between treatment classes rather than absolute values.

We used four pre-defined fire weather (wind and fuel moisture) conditions in this analysis for comparative purposes (Scott and Burgan 2005; Table 2). Overstory canopy characteristics were calculated from sample tree data according to FVS algorithms. We calculated live herb load using FVS; live woody understory loads were calculated using FVS shrub load plus tree regeneration load (Brown 1978). Surface wind adjustment factors ranged from 0.1 to 0.4, per overstory canopy cover (Rothermel 1983).

We report a suite of potential fire behavior metrics across the four weather scenarios. We tested for differences in mean surface fireline intensity across treatments using the linear model framework outlined above. The potential for crown fire was assessed by examining the variability of critical surface fire flame length for canopy ignition, critical fire rate of spread for sustained canopy fire, and transition ratio (predicted flame length divided by critical flame length). Transition ratio was modeled in the same fashion as fireline intensity.

Finally, we generated heat release profiles for each plot based on fuel availability and plot environmental conditions. Whereas heat release at time 0 is indicative of frontal flaming and fire spread, subsequent flaming and smoldering has substantial effects on biota and post-fire fuel loads. We assessed within and among treatment variability both visually and with general descriptive statistics.

Results

Fuel characteristics

The grand mean of total stand-level dead surface fuels across treatments and controls (12 years post-harvest, and 9-10 years post-burn) was 81.59 Mg·ha⁻¹ (average of treatment-level

values reported in Table 3). Total dead surface fuel loads ranged from 48.96 Mg·ha⁻¹ in one aggregated burned stand to 124.79 Mg·ha⁻¹ in a control stand (see treatment means in Table 3). Model residual standard errors (in Mg·ha⁻¹) were as follows: 0.19 for 1-hr current fuel load, 1.50 for 10-hr, 3.14 for 100-hr, 20.02 for 1000-hr, 29.28 for duff and litter, and 40.09 for total dead surface fuel. Squared predicted-to-observed correlations ranged from 0.084 for the 1-hr model to 0.32 for the 1000-hr model, but fixed-effects only contributed up to 0.09 to the squared correlations. Our model contrasts show that total dead surface fuel loads in treated stands were no different than untreated stands (statistical hypothesis H1; Table 4), though there is mild to strong evidence for differences in the 10, 100, and 1000-hr fuel classes. Dispersed retention treatments were associated with greater 1000-hr fuel load than aggregated treatments, but less 1-hr load (H2). The contrasts also indicate greater loading in unburned than burned stands, except for in the 1000-hr fuel class where the opposite case holds (H3). Interaction between the main effects was evident only in the 10-hr fuels (H4).

Average annual change in fuel load (Δ AFL) for individual stands varied from -0.07 to 0.00 Mg·ha⁻¹year⁻¹ within the 1-hr component and increased with fuel size to -0.69 to 1.77 Mg·ha⁻¹year⁻¹ within the 1000-hr component (means of treatment-level values reported in Figure 2). Total dead surface fuel load was most influenced by the change in combined litter and duff load, which ranged from -3.13 to 0.90 Mg·ha⁻¹year⁻¹ in individual stands (see treatment means in Figure 2). Model residual standard errors (Mg·ha⁻¹year⁻¹) were: 0.04 for 1-hr Δ AFL, 0.23 for 10-hr, 0.40 for 100-hr, 1.47 for 1000-hr, 3.14 for duff and litter, and 3.88 for total dead surface fuel. Squared predicted-to-observed correlations ranged from 0.03 for the total fuel model to 0.17 for the 1-hr model; fixed-effects contributed 0.02 to 0.10 to the squared correlations. Tests on estimated contrasts confirmed that Δ AFLs are significantly different from zero in the 1-hr (-), 10-

hr (-), 1000-hr (+), litter and duff (-), and total (-) fuel classes (Table 4). Treated stand Δ AFL was lower than untreated stands except for in the 1000-hr class, indicating that fuels less than 7.62 cm as well as litter and duff have been more rapidly accumulating in control stands. There was some weak evidence that 10-hr Δ AFL in aggregated treatments was greater than those in the dispersed. Burned stands had significantly greater Δ AFL than unburned in the 1-hr, 10-hr, and 1000-hr classes, which highlights that both fine and coarse woody debris falls from the canopy to the surface in the years after burning.

Means of live fuel characteristics indicate that stands exhibit distinct structural variability 12 years after harvest (Table 5). Since controls were not harvested or burned, overstory density and basal area were greatest in untreated stands. Despite identical basal area targets in the dispersed and aggregated retention prescriptions, residual stem density and basal area were two-thirds to one-half less in the dispersed stands than aggregated stands. Estimated canopy bulk densities follow accordingly; at the plot level they range from 0 to $0.20 \text{ kg}\cdot\text{m}^{-3}$ (see treatment-level means in Table 5). Herb loads were inversely related to overstory cover; as calculated by FVS, these values range from 0.16 to $0.40 \text{ Mg}\cdot\text{ha}^{-1}$ per plot. Due to dense patches of regeneration, live understory woody loads likewise had an inverse relationship with overstory cover that ranged from 0.05 to $4.49 \text{ Mg}\cdot\text{ha}^{-1}$ per plot (treatment means in Table 5).

Potential fire behavior

We simulated fire on all plots separately using BehavePlus and FOFEM, under each of the four moisture and wind scenarios (Table 2). Within each treatment \times scenario combination, simulated fireline spread rates, flame lengths, and intensities were heavily right skewed. These were greatest in the dry-high wind scenario, where pooled intensities averaged $693 \text{ kW}\cdot\text{m}^{-1}$ (range: $0.0 - 9686.0$) from 1.57 m flame lengths (range: $0.00 - 5.28 \text{ m}$). In the moist-low wind

scenario, intensities averaged $87 \text{ kW}\cdot\text{m}^{-1}$ (range: 0.0 – 1696.0), given an average flame length of 0.31 m (range: 0.00 – 2.37 m).

Levene's variance homogeneity test on fireline intensity in the each scenario (pooled within treatments) had p-values less than 0.001 ($F_{4,116}$ ranged from 5.82 to 8.65), indicating non-constant variance. Fireline intensity was modeled with treatment-level variances specified. Surface fireline intensity model residual standard errors were 354.8 for dry-low wind, 9991.9 for dry-high wind, 154.3 for moist-low wind, and 420.3 for moist-high wind. Squared predicted-to-observed correlations ranged from 0.14 for the moist-high wind model to 0.21 for the dry-low wind model; fixed-effects contributed 0.13 to 0.19 to the squared correlations. Unharvested stands are predicted to have significantly lower mean fireline intensities than harvested stands in all scenarios (Table 6). There was insufficient evidence of a difference between mean predicted fireline intensities among the cutting patterns in any scenario. Predicted fireline intensities in unburned stands are significantly greater than burned stands.

