Ecological Applications, 30(2), 2020, e02023

Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak

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Citation: Crotteau, J. S., C. R. Keyes, S. M. Hood, and A. J. Larson. 2020. Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak. Ecological Applications 30(2):e02023. 10.1002/eap.2023

Abstract. In the western United States, restoration of forests with historically frequent, low-severity fire regimes often includes fuel reduction that reestablish open, early-seral conditions while reducing fuel continuity and loading. Between 2001 and 2016, fuel reduction (e.g., thinning, prescribed burning, etc.) was implemented on over 26 million hectares of federal lands alone in the United States, reflecting the urgency to mitigate risk from high-severity wildfire. However, between 2001 and 2012, nearly 20 million hectares in the United States were impacted by mountain pine beetle (MPB; *Dendroctonus ponderosae*), compounding restoration effects in wildfire-hazard-treated stands. Knowledge of the effects of treatments followed by natural disturbance on long-term forest structure and communities is needed, especially considering that fuel treatments are increasingly being implemented and warming climate is predicted to exacerbate disturbance frequency and severity. We tested the interacting effects of treatments designed to reduce high-severity wildfire hazard in stands subsequently challenged by MPB outbreak on vegetation dynamics using a factorial experimental design (control, thin only, burn only, thin + burn) in a ponderosa pine (*Pinus ponderosa*)-dominated forest. Stands were treated by 2002, then impacted by MPB outbreak from 2005 to 2012. We assessed change in overstory and understory forest community structure, composition, and diversity over time. There were distinct thinning, burning, and year effects. Thinning immediately reduced overstory density; pine density then declined 4.5 times more in unthinned than thinned treatments due to MPB. Burning immediately reduced graminoid, shrub, and total understory cover by as much as 52%, resulting in greater species evenness than unburned treatments, but differences disappeared by 2016 due to growth and MPB outbreak. Similarly, multivariate analyses indicated forest communities were starkly different after treatment but became more similar over time, though key understory and overstory attributes still distinguish control and thin + burn. This study shows the value of long-term silvicultural experiments to evaluate treatment longevity and the compounded effects of treatment and natural disturbance. We demonstrate the homogenizing effects of treatment-induced growth coupled with MPB-caused tree mortality on management strategies that just treat the overstory (thinning) or understory (burning), showing that only combined treatments can provide the unique structural and compositional outcomes expected of restoration.

Key words: Dendroctonus ponderosae; *early seral restoration; Fire and Fire Surrogate study; fire exclusion, understory diversity; frequent-fire ecosystem;* Pinus ponderosa.

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, Stephens et al. 2018). Active restoration of fire-dependent forests can create conditions that foster low-severity fire and counter the successional effects of past management (Fulé et al. 2012, Hessburg et al. 2015, Kalies and Yocom Kent 2016); however, restoration efforts often do not acknowledge the need for maintenance treatments or examine longer-term impacts (Collins et al. 2016, Stephens et al. 2016). 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 fire resistance may be ephemeral if fire-sensitive communities quickly reestablish and grow.

Manuscript received 11 March 2019; revised 26 July 2019; accepted 27 August 2019. Corresponding Editor: Donald McKenzie.
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Although dry forest restoration anticipates subsequent disturbance by fire, western forests are subject to a variety of disturbance agents and their interactions (wind, beetles, freezing, and drought; e.g., Veblen et al. 1994), regardless of whether stands are treated. Furthermore, compounding disturbances may have antagonistic or synergistic impacts on tree mortality and forest communities (Pickett et al. 1989, Paine et al. 1998, Kane et al. 2017). As disturbance agents, bark beetles and fire have a complex relationship that has shaped many temperate forests (Bigler et al. 2005, Harvey et al. 2013, Stephens et al. 2018). The effects of bark beetle outbreaks on vegetation dynamics have been widely documented (Pec et al. 2015), as have been forest treatments for resistance to beetle outbreaks (Fettig et al. 2007, 2014). But the compounding effects of dry forest restoration, especially fuel treatments that aim to create resistance to high-severity fire, and bark beetle outbreak on vegetation dynamics in light of future fire and climate change are largely unknown, which presents an urgent and unsolved problem.

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 and fire exclusion (Hessburg et al. 2015). Whether informed by historical range of variability (Keane et al. 2009, Clyatt et al. 2016) or desired future structure and function (Fulé 2008, Janowiak et al. 2014, Maher et al. 2019), the long-term goal in the restoration of these forest types is to reestablish overstory resistance (i.e., ability to survive disturbance) and community resilience (i.e., ability to reorganize with similar attributes following disturbance) to future disturbance, especially fire. One crucial element in this is fuel reduction. 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, Reinhardt et al. 2008). Fuel reduction treatments have been widely implemented across the West over recent decades, sometimes with the aim to restore native ecosystem structure and process (Larson and Churchill 2012), and other times simply to provide a defensive framework to protect forests and properties (McKelvey et al. 1996, Schoennagel et al. 2009). Whether couched in ecosystem restoration or not, fuel treatments directly modify forest overstories and perturb understories in ways that are sure to influence community response (Anderson et al. 1969, Ellison et al. 2005, Abella and Springer 2015, Goodwin et al. 2018) and alter the outcome of subsequent disturbance.

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) is native to North America and frequently impacts dry, pine-dominated, forest types such as those with frequent, low-severity historical fire regimes. MPB periodically erupts into regional outbreaks and, between 2001 and 2012, outbreaks affected nearly 20 million hectares and killed many trees in the western United States (Karel and Man [2017], but see Hicke et al. [2016] for alternative estimate of MPB impact). The recent MPB outbreaks spanned landscapes consisting of multiple management strategies, killing trees in both unmanaged and managed stands, but causing the most mortality in stands with greater host densities (Klenner and Arsenault 2009, Klutsch et al. 2009, Egan et al. 2010, Hood et al. 2016).

Although MPB outbreaks reduce live tree density and live canopy fuel, increasing resources to remaining trees and understory species (Brown et al. 2010, Griffin et al. 2011, Pec et al. 2015) and addressing some of the primary objectives of silvicultural fuel reduction, there are important differences. Simard et al. (2011) argued that MPB outbreaks in untreated lodgepole pine stands eventually reduce canopy density and thereby potential for crown fire (but see Moran and Cochrane 2012), and physics-based fire modeling suggests that old MPB outbreaks likewise buffer residual overstory mortality in ponderosa pine stands (Sieg et al. 2017). The biophysical process of MPB-caused mortality and subsequent change in fuel structure in those studies suggest the process is independent of forest type, and that MPB outbreaks can confer some of the same fire same resistance elements that silvicultural practices like thinning provide in forests with more frequent fire. But unlike fuel treatment practices, which remove or consume surface and canopy biomass in a short pulse and generally retain large, early seral trees, MPB preferentially target and kill large, early seral pines over a lengthier period and do not remove biomass (Safranyik and Carroll 2006, Stephens et al. 2018). Because of host specificity, severe MPB outbreaks can quickly change species dominance if late-seral tree species are present (Hood et al. 2016). Furthermore, silvicultural practices typically aim to reduce surface fuel loadings and scarify forest understories with machinery or prescribed fire, whereas MPB outbreaks slowly add foliar and woody biomass to the forest floor as MPB-killed trees decompose and fall (Page and Jenkins 2007). Where silvicultural practices such as fuel reduction have subsequently been impacted by MPB outbreaks, community effects may be a composite of both disturbances, and the effects of either disturbance may mask the other (Crotteau et al. 2018*b*).