Where residual overstory trees were present on plots, the calculated critical flame lengths to ignite crowns were similar across plots (Figure 3). The median critical flame length in the control stands was 3.46 m (range: 1.52 – 4.67 m). Medians ranged from 2.74 to 3.51 m in the treated stands; the minimum and maximum critical flame lengths, averaged across treatments, were 1.71 and 4.64 m, respectively. Visual inspection of within-treatment distributions suggests medians were slightly lower in the unburned treatments. Much more variability was exhibited among treatments in the critical crown rate of spread (Figure 3). Critical rates of spread in the untreated units had the lowest median ($0.34 \text{ m}\cdot\text{sec}^{-1}$) and smallest range ($0.23 - 1.20 \text{ m}\cdot\text{sec}^{-1}$). Medians for the burned and unburned aggregated treatments were 1.6 and 3.6 times greater than that of the control, respectively. In the dispersed retention units, medians were 7.7 and 4.9 times

greater than the control. Maximum critical rate of spread was limited to $3.0 \text{ m}\cdot\text{sec}^{-1}$ because BehavePlus's minimum input value for canopy bulk density is $0.016 \text{ kg}\cdot\text{m}^{-3}$. Plots with zero residual overstory represented a minimum of 6% (in the unburned dispersed) and a maximum of 35% (burned dispersed) of plots measured within treatments. In these 'no-tree' plots, critical flame length and critical crown rate of spread could not be calculated as there were no overstory trees to ignite.

In the dry-high wind scenario, 'conditional' crown fire (per Scott and Reinhardt 2001) was predicted on 81.5% of the plots in untreated stands. In contrast, 34.3% and 16.7% of aggregated retention plots (burned and unburned, respectively) were predicted to have conditional crown fire. No plots in the dispersed treatment were predicted to have conditional crown fire. No active crown fire was predicted. Proportion of plots predicted to have conditional crown fire in the moist-high wind scenario were 73-83% lower than the dry scenario, and no conditional crown fire was predicted for the low wind scenarios.

We modeled crown fire transition ratio as a quantitative measure of fire ascension into crowns. Levene's variance homogeneity test on transition ratio (pooled within treatments) had a p-value of less than 0.01 ($F_{4,116}$ ranged from 3.54 to 7.98) for all but the wet-high wind scenario. Thus, even with a median-centered test, there is strong evidence that variability in transition ratio is not constant across treatment groups. Like the surface fireline intensity models, we modeled transition ratio with treatment-level variances specified. Harvested stands were predicted to have greater mean transition ratio than control stands in all but the moist-high wind scenario (Table 6). There appeared to be no effect of retention pattern on transition ratio, but unburned stands had greater mean ratios than burned stands, regardless of scenario.

In a plot of transition ratio (Figure 4), we observe with greater detail the relative susceptibility of plots to crown fire initiation (torching) in the dry-high wind scenario. Figure 4 illustrates more unstable fire behavior (points above 1.0 on the y-axis) is associated with low overstory densities, and also highlights the variability in transition ratio within and across treatments. The control and burned aggregated plots are most tightly clustered in a low susceptibility range (medians = 0.02 and 0.03 and third quartiles = 0.05 and 0.18, respectively), although both treatments still result in torching. Plots in burned and unburned treatments exhibited 1.9 and 13.5 times greater variance from zero than control plots, respectively. The greatest transition ratios across all treatment levels tended to be to the left of the maximum overstory threshold retained by the dispersed cutting method, i.e., 600 trees·ha⁻¹. Thus, even though dense clumps in the control and aggregated treatments exhibited the greatest CBDs and lowest crowning indices, predicted surface fireline intensities were much lower than the crown fire initiation thresholds in clumps with at least 600 trees·ha⁻¹.

We characterized post-frontal burning by generating heat release response profiles (Figure 5). The ratio of variance of heat release from t=20 minutes to t=2 minutes was 0.19 in control, 0.10 and 0.09 in aggregated burned and unburned, respectively, and 0.13 and 0.11 in dispersed burned and unburned plots, respectively. The ratio of median heat release at these times showcased similar relative values. Though heat release medians and variation tended to decay less rapidly in controls than treated units, median heat release values in controls were 2.4 to 4.3 times lower than treated units at t=2 minutes. Median biomass consumption associated with the heat release curves was greatest in the dispersed burned treatment (61.7 Mg·ha⁻¹) and lowest in the aggregated burned treatment (39.1 Mg·ha⁻¹).

Discussion

Control stands had lower 1-hr loading, but relatively similar 10-hr and 100-hr loading to the average condition identified by a study of four ‘typical’ cool, moist LP sites across Idaho, Montana, and Wyoming (Brown and Bevins 1986; Table 3). Fine fuel (1-, 10-, and 100-hr) loadings generated by FCCS for the typical TCEF stand condition and those presented by Baker (2009; generated by FCCS for a regional LP stand condition) were higher than our study site; 1000-hr and litter and duff loads were greater at our site than either set of FCCS-generated values. These may conflict because FCCS values apply to a broader ecoregion (stretching from northern Idaho down to Colorado and New Mexico) than typified by this study’s site or the northern Rocky Mountain stands characterized in Brown and Bevins (1986).

In addition to addressing the effects of wind and dead activity fuels on potential fire behavior, our study incorporates natural regeneration loads that resulted from treatment. However, we did not measure height of advance regeneration, and therefore potential fire behavior in control stands may be underestimated. Our calculations indicated that some surface fuelbeds (< 2 m) were more influenced by seedling biomass than by downed woody debris, live herbaceous load, or shrub load (compare Table 5 to published live woody loads in Anderson (1982), Scott and Burgan (2005)). Incorporating seedling-based fuel loads requires customization of fire behavior fuel models but is necessary for a comprehensive evaluation of silvicultural or fuels-reduction treatments on potential fire behavior.

Application of this study’s VRH and burn treatments in other LP forests may result in similar fuels dynamics, but potential fire behavior may be quite different from these predictions. For instance, a stand representative of FCCS identified fuelbed characteristics (Table 3) will result in more rapid predicted surface fire spread and unstable behavior than presented

predictions, owing to increased 1- and 10-hr fine surface fuels. Care must be taken in inference and extrapolation of the potential fire behavior predictions because this study's fire behavior fuel models have not been field validated.

Directly modeling fire effects (i.e, tree mortality) was beyond the scope of our study. Our analytical framework assumes that crown fire initiation and spread are the ultimate concern for the manager, although we present heat release and biomass consumption for better characterization of fire behavior. Such an additional analysis would be useful given sensitivity of trees in our study site to even a low-intensity fire.

Treated versus untreated

The tests on estimated contrasts in this study revealed first that there was no difference in total dead surface fuel loads between treated and untreated stands 12 years after harvest (Table 4). This conclusion suggests that activity fuels from harvesting and burning were no different than adjacent natural fuelbed aggradations. This is at least partially due to the study's harvest and burn prescriptions, which aimed to minimize activity residues. By whole-tree yarding to a centralized landing, fuel from non-merchantable materials such as tree branches and tops did not overload the surface fuel complex as a typical cut-to-length operation might do.

Second, testing revealed that the annual change in 10- and 100-hr fuel load components differs because of treatment (only weak evidence for 1-hr fuels). Treated stand Δ AFLs were 22.5 and 1.8 times less than the untreated stands, for respective 10- and 100-hr fuels. This suggests that initial activity fuels may have been slightly higher among the treated stands, but accumulation rate has decreased due to overstory removal. Since surface fire spread is predominately influenced by 1- and 10-hr timelag class fuels, dead fuel loadings would have been conducive to carrying a surface fire immediately post-treatment. Twelve years later, dead

surface fuel connectivity has been influenced by the reduction of fine fuels. In fact, we observed a number of plots where either 1- or 10-hr fuels were not found (9.25% of plots), which will continue to hinder surface fire spread where mature trees were removed. Also, fine woody debris (i.e. less than 7.62 cm) decomposition rate may have increased due to particle fragmentation and forest floor insolation. Increased decomposition would suggest that the post-treatment environment increased microorganism activity on the forest floor. This hypothesis addresses the reduction of small woody fuel loads, yet historical chronosequence and process-based experiments arrive at contrasting conclusions regarding post-harvest surface fuel decay (Yanai et al. 2003). Regardless of the mechanism, these rates may continue until the regenerating cohort enters into a crown competition growth phase.

Modeled fire behavior confirmed that potential surface fire flaming front intensities are influenced by the treatment at TCEF, particularly in low moisture conditions (Table 6, Figure 4). Model results suggest greater fireline intensities in treated stands, which is consistent with other post-treatment fire behavior studies in the western U.S. (e.g., Agee and Lolley 2006). This result was expected because of the increased live surface fuel load and within-stand wind penetration after partial overstory removal. BehavePlus predicted that “conditional” crown fire was possible in each of the stand types given 40 km·hr⁻¹ wind scenarios, but most prevalent in untreated stands. Furthermore, median values indicate that treatments raised critical crown fire rate of spread overall. These results imply that a variety of LP stand configurations support sufficient canopy bulk density to carry crown fire given abnormally strong winds, but the VRH treatments evaluated can play a role in reducing that probability. However, this is further complicated by surface fire behavior since the relative potential for crown fire initiation (transition ratio) increased by treatment in all four weather scenarios (Table 6). We acknowledge there are

tradeoffs between reduced potential for crown fire spread and increased potential for canopy ignition, both of which are largely driven by wind dynamics. Considering fine-scale resolution of intra-stand wind conditions may be very useful to increase stand resistance to crown fire in the treatment design phase.

The heat release profiles we generated highlight the wide range of variability of post-frontal burning within and among treatments. We identified two key differences in heat profiles and associated consumed biomass between treatments and controls. First, the median of control plots decayed more rapidly than medians in the treated units. The median heat release in the control remained below $23 \text{ kW}\cdot\text{m}^{-2}$ shortly after two minutes, whereas the same heat flux threshold was reached in about four minutes in aggregated and eleven in dispersed units. Second, biomass consumption medians were more or less similar across treatments, but the few plots that approached or surpassed $150 \text{ Mg}\cdot\text{ha}^{-1}$ of consumption were in the treated units. These plots reflect greater stockpiles of large woody debris that can profoundly impact subsurface heating. Our predictions highlight that although quantity of biomass consumption may vary only slightly, differences in the quality (e.g., time-lag class) of consumed materials may result in more adverse fire effects from the post-flaming front in treated units, particularly in the dispersed retention.

Burned versus unburned

Despite the seemingly detrimental differences in ΔAFL rates due to prescribed fire, 12-year post-treatment total dead surface fuel loads were generally greater in unburned treatments. Fine woody debris (1-hr, 10-hr, and 100-hr fuel classes) was highly influenced by burning (Table 4). Burn treatments resulted in 23 to 35% lower loads in these classes, but treatment interaction suggests burn effect was greater in the dispersed retention treatment for 10-hr fuels. Although burning resulted in lower 1-hr and 10-hr loads after 12-years, ΔAFLs in unburned stands were

48% and 46% lower than burned stands. It is clear that burning plays a very influential role in the immediate removal of fine woody debris, but delayed recruitment of fuels from fire-killed trees added fuels to this pool, reducing the effect that the mechanical treatment had in increasing decomposition rates. Burning was also associated with lower current litter and duff loads (22% less than unburned stands), but the rate of change over the measurement period was not significantly different from zero (Table 4). As for the largest fuel class, current burned and unburned 1000-hr fuel loads were no different. Recruitment rate (Δ AFL) of 1000-hr fuels was notably greater in burned than unburned stands, however. Recruitment of 1000-hr fuels was greater in burned stands because of fire-induced tree mortality and subsequent translocation of fuels to the surface fuel complex. It is likely that tree mortality was driven by both first-order and second-order fire effects, but we were unable to quantify the relative rates of occurrence in this study. See Hardy et al. (2006) and Hood et al. (2012) for further assessment of fire-induced mortality in the study area.

In review, fuels less than 2.54 cm in diameter (1-hr and 10-hr classes) and fuels greater than 7.62 cm (1000-hr class) tended to stockpile more rapidly after burning. These results suggest that the structural benefit of fuels reduction in burn treatments was curtailed by post-treatment recruitment of woody fuels from the fire-damaged stand. Yet current fine woody debris loading in burned stands is still less than that of unburned stands. If prescribed burn severity was greater than what we observed, then the recruitment of fine and large woody debris might have profound impacts on future fire effects. The burning prescription for these stands was for low-intensity fire, but the applied fire was more intense than anticipated resulting in greater overstory mortality and subsequent fuel accumulation. Future surface fire in these stands may again result

in higher fire intensity than expected, but also greater soil heating and overstory severity because of large fuel loads from past mortality.

Our models confirmed that unburned stand surface fireline intensity would be greater than burned stands (Table 6) because treatments were designed to minimize post-treatment surface fuel loading. This supports that the burn treatment adequately decrease surface fireline intensity to reduce transition from surface to crown fire. We note that some of the difference in transition ratio due to burning treatment may be due to the fact that stands were burned 2-3 years after harvest, thus setting back the development of natural regeneration fuel loads. More conditional crown fire was predicted in burn treatments, but we believe this may be driven by tree density more than the burning treatment.

Aggregated versus dispersed

Only 1-hr and 1000-hr fuels differed in the current surface fuel profile by retention pattern. We observed 21% lower 1-hr and 39% greater 1000-hr fuel loads in dispersed treatments. Current 1000-hr load was high in dispersed stands because of a windthrow event immediately after harvesting and prior to sampling (Hood et al. 2012). Clump structures in the aggregated treatment drastically improved stem stability, as windthrow in these treatments was limited to clump edges. We did not observe significantly greater recruitment by retention pattern although we expected it. More trees in the dispersed treatment were directly exposed to prescribed fire (which influenced mortality), whereas interiors of clumps in the aggregated treatment had poor fire coverage because of moisture conditions. Nevertheless, 1000-hr fuel recruitment was similar between treatments because when fire did kill aggregated trees, it killed many of them.

Our analysis partly elucidated potential fire behavior differences between retention patterns. Although contrast tests between retention patterns revealed no differences in mean effects, Levene's test of variance homogeneity indicates greater variability in aggregated treatments. This emphasizes that predicted fire behavior based on averaged data from pooled plots masks important treatment differences identified among plots (see also Harrington et al. 2007), particularly where treatments were designed for structural irregularity. Aggregated treatment stands were defined by clumps and openings. Interiors of the leave-tree clumps tended to have predicted fire behavior akin to the untreated controls, i.e., low surface fire spread rate and low transition ratio. Openings where all overstory trees were removed had the greatest surface fire spread rate and flame length due to increased open windspeed. Clump edges were predicted to have fire behavior most similar to stands in the dispersed treatment. Where stands are designed for structural diversity, measures of central tendency (mean, median) of stand condition are clearly insufficient to assess the scope of potential fire behavior. Greater resolution of within-stand variability and appropriate replication will aid the development of within-stand potential fire behavior distributions after aggregated VRH.