Little is known about long-term vegetation and community dynamics after fuel treatments, and even less is known about the combined impact of these treatments and MPB outbreak on vegetation structure, composition, and dynamics. Here, we report 14-yr vegetation response to the Fire and Fire Surrogate study, a replicated, randomized, operational-scale fuel reduction experiment (McIver et al. 2013) designed to restore ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson var. *scopulorum* Engelm.) forests that were challenged by a regional MPB outbreak. The unique combination of experimental fuel reduction treatments and an MPB outbreak created novel forest conditions, which have been largely undocumented. In a companion piece to this study from the fire and fuels perspective, Crotteau et al. (2018*b*) found that combined thinning and burning treatments best mitigated fire hazard development after MPB outbreak, because thinning reduced canopy fuels, thinning increased overstory survival and thus limited mortality-induced surface fuel accumulation, and burning reduced ladder fuels. Here, we analyze data from 14 yr after silvicultural treatment with the broad research question: what impact does the combination of fuel reduction and MPB outbreak have on live vegetation dynamics? We sought to understand how the combination of treatment and MPB 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 MPB-caused mortality, which in turn also impacts residual growth. Further, we expected that understory functional composition and diversity would develop on different trajectories across treatments because of trait-mediated responses to initial treatments followed by changes in 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 MPB outbreak reduced overstory density and stimulated understory development as expected by fuel treatments. To our knowledge, this study is unprecedented. None have ever revealed the cumulative effects of fuel treatment modified by a MPB outbreak on forest vegetation dynamics, therefore our results are highly 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 to 1,388 m above sea level; vegetation comprises *Pseudotsuga menziesii*/*Vaccinium caespitosum* Michx. and *Pseudotsuga menziesii*/*Spiraea betulifolia* Pall. 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, nearly one-half of which falls as snow (Schneider et al. 2019; precipitation data *available online*).[5] 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 d. Grissino-Mayer et al. (2006) identified that historical fire frequency at Lubrecht prior to the 20th century ranged from 2 to 14 yr, with a mean composite fire return interval of 7 yr, but the last natural fire prior to treatment was approximately 70 yr ago.

Early 20th-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 and cattle grazing (Keeley et al. 2009). The overstory is dominated by second-growth ponderosa pine, 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. Pretreatment overstories were mostly continuous, with stem densities near 400 trees/ha and basal area of 22.1 m^2/ha. Stands were dense (5,000–11,000 stems/ha) with advance regeneration of Douglas-fir, and occasional thickets of ponderosa pine regeneration.

Silvicultural treatment and natural disturbance

Lubrecht Experimental Forest was selected as the northern Rocky Mountains' site for the Fire and Fire Surrogate study, a multidisciplinary research project that aimed to quantify the short-term effects of fuel reduction treatments in frequent-fire forests across the United States (Weatherspoon 2000, McIver and Weatherspoon 2010). The Fire and Fire Surrogate study provides a framework to examine the effects of 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 12 9-ha experimental units. The cutting prescription was a combined low thinning and improvement cut to a residual basal area of 11.5 m^{2}/ha, favoring retention of large ponderosa pine and western larch over Douglas-fir. Broadcast burns were conducted in the spring with wind speeds <13 km/h. Fires were generally kept to a low intensity to maintain operational control, resulting in low-severity burns that consumed the forest floor and killed small-diameter ladder fuels, with pockets of moderate to 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 short pulse of activity associated with burning. Finally, Schwilk et al. (2009)

[5] http://prism.oregonstate.edu

and McIver et al. (2013) compared this site's vegetative and fuel responses with other sites from the national Fire and Fire Surrogate study.

Not long after researchers completed measurements of short-term treatment responses (i.e., 4 yr after treatment), a regional MPB outbreak began affecting the Lubrecht Experimental Forest (Gannon and Sontag 2011). MPB-caused overstory mortality levels were high in Control and Burn only units over the course of 2006 to 2012, leading to similar live ponderosa pine basal area across all treatments by the end of the outbreak (Hood et al. 2016). In the present study, we used Hood et al.'s (2016) MPB-caused tree mortality data to infer cause of tree death. After the MPB outbreak, changes in vegetation dynamics are no longer a pure effect of fuel reduction treatments, but rather restoration compounded by MPB outbreak (Crotteau et al. 2018*b*).

Field methods

We measured all live aboveground forest vegetation at our study site except for bryophytes. We divided life forms into two broad classes for measurement and analysis: tree and nontree (hereafter, "understory") vegetation. The tree class was then subdivided by size into overstory (diameter at breast height [dbh; height 1.37 m] $\geq$ 10.16 cm) and regeneration (height $\geq$ 10 cm and dbh < 10.16 cm), the latter comprised of five subclasses (seedling, 10 cm $\leq$ height < 50 cm; large seedling, 50 cm $\leq$ height < 137 cm; small sapling, 0.1 cm $\leq$ dbh < 3 cm; medium sapling, 3 cm $\leq$ dbh < 6 cm; large sapling, 6 cm $\leq$ dbh < 10.16 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 nonwoody, nongraminoid 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 (Metlen and Fiedler 2006). These were 10 randomly selected plot locations from 36 systematically located grid points within each of the 12 treatment units, for a total of 120 measured plot locations. Species, dbh, total height, and crown width were recorded for overstory trees on one 0.04-ha subplot per Whittaker plot. Saplings were tallied on five 100-m^2 subplots per plot; seedlings were tallied on 20 1-m^2 subplots per plot. Understory vegetation was identified by species (or by genus for difficult to identify species) and cover was estimated on 12 1-m^2 subplots per plot.

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

To assess the spatial variability within treatments, we also measured overstory trees on each of the 36 grid point locations per unit (total of 432 plots). In that spatially extensive 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 harvested or fire-killed trees. Trees were then remeasured in 2015.

We refer to the earliest data (2000, 2001, 2002) as "2002" to represent the collective immediate post-treatment data and most recent data (2014, 2015, 2016) as "2016" for the post-MPB outbreak data. By the time of final measurement, stands were in the post-MPB outbreak, leaf-off, "gray phase" of the disturbance cycle (Jenkins et al. 2008).

Analytical and statistical methods

To understand how the combination of fuel treatment and MPB 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 stand density index as a relative density metric that incorporates overstory tree size and density, scaled by an a priori maximum stocking value for ponderosa pine of 900 (rSDI; 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 our spatially extensive data set to address spatial variability of stand structure within treated areas. We summed tree volumes to estimate stand volume 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 (SCI). In-stand standard deviation is 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. We calculated SCI for each unit (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 nonoverlapping 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 (m) and considered volume as the z coordinate (m^3/ha; see Appendix S1: Fig. S1 for an example). We present SCI as the percentage >1, with higher numbers signifying a more rugged surface.

We analyzed understory vegetation total percent cover and cover by class to understand how the combination of fuel treatment and MPB 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 evidence of significance at the 90% confidence level (alpha = 0.10).

Finally, we identified change to overall forest communities by treatment 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 two dimensions, first for the overstory community (16 dimensions) and then the understory (nine 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 multiresponse permutation procedure (MRPP), which is a nonparametric alternative to multivariate ANOVA. Whereas the combination of 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

Immediately following treatment, in 2002, diameter distributions on the Whittaker plots varied by treatment (Fig. 1). In particular, unthinned treatments (Control and Burn-only) had high densities of small overstory trees and low densities of large overstory 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, as Douglas-fir was specifically targeted for removal. Regeneration size-class distribution also varied by treatment in 2002 (Fig. 2). Burned treatments had less small regeneration than unburned treatments, and density across all classes in the thin + burn treatment was much lower than other treatments.