Structural complexity and disturbance

We found that nearly all untreated plots, less than half of aggregated treatment plots, and very few of dispersed treatment plots had low critical crown rate of spread thresholds (< 0.75 m·sec⁻¹; Figure 3). Since removal of 50% of the stand basal area was the treatment prescription, it is no surprise that many of the plots in treated stands had low to no CBD values, and thus high critical crown rates of spread. Not evident in Figure 3 is the spatial discontinuity inherent to clumps of trees within aggregated treatment stands. Aggregated retention *stands* are likely more resistant to crown fire than Figure 3 indicates because the spatially discontinuous pattern of the

retention layout reduces crown fire contagion. At this stage in stand development, aggregated clump disconnectedness is a major driver of structural resilience to fire.

Homogeneous, even-aged LP forests are often highly susceptible to severe and widespread disturbance events, but structural diversity and resilience can be improved by creating multiaged stands (Safranyik and Carroll 2006; Axelson et al. 2010). At TCEF, VRH techniques increased stand complexity by reducing overstory densities and promoting a new cohort. These treated stands also reduced the amount of forested area susceptible to mortality caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins), since these insects generally cannot amplify populations to epidemic levels within LP trees less than 20 cm dbh or in stands younger than 80 years old (Safranyik and Carroll 2006; Axelson et al. 2010). Furthermore, the structural complexity created likely increased resistance to beetle attack in the retained overstory portions of the aggregated retention stands. This residual structure has been shown beneficial in a forest patch-cutting experiment in Wyoming, where tree mortality caused by biotic agents (including mountain pine beetle) was reduced within overstory retention groups similar to those created at TCEF (Johnson et al. 2014).

We also expect improved resistance to some biotic and abiotic disturbances in the dispersed retention stands, since its structure is similar to shaded fuelbreaks designed to hinder stand-replacing crown fires (Agee et al. 2000) and thinning treatments implemented to reduce stand susceptibility to mountain pine beetle attack (Whitehead and Russo 2005; Whitehead et al. 2007). However, dispersed retention treatments may exacerbate wind and snow-related tree mortality, as observed in partial cutting of old-growth LP stands in the central Rocky Mountains (Alexander 1966). In general, flexible saplings are resilient to windstorms and heavy snow loads, whereas windthrow can be common in mature trees (Johnson 1987). Substantial windthrow was

observed in multiple dispersed retention plots at this study site following harvesting (Hood et al. 2012). As such, aggregated retention may be preferred over the dispersed stand structure when converting to multiple cohorts in locations prone to high windspeeds or snow damage. This is especially true in dense, previously unthinned stands with high height to diameter ratios.

We suggest that the VRH treatments implemented at TCEF can effectively improve forest heterogeneity in such a manner that mitigates stand-level susceptibility to severe biotic and abiotic disturbances. However, these treatments increase within-stand variability in surface fireline intensity and crown fire initiation ratio after 12 years. We believe it is critical to acknowledge the tradeoffs in overstory retention structure (i.e., for stand growth and disturbance susceptibility) when using VRH to create multiaged stands.

Conclusion

This study provides much needed insight into the change in fuel loadings for 12-year fuel dynamics after variable-retention harvests. Our results suggest that operational efforts to reduce fuel loading were countered by post-treatment mortality. We observed lower accumulation of fine woody debris due to treatment, but burning greatly increased large woody debris accumulation. Our potential fire analysis shows that that averaged fuel and fire behavior metrics are insufficient to characterize the scope of potential fire behavior in highly irregular stands. Treatments increased likelihood of crown ignition because of increased live surface fuels and sub-canopy wind penetration. However, critical crown fire spread rates generally indicated higher windspeeds needed in treated vs. untreated to facilitate crown fire spread.

Acknowledgements

This was a study of the Applied Forest Management Program at the University of Montana, a research and demonstration unit of the Montana Forest and Conservation Experiment Station. Support for this study came from the USDA Forest Service, Forest Health Protection, Special Technology Development Program (grant R1-2011-03). The study was made possible with contributions by Forest Health Protection, Northern Region, USDA Forest Service, and the Rocky Mountain Research Station (RMRS), USDA Forest Service. We are indebted to Tom Perry (University of Montana College of Forestry and Conservation), who provided integral technical leadership; Helen Smith (RMRS), gracious provider of historic data; Duncan Lutes (RMRS) and Bob Keane (RMRS), who administered very helpful guidance; and two anonymous reviewers.

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Table 1. Custom fire behavior fuel model assignment coefficients calculated or assumed for fire behavior simulations within BehavePlus and FOFEM. Fuel models were assigned to each measured plot. SAV is surface area to volume ratio.

Characteristics	Metric	English	Value (English)	Derivation
	Units	Units		
1-hr fuel load	Mg·ha ⁻¹	tons·ac ⁻¹	[plot-specific]	Calculated after Brown 1974
10-hr fuel load	Mg·ha ⁻¹	tons·ac ⁻¹	[plot-specific]	Calculated after Brown 1974
100-hr fuel load	Mg·ha ⁻¹	tons·ac ⁻¹	[plot-specific]	Calculated after Brown 1974
Live herbaceous fuel load	Mg·ha ⁻¹	tons·ac ⁻¹	[plot-specific]	FFE-FVS FUELOUT herb load
Live woody fuel load	Mg·ha ⁻¹	tons·ac ⁻¹	[plot-specific]	FFE-FVS FUELOUT shrub load + calculated seedling load (foliage + half of 1-hr branch load; Brown 1978)
Fuel model type	-	-	"static"	-
1-hr dead SAV	cm ⁻¹	ft ⁻¹	60,960 (2,000)	Anderson 1982, Scott and Burgan 2005
Live herbaceous SAV	cm ⁻¹	ft ⁻¹	50,292 (1,650)	Compromise between Anderson 1982, Scott and Burgan 2005
Live woody SAV	cm ⁻¹	ft ⁻¹	47,244 (1,550)	Compromise between Anderson 1982, Scott and Burgan 2005
Fuel bed depth	cm	ft	[plot-specific]	Seedling density modified seedling height
Moisture of extinction	%	%	[plot-specific]	Modified by overstory canopy cover, as reflected in Anderson 1982, Scott and Burgan 2005
Dead heat content	J·kg ⁻¹	BTU·lb ⁻¹	18,607,978 (8,000)	Anderson 1982, Scott and Burgan 2005
Live heat content	J·kg ⁻¹	BTU·lb ⁻¹	18,607,978 (8,000)	Anderson 1982, Scott and Burgan 2005

Table 2. Live and dead fuel moistures and wind scenarios modeled using BehavePlus and FOFEM. Fuel moistures are based on Scott and Burgan (2005).