By 2016, 14 yr after treatment and approximately 5 yr after MPB outbreak, changes to diameter distributions were most evident in the unthinned treatments, where the MPB outbreak caused sizable mortality to ponderosa pine trees from 20 to 55 cm dbh (Fig. 1; also see

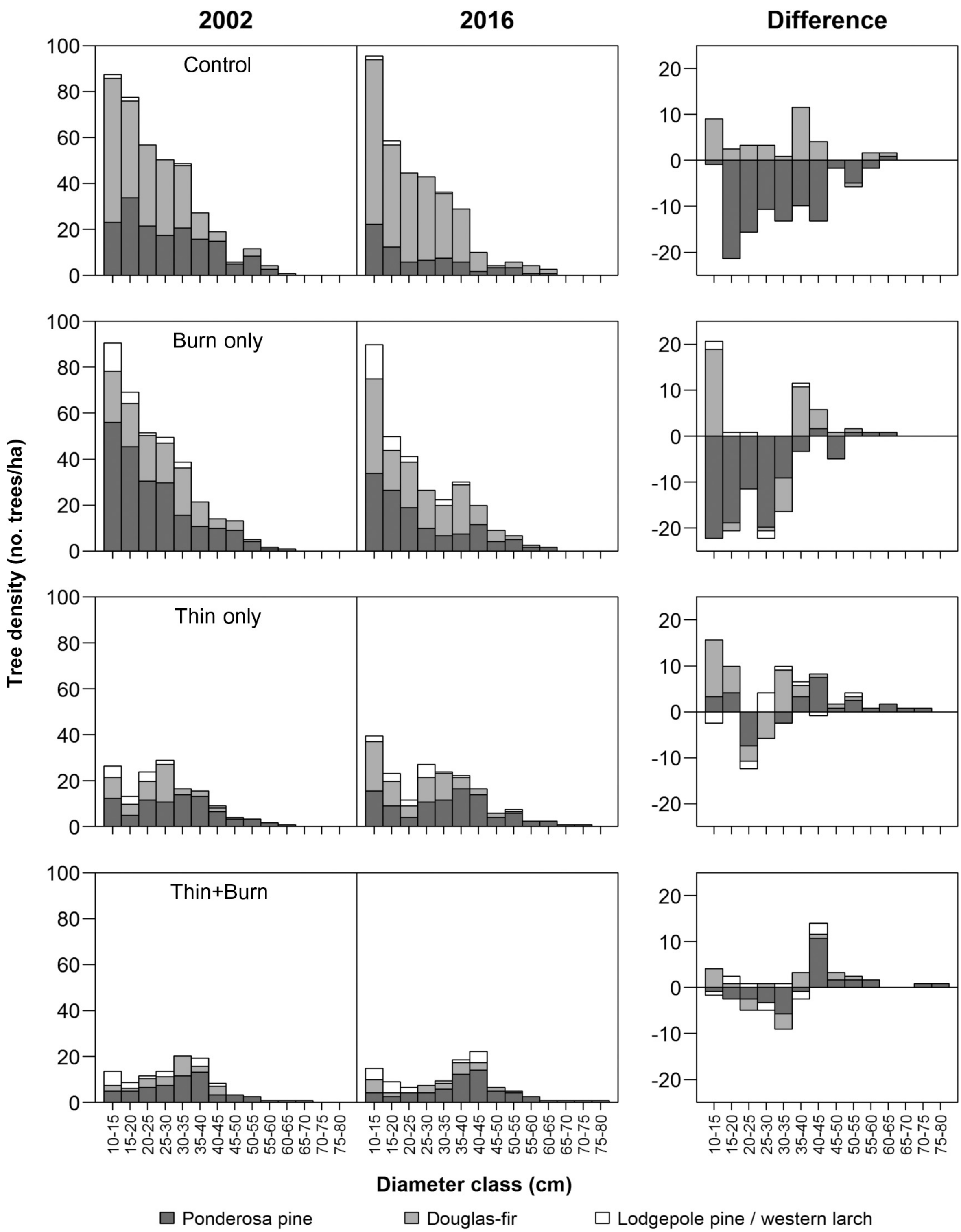

FIG. 1. Overstory diameter distribution by species (stacked) after treatment at Lubrecht Forest's Fire and Fire Surrogate study. From left to right panels show distribution in 2002 (immediately after treatment), 2016, and gains/losses per class between 2002 and 2016.

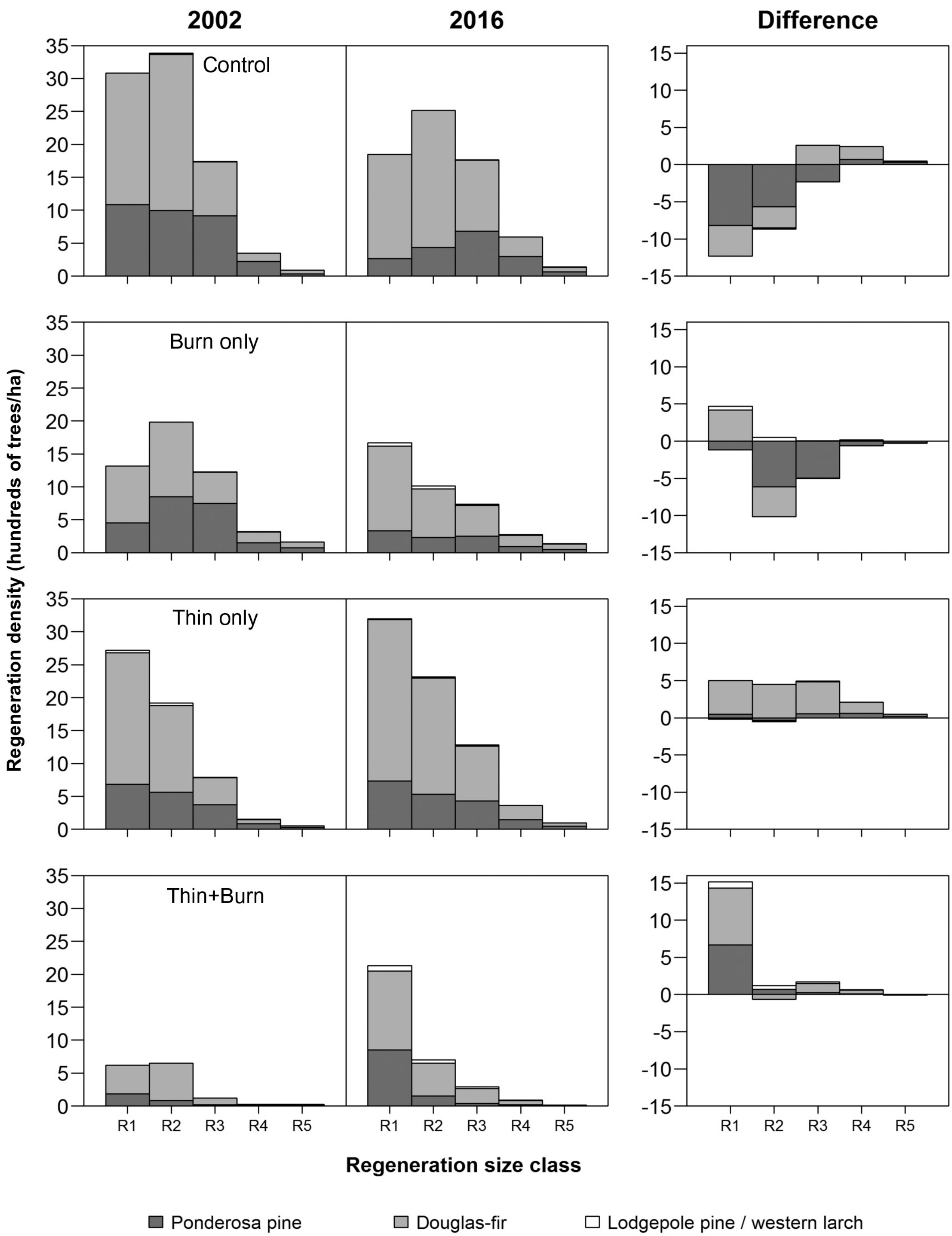

FIG. 2. Regeneration size class distribution by species (stacked) after treatment at Lubrecht Forest's Fire and Fire Surrogate study. From left to right, panels show distribution in 2002 (immediately after treatment), 2016, and gains/losses per class between 2002 and 2016. Regeneration size classes are 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).