Scenario name	Moisture content (%)						6.1 m Wind speed (km·hr ⁻¹)
	1-hr fuels	10-hr fuels ^a	100-hr fuels	Live herbaceous fuels ^d	Live woody fuels ^d	Canopy foliar	
Dry-low wind	3	4 ^b	5	60	90	100	16.1
Dry-high wind	3	4 ^b	5	60	90	100	40.2
Moist-low wind	12	13 ^c	14	60	90	100	16.1
Moist-high wind	12	13 ^c	14	60	90	100	40.2

^a Plots with canopy cover > 50% were assigned 3.25% greater 10-hr moisture, per Rothermel 1983

^b Based on Scott and Burgan (2005) dead fuel moisture scenario D1

^c Based on Scott and Burgan (2005) dead fuel moisture scenario D4

^d Based on Scott and Burgan (2005) live fuel moisture scenario L2

Table 3. Treatment means and standard errors of downed woody debris by fuels class, 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF.

Three sets of no-treatment reference means are provided for comparison. The Brown and Bevins (1986) lodgepole pine fuelbed means were developed using an average of four sites across Idaho, Montana, and Wyoming. The means presented by Baker (2009) were derived using the Fuel Characteristic Classification System (FCCS; [Ottmar et al. 2007]) for lodgepole pine fuelbeds across the entirety of the United States Rocky Mountain range. The reference means in the final row of the table were calculated using FCCS given the typical overstory condition of this study's control units.

	Litter and duff	1-hr	10-hr	100-hr	Sound 1000-hr	Total
 <i>Mg ha⁻¹</i>					
Control	48.16 (5.43)	0.24 (0.03)	1.69 (0.27)	3.64 (1.21)	34.07 (7.73)	87.83 (11.15)
Aggregated:B	40.35 (5.31)	0.22 (0.03)	1.96 (0.26)	3.88 (1.24)	25.54 (7.69)	72.07 (11.05)
Aggregated:U	49.13 (5.19)	0.25 (0.03)	2.41 (0.25)	5.92 (1.28)	22.73 (7.65)	80.46 (10.94)
Dispersed:B	36.20 (5.43)	0.15 (0.03)	1.38 (0.27)	4.41 (1.22)	36.40 (7.73)	78.67 (11.16)
Dispersed:U	49.57 (4.98)	0.23 (0.03)	2.72 (0.24)	6.02 (1.29)	30.51 (7.58)	88.91 (10.76)
Brown and Bevins 1986	1.26 (Litter only)	0.40	1.50	4.34	--	--
Baker 2008	35.4	1.1	6.0	7.6	25.9	76.0
FCCS	32.45	0.90	4.93	6.28	21.30	33.40

Table 4. Estimated linear contrasts of dead surface fuel loads (Mg ha^{-1}) from mixed-effects models 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF.

Response variables were modeled first at the year 2012, and second as net annual fuel load evaluated over post-treatment years.

Contrast test	1-hr		10-hr		100-hr		sound 1000-hr +		litter and duff		total dead surface fuel	
	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value
<i>Year 2012</i>												
Grand mean	0.218	<0.001	2.033	<0.001	4.773	<0.001	29.851	<0.001	44.681	<0.001	81.589	<0.001
Control - Treated	0.027	0.362	-0.427	0.070	-1.415	0.005	5.274	0.093	4.347	0.343	7.796	0.214
Aggregated - Dispersed	0.050	0.045	0.134	0.500	-0.317	0.554	-9.317	0.001	1.856	0.632	-7.527	0.157
Burned - Unburned	-0.056	0.025	-0.899	<0.001	-1.824	0.001	4.351	0.103	-11.075	0.005	-9.315	0.082
Treatment interaction	0.025	0.310	0.440	0.028	-0.211	0.695	-1.544	0.561	2.301	0.553	0.928	0.861
<i>Net annual fuel load</i>												
Grand mean	-0.042	<0.001	-0.125	<0.001	-0.041	0.237	0.472	<0.001	-1.096	0.002	-0.838	0.015
Control - Treated	0.012	0.065	0.148	<0.001	0.166	0.009	-0.374	0.106	1.312	0.008	1.270	0.037
Aggregated - Dispersed	0.005	0.379	0.067	0.064	0.074	0.165	-0.225	0.248	-0.067	0.872	-0.157	0.758
Burned - Unburned	0.028	<0.001	0.094	0.010	0.042	0.432	0.714	<0.001	-0.261	0.530	0.599	0.243
Treatment interaction	0.000	0.990	0.038	0.301	0.027	0.614	0.011	0.957	0.017	0.968	0.098	0.848

Table 5. Live vegetation characteristics (mean and standard error) 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF. BA is stand basal area, QMD is quadratic mean diameter, CBD is canopy bulk density, CBH is canopy base height. Understory herb and woody load represent the aboveground plant biomass that contributes to surface fire spread.

Treatment	Overstory						Understory	
	Stem density	BA	QMD	Top height	CBD	CBH	Herb load	Woody load
	<i>trees ha⁻¹</i>	<i>m² ha⁻¹</i>	<i>cm</i>	<i>m</i>	<i>kg m⁻³</i>	<i>m</i>	<i>Mg ha⁻¹</i>	<i>Mg ha⁻¹</i>
Control	745 (94)	30.2 (1.8)	19.4 (0.3)	23.3 (0.9)	0.118 (0.011)	7.1 (0.7)	0.55 (0.04)	0.76 (0.16)
Aggregated:B	497 (88)	18.4 (3.2)	15.0 (0.9)	17.8 (1.7)	0.069 (0.014)	6.3 (0.6)	0.70 (0.04)	1.36 (0.22)
Aggregated:U	364 (150)	11.3 (2.8)	13.5 (0.8)	15.3 (1.7)	0.042 (0.009)	5.0 (0.7)	0.74 (0.03)	2.37 (0.50)
Dispersed:B	108 (32)	4.9 (1.1)	12.8 (2.8)	16.8 (3.4)	0.016 (0.003)	5.5 (0.8)	0.85 (0.01)	2.17 (0.17)
Dispersed:U	194 (25)	8.9 (1.0)	18.0 (0.6)	22.7 (1.1)	0.030 (0.003)	6.0 (0.7)	0.80 (0.02)	2.10 (0.48)

Table 6. Estimated linear contrasts of potential fire characteristics from mixed-effects models 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF.

Response variables were surface fireline intensity and crown fire transition ratio.

Contrast	Dry-low wind		Dry-high wind		Moist-low wind		Moist-high wind	
	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value
<i>Surface fireline intensity (kW m⁻¹)</i>								
Grand mean - 0	265.4	<0.001	742.9	<0.001	93.7	<0.001	235.8	<0.001
Control - Treated	-240.4	<0.001	-675.9	<0.001	-87.1	<0.001	-220.5	<0.001
Aggregated - Dispersed	-114.6	0.126	-319.0	0.166	-39.3	0.251	-103.2	0.284
Burned - Unburned	-270.4	<0.001	-784.0	0.001	-121.5	<0.001	-313.0	0.001
Treatment interaction	29.8	0.689	101.7	0.658	33.3	0.330	98.2	0.308
<i>Transition ratio</i>								
Grand mean - 0	0.119	<0.001	0.327	<0.001	0.053	<0.001	0.135	<0.001
Control - Treated	-0.089	<0.001	-0.243	<0.001	-0.032	0.031	-0.085	0.120
Aggregated - Dispersed	-0.047	0.201	-0.122	0.252	-0.015	0.398	-0.046	0.445
Burned - Unburned	-0.124	0.001	-0.378	<0.001	-0.068	<0.001	-0.176	0.004
Treatment interaction	-0.003	0.942	0.007	0.951	0.006	0.749	0.017	0.770