Hood et al. [2016]), a class that includes many of the trees that had been targeted for retention in the treated units. 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 (Fig. 2). We observed greater decline across regeneration classes in the unthinned treatments than the thinned treatments likely due to overstory competition, which likely reduced pine regeneration densities, 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.

Stand structure and composition metrics changed notably from 2002 to 2016 (Fig. 3). In 2002, the average stand across all treatments had 242 overstory trees/ha, with a QMD of 29 cm, volume of 102 m^3/ha, rSDI of 31%, 25% canopy cover, and was composed of 60% ponderosa pine. The regeneration class (includes advance regeneration) had 5,275 trees/ha and was 39% ponderosa pine. Year or year × 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 (Fig. 3). Thinning immediately reduced these metrics between 46% and 61% over the unthinned treatments. Burning reduced overstory density, regeneration density, and canopy cover between 15% and 54% over unburned treatments. Responses decreased 6% to 22% in unthinned treatments over time (2002–2016), whereas they increased 22% to 50% in thinned treatments.

Overstory and regeneration composition did not respond to the same across treatment and year (Fig. 3). Across years, thinning increased overstory ponderosa pine composition 40% over unthinned treatments. 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 >50% ponderosa pine composition by 2016.

Structural variability (i.e., variability of overstory volume across 36 points per stand) generally increased over time across treatments. Treatment and year had nearly identical effects on in-stand standard deviation and SCI (Fig. 4). Those two metrics show that thinning reduced structural variability: thinned treatments had 27–34% lower structural variability than unthinned treatments (control and burn only). Variability across all treatments, however, increased 21–27% over time. Although the gap in structural variability between thinned and unthinned treatments was reduced by 2016, lack of a significant interaction term shows these statistical differences persist over time. The striking similarity between averaged in-stand standard deviation and "global" SCI indicates that spatial referencing provided little additional information to variability when summarized to the stand scale. Coefficient of variation (variability of stand volume 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

Understory cover and diversity metrics demonstrated both similarities and differences across treatments and over time (Fig. 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 × time was a significant factor for graminoid cover, exotic cover, richness, and Shannon's H. Burning or burning × time 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.

Cover of all functional types (graminoids, forbs, and shrubs) increased over time, between 102% and 558% from 2002 to 2016 (Fig. 5). Graminoids were the only functional type influenced by thinning. The thinning × 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 burn only), respectively. The burning × 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

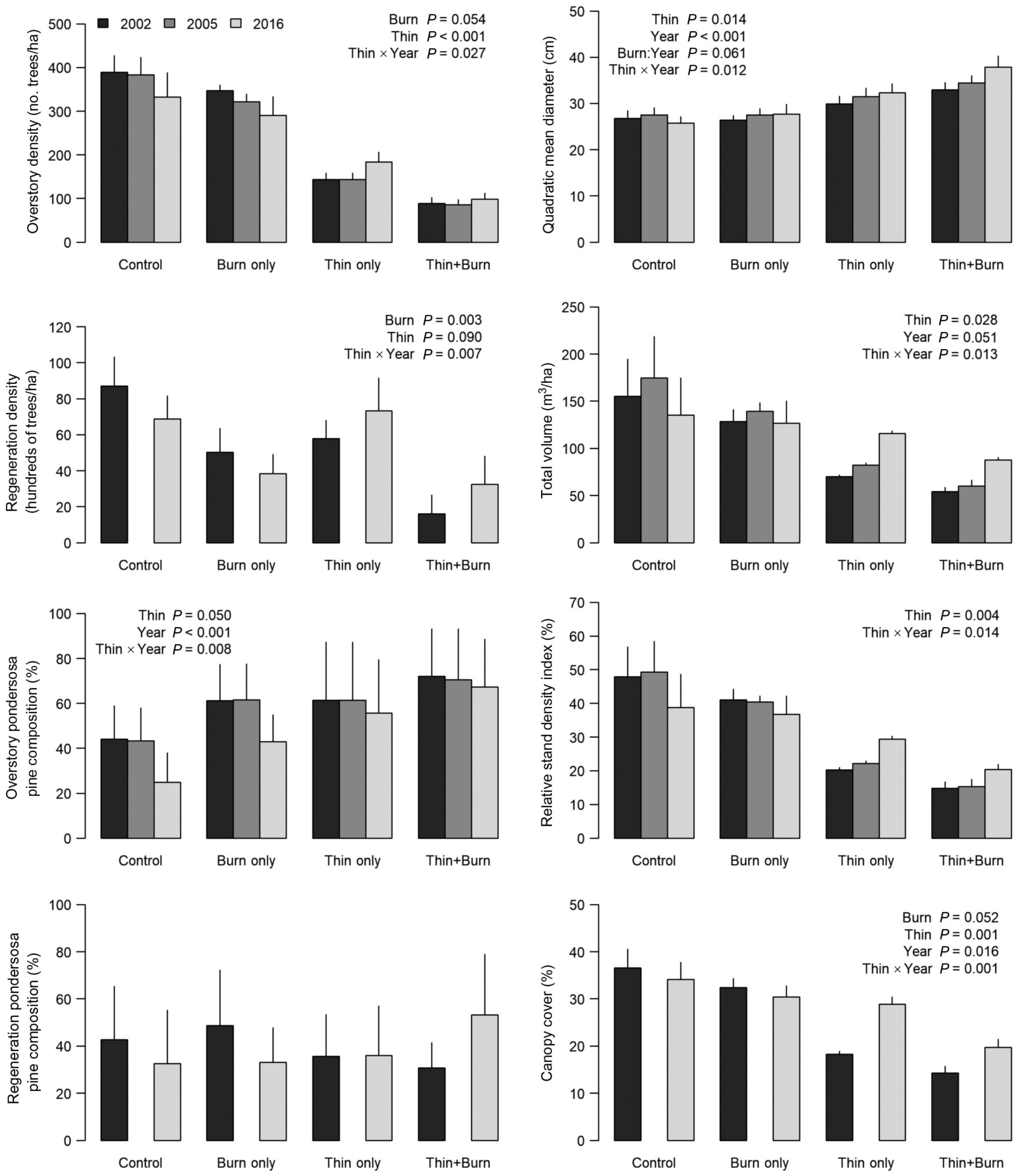

FIG. 3. Forest structure and composition (by number of trees) at Lubrecht Forest's Fire and Fire Surrogate study. Bars show treatment means and standard error by year: 2002 (immediately after treatment), 2005, and 2016. Regeneration density, regeneration composition, and canopy cover were not measured in 2005. Significant ANOVA factors ($P < 0.1$) are shown at the top of each panel.

unburned (control and thin only) treatments in 2002, 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