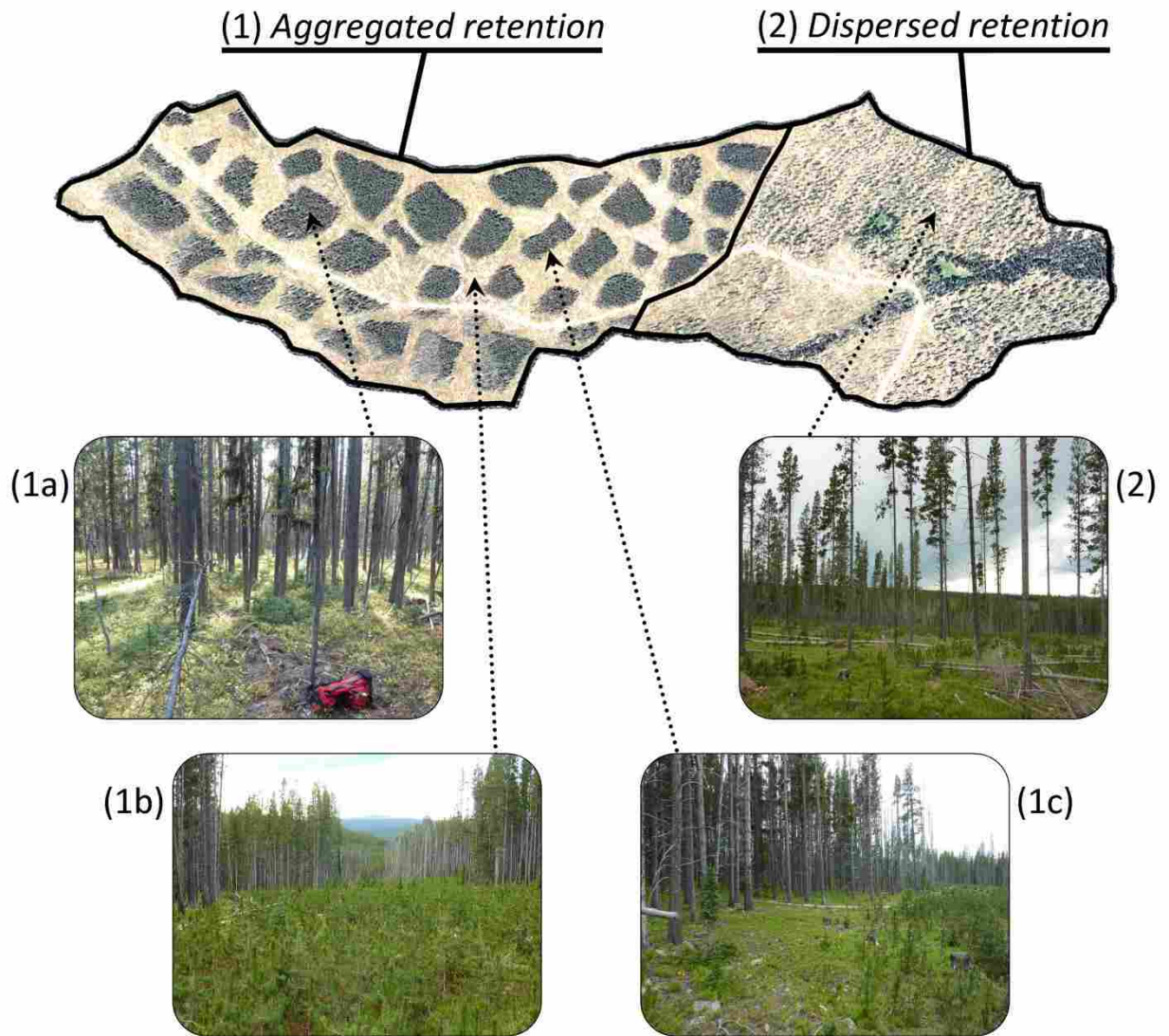


Figure 1. Photo-diagram of variable-retention harvest structural conditions: aerial perspective and typical stand profiles of points within aggregated (1) and dispersed retention (2) management units. Note that the natural consequence of the aggregated retention is three distinct within-stand structural elements: (1a) retained patch interior, (1b) clearing, and (1c) the patch-to-clearing edge interface.

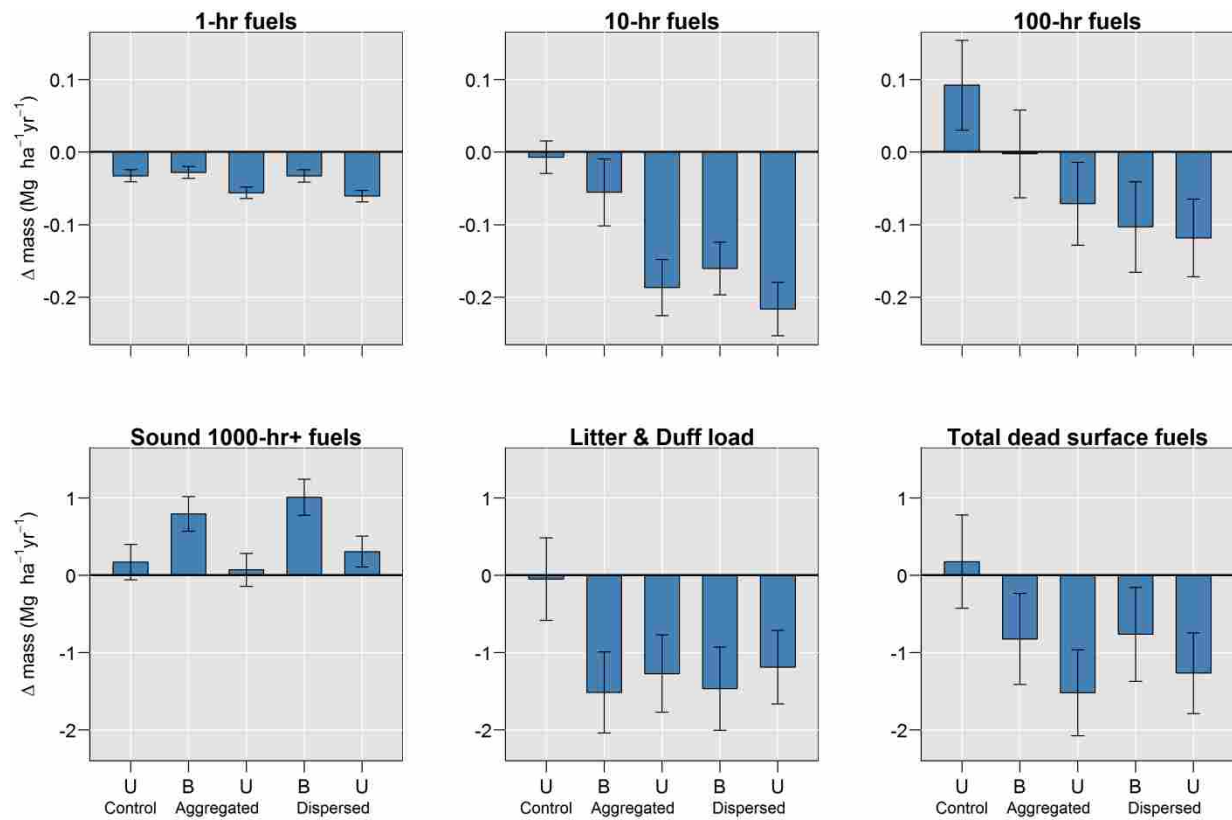


Figure 2. Net annual fuel load (Δ AFL) of surface fuel components in 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF.

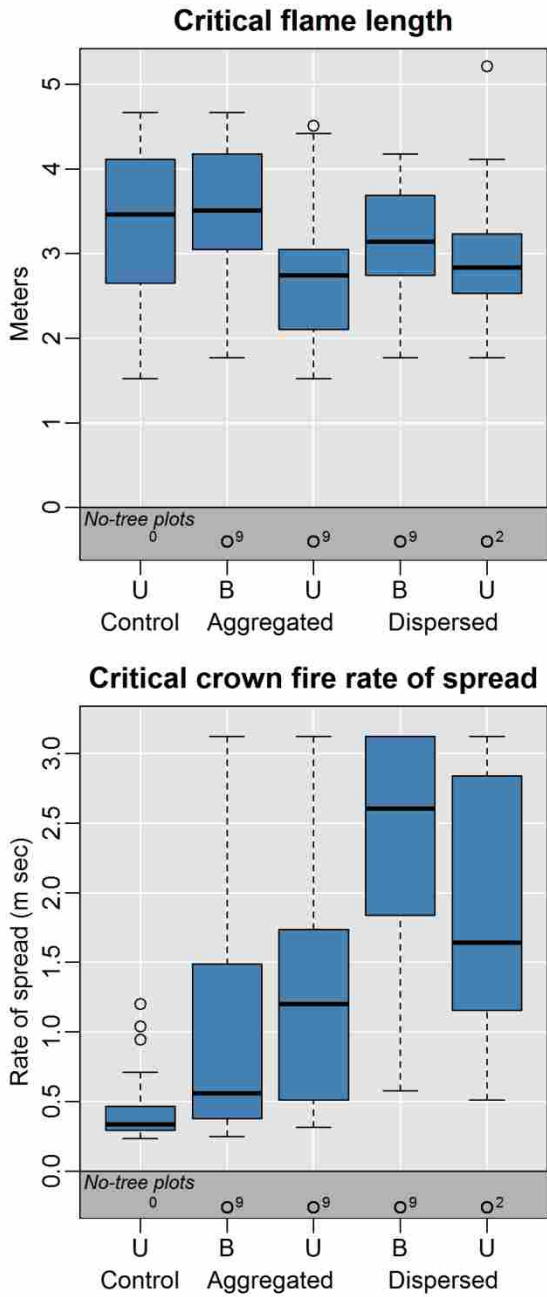


Figure 3. Critical flame length to initiate crown fire (top panel) and critical crown fire rate of spread (bottom panel), 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF. Critical flame length is defined as the surface fire flame length necessary for fire to transition into tree crowns. Critical crown fire rate of spread is the rate necessary for fire to perpetuate in the canopy.

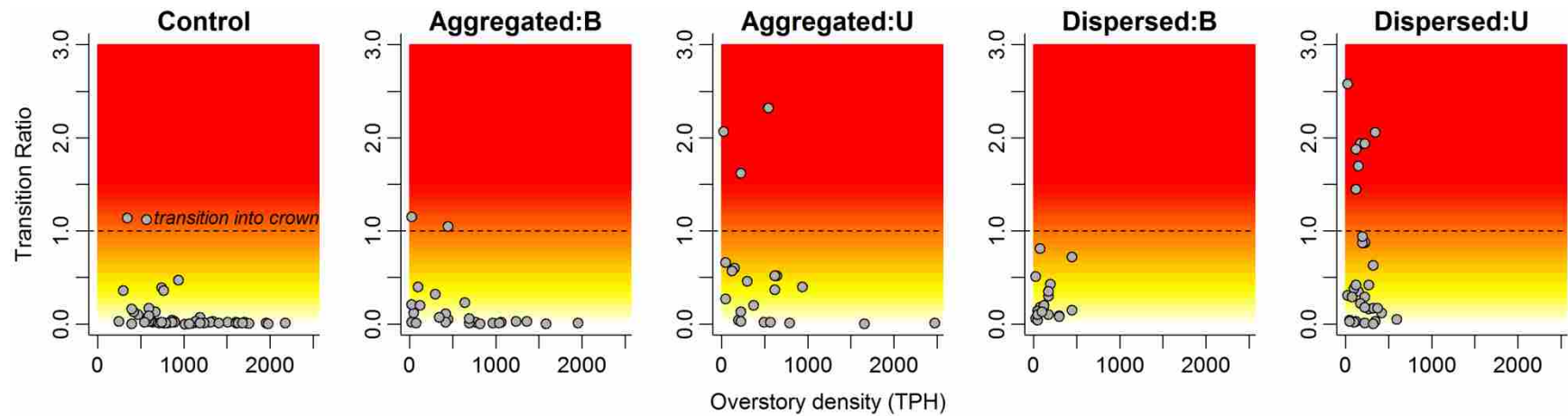


Figure 4. Transition ratios (predicted to critical surface fire flame length needed to ignite overstory crowns) in the dry-high wind scenario (see Table 2), 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF. Points represent plot-level ratios from four experimental units.

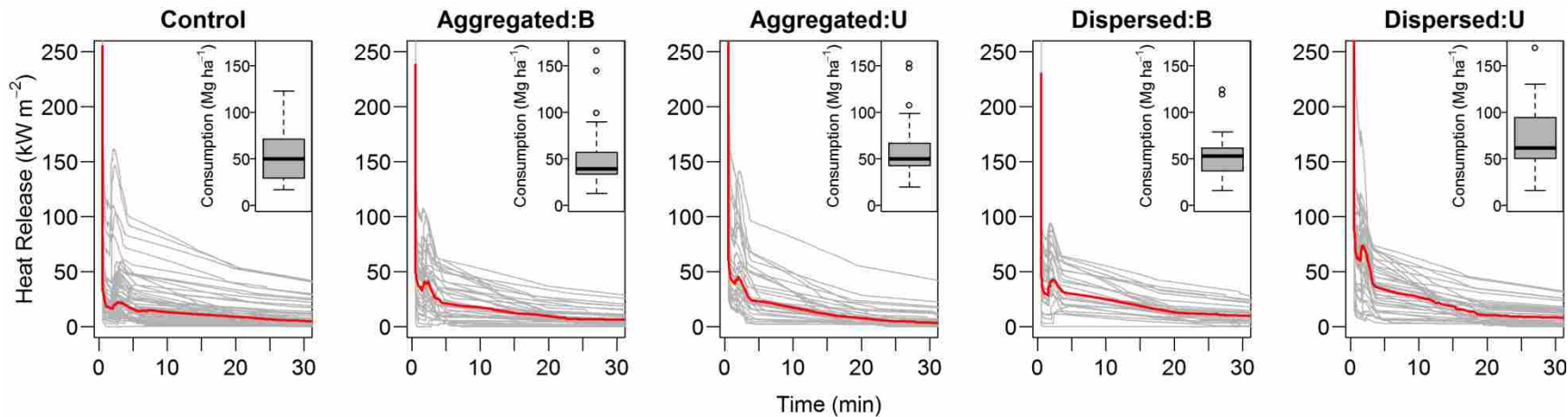


Figure 5. Predicted heat release profile (truncated) in the dry-high wind scenario (see Table 2), 12 years after variable-retention harvest and 9-10 years after prescribed fire in TCEF. Gray lines represent plot-level responses from four experimental units. Red lines represent median heat release from pooled responses. Inset box and whisker plot represents biomass consumed from predicted flaming and smoldering from pooled responses.