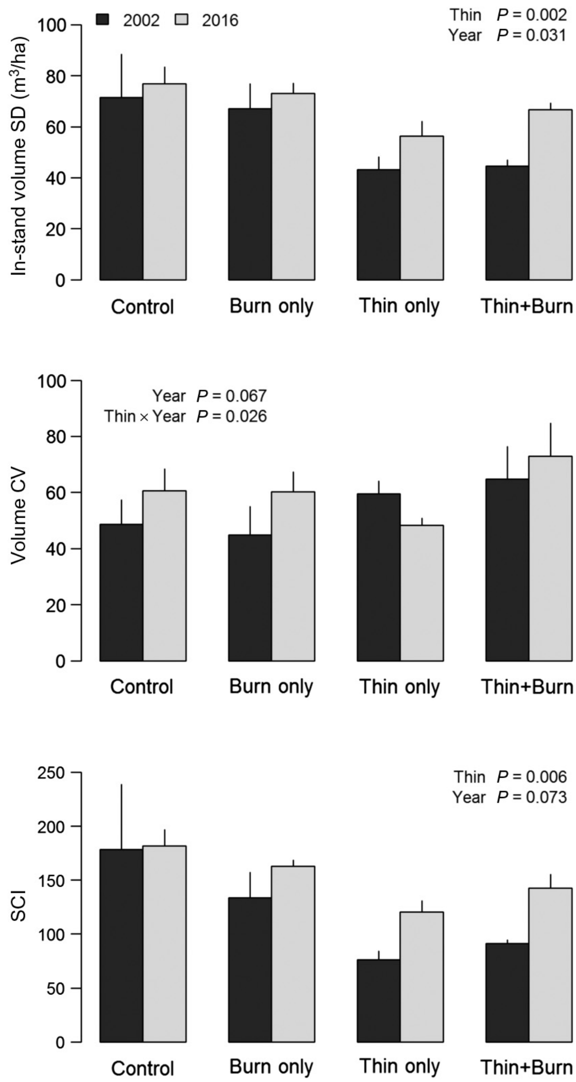

FIG. 4. Structural variability at Lubrecht Forest's Fire and Fire Surrogate study. Bars show treatment means and standard error by year, 2002 (immediately after treatment) and 2016, for in-stand standard deviation of volume, coefficient of variation (variability of stand volume relative to the mean), and structural complexity index (SCI, percentage of area greater than flat surface; see *Methods: Analytical and statistical methods*). Significant ANOVA factors ($P < 0.1$) are shown at the top of each panel.

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 S1: Table S1). 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 from 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

Overstory and understory vegetation communities changed over this study's timeframe. Overstory communities exhibited strong separation by treatment in 2002 ($A_{2002} = 0.273$, $P_{2002} = 0.002$), but by 2016 they were more similar ($A_{2016} = 0.086$, $P_{2016} = 0.188$; Fig. 6). 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. Axis 1 is best characterized as a species composition gradient, differentiating ponderosa pine (−) and Douglas-fir (+) overstory and regeneration. While axis 2 is more complicated than structure alone, it contrasts major structural attributes such as large trees (+) with high densities of overstory trees and saplings (−). 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; Fig. 7). By 2016, however, treatments were only differentiated along one axis ($P_{axis1} < 0.001$ and $P_{axis2} = 0.163$), meaning that treatments grew more similar over time. In 2002, tree densities (−) and diversity metrics (+) comprised the first axis that best differentiated between

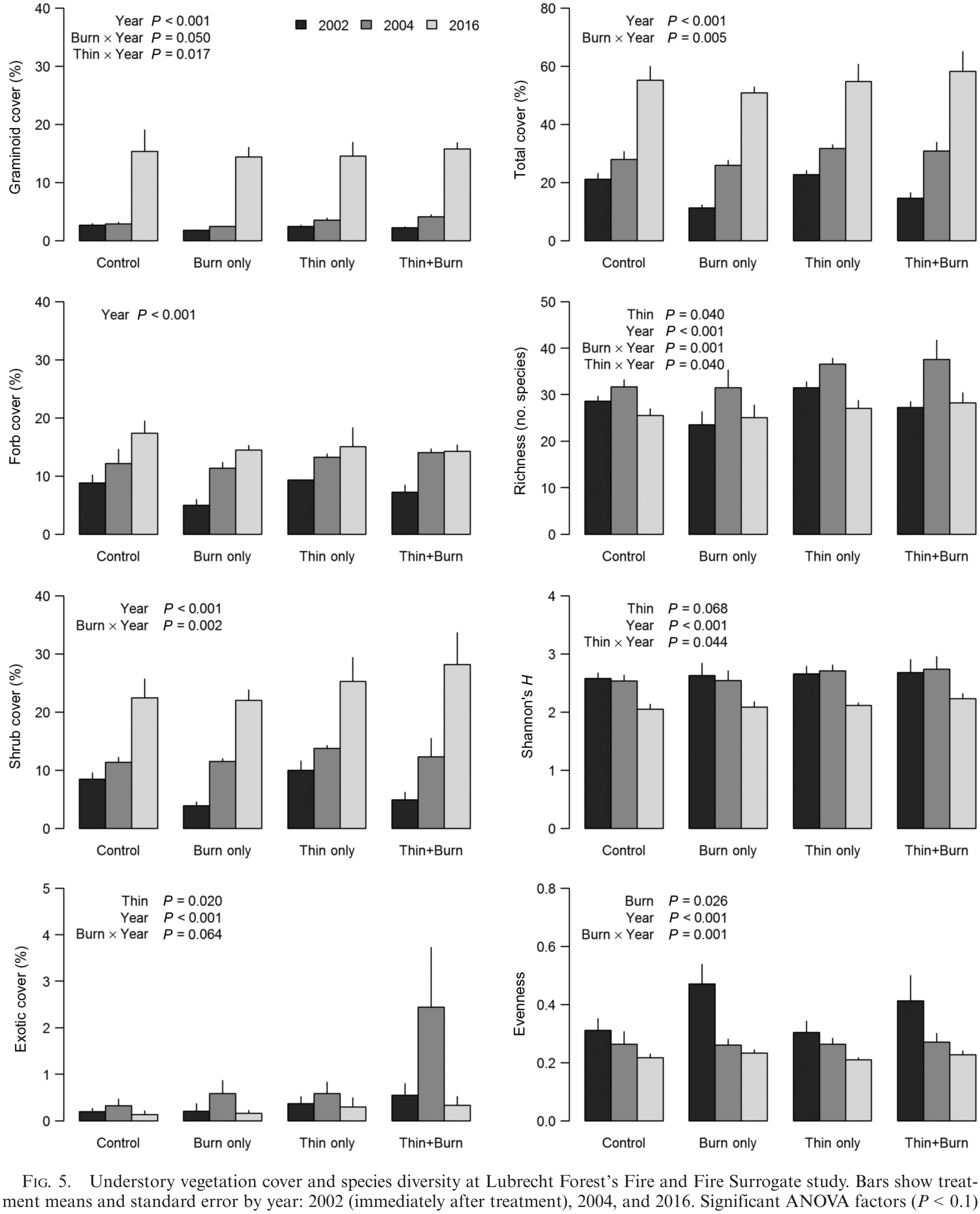

FIG. 5. Understory vegetation cover and species diversity at Lubrecht Forest's Fire and Fire Surrogate study. Bars show treatment means and standard error by year: 2002 (immediately after treatment), 2004, and 2016. Significant ANOVA factors ($P < 0.1$) are shown at the top of each panel.

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

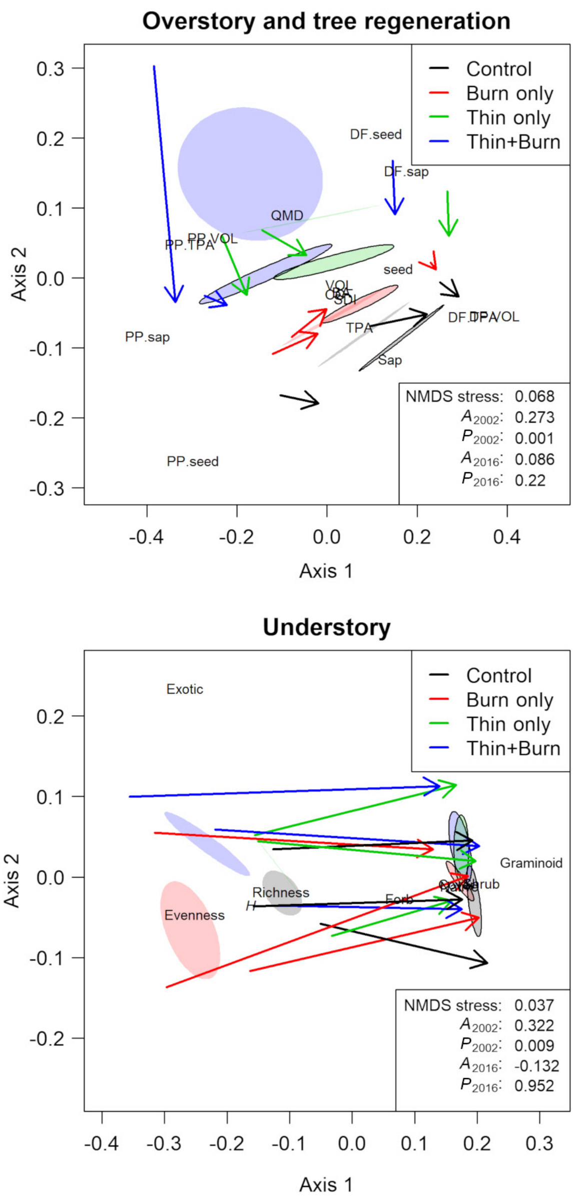

FIG. 6. Two-dimensional projection of nonmetric multidimensional scaling (NMDS) ordination, showing overall vegetation community shifts by experimental unit from 2002 (arrow tail) to 2016 (arrowhead) at Lubrecht Forest's Fire and Fire Surrogate study. Projected one standard errors are shown with ellipses by treatment (black, Control; red, Burn only; green, Thin only; blue, Thin + burn) and year (no outline, 2002; black outline, 2016). On-figure text shows total NMDS configuration stress, test statistic (A) for multiresponse permutation procedure (MRPP) by year, and P value for MRPP test statistic by year. Variables in top panel include overall overstory density (TPA), stand density index (SDI), volume (VOL), quadratic mean diameter (QMD), sapling density (Sap), seedling density (seed), and the proportion of ponderosa pine or Douglas-fir in these variables (when preceded by PP or DF, respectively). Variables in bottom panel include Shannon's H, richness, evenness, and cover for total, forb, shrub, graminoid, and exotic plants.

most negative and most positive influential loadings were the same as in 2002.

Discussion

Fourteen years since fuel treatment, and at least 4 yr after MPB outbreak, the suite of forest stands in this experiment were clearly a result of management compounded by natural disturbance. Coarse vegetation structure metrics were more similar across treatments in 2016 than in 2002 because of MPB-caused tree mortality. However, key differences between treatments persisted amid the MPB pressure, especially between the no-action control and the thin + burn treatment. Framed in light of treatment longevity, both observed growth and MPB-caused tree mortality have caused treatment convergence, negatively impacting the relative effectiveness of some of the restoration treatments (i.e., burn-only and thin-only treatments). This has important implications for management needs and future management strategies. This study shows that combined treatment of both overstory and understory (thinning and prescribed burning, here) is best able to meet live vegetation structural and compositional restoration goals despite pressure from MPB.

Fuel treatment × MPB interaction

Little has been published on the comparative effects of MPB outbreak on dynamics in stands experimentally treated with fuel reduction. In this study, we found that MPB-caused overstory mortality, which was 4.5 times greater in unthinned stands than thinned (Hood et al. 2016), was a major driver in between-treatment vegetation homogeneity, particularly for coarse structure and diversity metrics. Thinning to reduce crown fire hazard (often a more intensive treatment than prescribed burning alone) lessens overstory competition and reduces canopy and ladder fuels (Stephens et al. 2009, Fulé et al. 2012), but then also stimulates tree growth and recruitment (as in this study, also Keyes and Varner 2006). Thus, thinning as a fuel treatment initially opens forest structure, but new and advance regeneration develops increasingly dense stands. MPB outbreak with subsequent overstory mortality "thinned" the unthinned units, following a 5–7 yr lag period, but did so in a way that undermined ecosystem restoration and resilience goals. Similar to the postrestoration thinning environment, the MPB outbreak altered light and water conditions because of overstory loss, likely stimulating both residual overstory and understory growth (Heath and Alfaro 1990, Stone and Wolfe 1996, Hansen 2014). Therefore, by 2016, thinned and unthinned treatments are more similar in structure (i.e., overstory tree density, total understory cover) and understory diversity (i.e., evenness); if MPB had not reduced overstory densities in

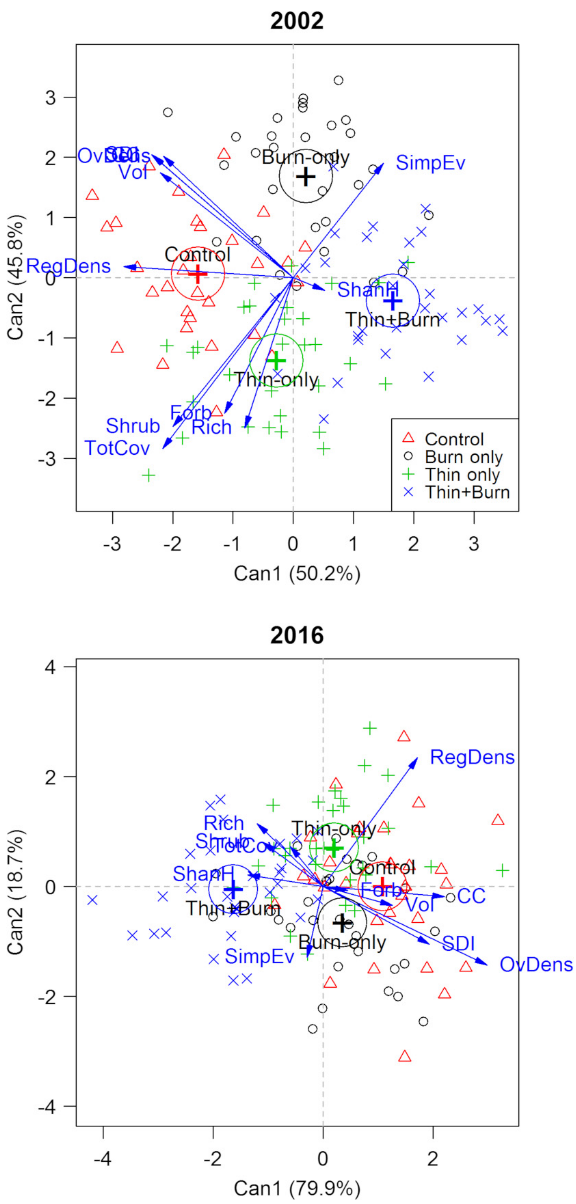

FIG. 7. Canonical discriminant analysis of plot-scale multivariate communities in 2002 (top panel) and 2016 (bottom panel) at Lubrecht Forest's Fire and Fire Surrogate study. First two canonical axes are shown for each year ($P < 0.05$ except Can2 in 2016), labeled with percent variance explained by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

unthinned stands then structure and diversity would have diverged according to prior differences in vegetation structure, composition, and fuel characteristics (e.g., Fig. 8, and those identified by Metlen and Fiedler [2006] and McIver et al. [2013]). This study expands upon the structural and compositional changes in the overstory due to treatment and MPB outbreak that Hood et al. (2016) report, and includes the dynamic understory conditions following these disturbances.