Summary and synthesis

There is a dearth of empirical studies examining the mid- to long-term effects of forest structural restoration within forests that have non-stand-replacing fire regimes. This dissertation improves understanding of forest development following restoration treatments that reduce the probability of crown fire.

In Chapters 1 through 3 I investigated forest change following restoration treatments designed to emulate structure from a frequent, low-severity fire regime, that is, after fuel reduction treatment and subsequent mountain pine beetle outbreak in a ponderosa pine/Douglas-fir forest. I found that vegetation communities across treatments had become more similar in the years since treatment, but that overstory and understory structural and compositional traits still distinguish the no-action Control from Thin+Burn stands in 2016. Treatments became more similar over time because of ingrowth stimulated by treatment and overstory mortality from the beetle outbreak. However, both the Thin-only and Thin+Burn resulted in greater stem and crown growth than the unthinned treatments at the individual tree scale. Beetle outbreak had a major impact on forest fuels and crown fire hazard in unthinned treatments because fuel from beetle-killed trees was transferred from canopy to surface profiles, reducing potential for horizontal crown fire spread but increasing potential for crown fire initiation. Thinned treatments were less impacted by beetle outbreak and more impacted by ingrowth. Ingrowth in the Thin-only treatment elevated canopy fuel loads and probability of in-canopy fire transfer, but prescribed fire in the Thin+Burn treatment eliminated advance regeneration such that fuel and potential for crown fire was low and varied little over time.

In Chapters 4 and 5 I similarly investigated forest change following restoration treatments, but these treatments were designed to emulate structure from an infrequent,

mixed-severity fire regime, that is, retention harvest in a lodgepole pine forest. Overstory structures varied widely by treatment, and deteriorated over time, though structure and variability was more stable after Aggregated than Dispersed treatments. Individual overstory trees in the Dispersed treatment had high mortality rates over the years since treatment, but those that survived had high growth rates because of the wide spacing; the open canopies in the Dispersed treatment also resulted in greater regeneration stocking than in Aggregated treatments. I found that stand dynamics processes were fully explained by ecological predictors instead of treatment scale harvest pattern factors, except for overstory tree growth, which was better explained when harvest spatial pattern was included in a predictive model. High overstory mortality rates and structural degradation lead to greater concentration of large woody debris in Dispersed than Aggregated treatments by 2012. The most consistent trend in fuel dynamics was reduced fuel degradation or increased fuel aggradation in burned treatments, however, fuel loads were still lower in burned treatments by 2012. All retention harvest treatments resulted in greater predicted fireline intensities and heat release, though these were greater in unburned treatments, where there were greater stockpiles of surface fuels. Crown fire hazard was lowest in Dispersed treatments because of low residual overstory densities; though mean hazard was greater in Aggregated treatments, canopy variability may aid stand resistance to crown fire.

Both the low- and mixed-severity fire regime restoration treatments that I studied demonstrated a simple, key theme: treatment influences both vegetation development and mortality, which in turn have lasting repercussions on crown fire hazard. Because they removed so much standing biomass, cutting treatments generally influenced forest growth and crown fire hazard more than prescribed burning treatments. Yet treatments as a whole had

progressively greater effects on forest growth as they increased in intensity (Figure 1).

Although treatments were not designed to assess forest dynamics across a smooth gradient of overstory removal, they effectively spanned a range of overstory removal densities, showing that overstory and regeneration growth increased with removal.

Restoration treatments demonstrated similar effects on residual tree growth and regeneration with increasing overstory removal, but they demonstrated contrasting effects on overstory mortality and fuel deposition (Figure 1). This is primarily because the restoration treatments were executed on two different forest types and subject to two different disturbance agents during the measurement period. Overstory mortality and fuel deposition was high for the low-intensity fuel reduction treatments (Control and Burn-only) because of beetle-caused mortality. On the other hand, mortality and fuel deposition was high for high-intensity retention harvests (Dispersed treatments removed more basal area than Aggregated) because of windthrow and lodgepole pine's limited fire tolerance.

Finally, this body of work highlights that forest restoration treatments require upkeep to maintain expected effects on crown fire hazard. As ingrowth ascends into residual overstory canopies crown fire hazard will continue to increase. Ingrowth is a low priority management goal in many fuel reduction treatments, but establishment and development of a new cohort is an expectation for retention harvests. It is important to recognize the distinct tradeoff of new cohort development for increased fire hazard in either restoration approach, and shrewd to plan for treatment maintenance as stands develop.

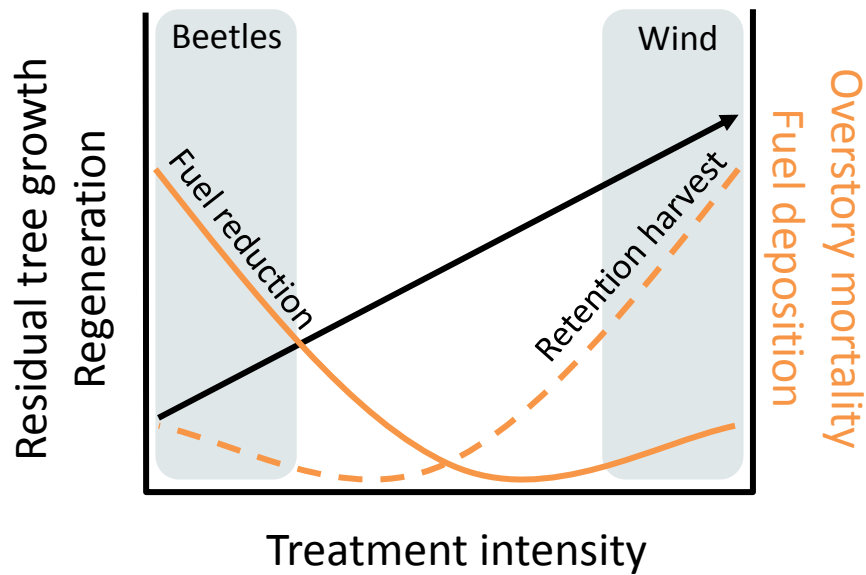


Figure 1. Conceptual diagram demonstrating the effect of treatment intensity (i.e., overstory removal) on residual tree growth and regeneration (black line, both on left y-axis) as well as on overstory mortality and fuel deposition to the surface (orange lines, both on right y-axis). For fuel reduction, treatment intensities ranked from lowest to highest were: Control, Burn-only, Thin-only, Thin+Burn. For retention harvest, ranked intensities were: Control, Aggregated:Unburned, Aggregated:Burned, Dispersed:Unburned, Dispersed:Burned. Shaded areas represent disturbance by beetles (influenced fuel reduction treatments) or wind (influenced retention harvests), two agents that affected overstory mortality and fuel deposition.