We found there were still some key treatment-created differences that persisted in spite of the MPB outbreak. This supports Hood et al.'s (2016) findings on the lasting effects of fuel treatment on stand resistance to subsequent disturbance, as well as Crotteau et al.'s (2018*b*) findings on the mitigating effect that treatment had on post-MPB fuel development. The persisting and emerging differences between control and thin + burn treatments emphasize the trade-offs between managing for dense or sparse tree layers, as well as demonstrate the contrast's insensitivity to MPB outbreak. Dense overstories like the control prioritize biomass and canopy cover of shade-tolerant tree species but limit understory biomass and diversity, while sparse tree layers like the thin + burn permit understory development as a trade-off with shade-intolerant tree layers (Ahmad et al. 2018, Goodwin et al. 2018). In 2016, the control and thin + burn were still significantly different from each other after positively weighting overstory density, canopy cover, and rSDI (greater in control), and negatively weighting Shannon's H, richness, and shrub cover (more in thin + burn) in CDA, which is similar to many findings from fuel treatments not impacted by MPB (Schwilk et al. 2009, Strahan et al. 2015*b*), though insignificant in others (Nelson et al. 2008). Thus, some ecological differences between treatments were resistant to the effects of MPB outbreak, just as Crotteau et al. (2018*b*) reported for fuel and fire hazard.

Differences due to burning diminished with time. By 2016, the effects of burning were primarily evident through the combined thin + burn, whereas, in the burn-only treatment, they generally disappeared prior to MPB outbreak (Fig. 3). The abatement in burn-only differences may be masked by the MPB activity in the middle of this study's response period, but the treatment effects are likely ephemeral because experimental burns were mostly low-severity underburns (Schwilk et al. 2009). Balancing fire control and fuel reduction objectives is a challenge for burn-only treatments in long-unburned stands. Reinhardt et al. (2008) suggest that subsequent burns in the form of management regimes are necessary to fully meet fuel reduction objectives with fire, and maintain stand resistance to fire into the future. In that vein, some have found that effects of a single prescribed burn on understory vegetation fade with time since treatment (Nelson et al. 2008, Kerns and Day 2018), while others report sustained richness improvements over unburned stands (Webster and Halpern 2010, Rossman et al. 2018). Overall, it appears that the impact of MPB outbreak on burning treatments in this study did not modify the understory vegetation compared with the untreated stands, but MPB outbreak did negatively interact with overstory structure and composition in the control and burn-only treatments by killing many of the ponderosa pines up to 55 cm dbh.

The interaction of fuel treatment and MPB outbreak caused lasting differences in structural variability. One key finding was that thinning reduced absolute

TABLE 1. Variable abbreviations and loadings from canonical discriminant analysis of plot-scale multivariate communities in 2002 and 2016 at Lubrecht Forest's Fire and Fire Surrogate study.

Vegetation type and variable	Abbreviation	2002 Can1	2002 Can2	2016 Can1	2016 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	*−0.614*	**0.534**	**0.582**	−0.049
Stand density index	SDI	*−0.618*	**0.538**	**0.508**	*−0.277*
Regeneration density	RegDens	*−0.741*	0.048	0.452	**0.616**
Understory					
Total cover	TotCov	−0.570	*−0.748*	−0.157	0.191
Forb cover	Forb	−0.300	−0.594	0.118	−0.020
Shrub cover	Shrub	−0.526	*−0.651*	*−0.291*	**0.213**
Richness	Rich	−0.212	*−0.657*	*−0.316*	**0.301**
Shannon's *H*	ShanH	**0.137**	−0.056	*−0.362*	0.056
Simpson's evenness	SimpEv	**0.394**	0.500	−0.076	*−0.339*

Notes: First two canonical axes (Can1 and Can2) are shown for each year (axis $P < 0.05$ except Can2 in 2016). Up to three most positive loadings are portrayed in boldface type and three most negative loadings are portrayed in italic type.

structural variability (thin only and thin + burn vs. control and burn only). This was expected since many forest treatments simplify forest structure by prescribing average densities and even spacing (Puettmann et al. 2009, Churchill et al. 2013), which is a simple and effective way to reduce crown fire hazard. In contrast, prescribing structural complexity (not a treatment objective here) requires more effort and may have a less beneficial effect on fire hazard reduction depending on ladder fuel proximity to overstory trees. Structural 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 MPB outbreak (as in Dordel et al. 2008). Increases in structural variability proved to be a unique way that MPB outbreak actually perpetuated differences between treatments, though differences may not have existed if thinning treatments prioritized clumpy spatial patterns (e.g., per Churchill et al. 2013).

Treatment convergence and longevity

These trends in vegetation dynamics have significant ecological and managerial implications. Our NMDS analyses showed that treated stands are converging toward a similar forest structure and composition with higher overstory Douglas-fir densities and understory cover (similar to post-treatment convergence in Campbell et al. 2016, Clyatt et al. 2017, Hu et al. 2018, Peter and Harrington 2018). Additional support comes from our analysis of individual forest components, showing thinned stands increased in overstory density over time while unthinned stands decreased, and the proportion of overstory ponderosa pine declined while Douglas-fir increased across treatments. Treatment differences for understory cover and diversity either diminished with time (e.g., decline in effect of burning on evenness; Kerns and Day 2018) or were of minimal consequence (e.g., 2016 richness of 28 genera in thin only and thin + burn vs. 25 genera in control and burn only). Whereas small differences in structure or species assemblages can escalate community uniqueness and divergence over time (Samuels and Drake 1997), this study suggests that developmental trajectories were not sufficiently modified by treatment to initiate such differentiation or that compounded disturbance subdued differentiation.

Treatment convergence may also be due to cattle grazing or climate influences on productivity. Similar to many public lands in the West, cattle have grazed Lubrecht Experimental Forest for at least one-half century. However, fenced exclosures were installed around the entire Fire and Fire Surrogate study immediately after treatment implementation in order eliminate cattle. Understory development has been generally unhindered by cattle grazing, potentially explaining the increase of understory cover across functional classes since treatment. Similar understory gains were identified after excluding cattle in ponderosa pine forests in Idaho and Arizona, especially for graminoids (Zimmerman and Neuenschwander 1984, Strahan et al. 2015*a*). It is also possible that increases in cover by 2016 were due to favorable growing season climate. Lubrecht Experimental Forest had a relatively dry spring in 2015 but received twice as much precipitation in spring 2016 (prior to measurement in June 2016). Additionally, snowpack was greater in early 2016 than 2015 (Schneider et al. 2019), increasing soil water availability into the summer. The increase in precipitation from 2015 to 2016 may have stimulated a widespread understory growth response (Strahan et al. 2015*b*). Thus, understory convergence across treatments may be attributable to overstory loss

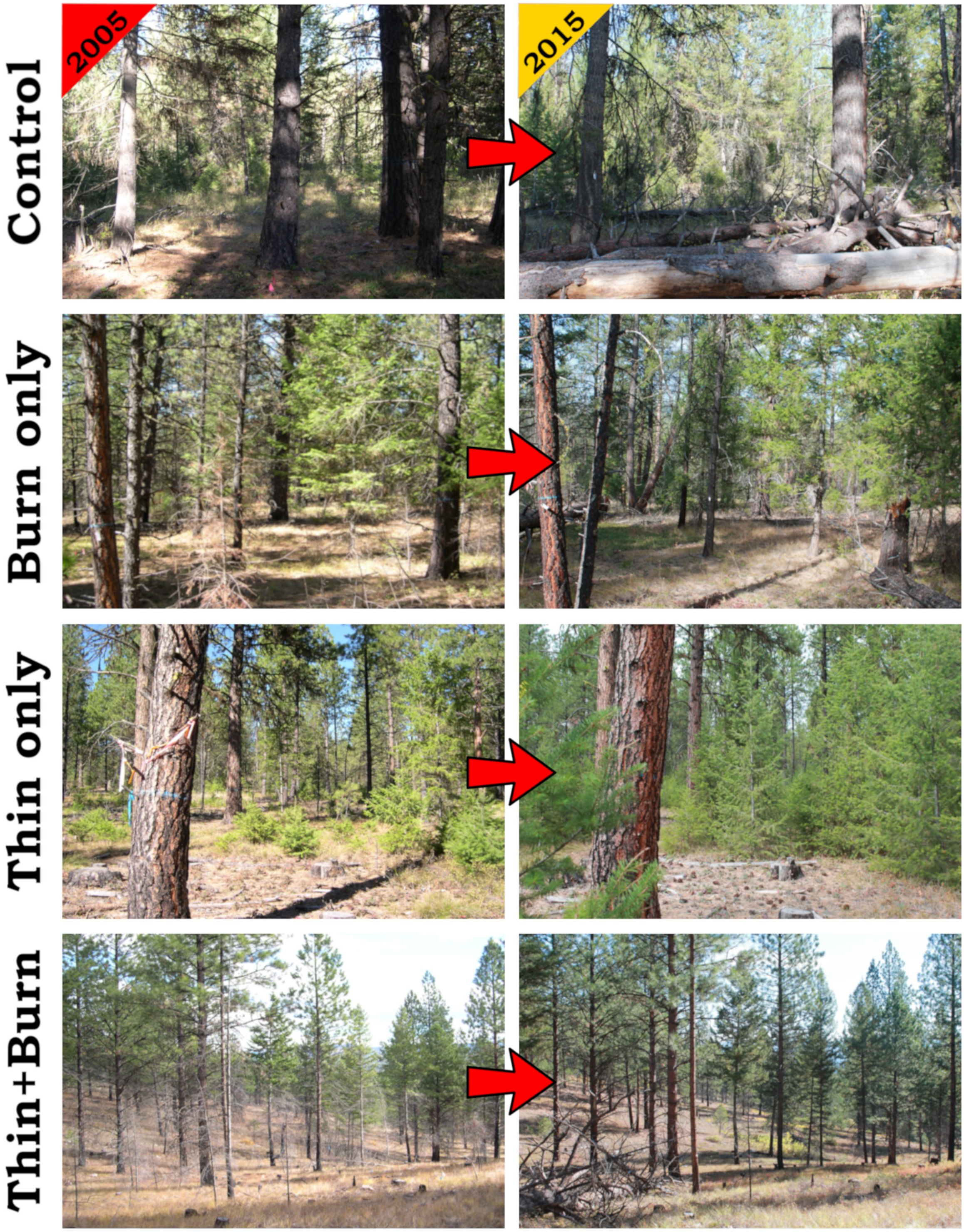

FIG. 8. Repeat photographs from representative photo points within Lubrecht Forest's Fire and Fire Surrogate study. Left column shows forest conditions from 2005 (3 and 4 yr after burning and cutting, respectively; just prior to mountain pine beetle [MPB] outbreak), whereas right panel shows conditions a decade later. Note the stumps as evidence of thinning, reduced understory and regeneration as evidence of prescribed burning, downed wood and delayed openings as evidence of MPB outbreak, and tree regeneration growth over time as evidence of growth response.

from MPB, change in grazing pressure, wet months prior to measurement, or some combination thereof.

Treatment convergence provides an important cue to managers, especially when developing silvicultural timelines and weighing treatment alternatives. This study is in a unique position to inform management of forest dynamics following compound disturbance over a relatively long time period (Moore et al. 2006; Fig. 8). The most important message is that post-treatment growth compounded by MPB outbreak has decreased treatment longevity and made treated stands more similar to untreated stands (Jain et al. 2012). Of all treatments, burn-only communities are already most similar to the 2016 control treatment as reflected in the overstory NMDS analysis. But in the upcoming decade, we anticipate the thin-only stands will rapidly advance toward the control as Douglas-fir saplings grow into the overstory stratum (as following logging in Crotteau et al. 2018*a*). Although the thin + burn best retained a distinct identity from the control and delayed understory dominance by Douglas-fir, we eventually expect Douglas-fir regeneration to establish and recruit en masse into the midstory and overstory in subsequent decades. Douglas-fir sapling growth in the post-treatment growth period increased crown fire hazard by reducing the gap between surface and canopy fuels (this study and Crotteau et al. 2018*b*), and if not tended soon, saplings will resist future low-intensity prescribed fire as bark thickens, making future fire-only management strategies more challenging. Compounded growth and MPB outbreak have reduced the relative longevity of the thinned units, but the thin + burn is still sufficiently different because of the combined overstory and understory treatment (similar to studies without MPB outbreak, e.g., Stephens et al. 2012, Rossman et al. 2018). Given that historical fire return intervals at Lubrecht Experimental Forest ranged up to 14 yr (Grissino-Mayer et al. 2006), the same period over which this study reports an overall trend toward convergence, this interval may also be appropriate as a treatment regime return interval to improve long-term resilience in this forest type (Reinhardt et al. 2008), though increased fire frequencies with warming climate may require shorter treatment return intervals.

Conclusion

Following fuel treatment and MPB outbreak, vegetation is becoming more similar across treatments over time, but specific and nuanced differences between treatments demonstrate lasting effects to structure and composition (Fig. 8). Crotteau et al. (2018*b*) indicated that combined thinning and burning provided the longest lasting benefit for reducing fuel and fire hazard in treatments compounded by MPB outbreak, yet, promoting lasting seral overstory trees and diverse understory cover are two equally important management objectives in treatments 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 MPB outbreak, we conclude that the combination of overstory and understory treatment has the greatest longevity and enduring effectiveness. This fills a significant knowledge gap because no other studies have examined live vegetation dynamics in experimental fuel treatments that have been compounded by MPB outbreak. Managers weighing treatment options in these forest types might consider that (1) MPB outbreaks reduce overstory densities and produce irregular spatial structure, but cannot meet the early-seral composition and structure goals that silvicultural thinning accomplishes, and (2) understory treatment (broadcast burning, in this experiment) 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 immediately meets most live vegetation restoration goals, and reduces MPB-caused overstory mortality (Hood et al. 2016) that results in subsequent fuel accumulation and increased fire hazard (Crotteau et al. 2018*b*), but we found following thinning with burning delays succession and ensures that restoration goals are met for years to come. Finally, it appears treatment regimes will be necessary to maintain the ecological and practical benefits afforded by dry forest restoration.

Acknowledgments

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. Funding came from the USDA National Institute of Food and Agriculture, McIntire Stennis project 233356 (awarded to C. Keyes). The study was made possible with the foresight of past scientists who designed and implemented the Fire and Fire Surrogate study, a nationwide project funded by the Joint Fire Sciences Program (FFS 99-S-01). D. Affleck and A. Sala provided valuable guidance for this study.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2023/full

Data Availability

Data associated with this paper are available from the USDA Forest Service Research Data Archive at https://doi.org/10.2737/rds-2019-0040