



# Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA



Eric E. Knapp<sup>a,\*</sup>, Jamie M. Lydersen<sup>b</sup>, Malcolm P. North<sup>b</sup>, Brandon M. Collins<sup>c</sup>

<sup>a</sup> USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

<sup>b</sup> USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA

<sup>c</sup> Center for Fire Research and Outreach, University of California, Berkeley, CA 94720, USA

## ARTICLE INFO

### Keywords:

Frequent-fire forest  
Prescribed fire  
Restoration  
Silviculture  
Spatial structure

## ABSTRACT

Frequent-fire forests were historically characterized by lower tree density, a higher proportion of pine species, and greater within-stand spatial variability, compared to many contemporary forests where fire has been excluded. As a result, such forests are now increasingly unstable, prone to uncharacteristically severe wildfire or high levels of tree mortality in times of drought stress. While reducing tree density might help to restore resilience, thinning treatments are frequently seen as conflicting with management for other resources such as wildlife habitat, in part because standard thinning prescriptions don't typically produce the degree of within-stand heterogeneity found in historical forests. In this study, we compare stand structures and heterogeneity produced by two different mechanical thinning treatments and in an unthinned control, all with or without prescribed fire as a follow-up treatment. The "high variability" thinning treatment was designed to produce the spatial variability once found in frequent fire forests and was based on historical data from nearby old-growth stands, while the "low variability" thinning treatment retained a similar number of trees but at a relatively even crown spacing. Stand averages and degree of variation for common forest metrics were calculated and values compared to a historical old-growth reference stand. Both thinning treatments reduced tree density and basal area, and shifted species composition towards historical values. Thinning treatments contained a deficit of trees in both the smallest (< 25 cm) and largest (> 80 cm) size classes, relative to historical conditions. The high variability thinning treatment increased forest structure variation more than the low variability thinning treatment for most measures and retained a broader distribution of canopy closure values across the treatment units. While prescribed fire also reduced stand density and increased the amount of within-stand heterogeneity (when delayed mortality was included), the magnitude was much less than that produced by thinning. Prescribed fire did not significantly reduce basal area or alter the species composition. Prescribed burning did significantly reduce surface fuel loads, while thinning alone had no effect for most fuel classes. Our results show that high variability thinning coupled with prescribed burning resulted in a forest better aligned with the conditions present in historical frequent-fire forests, which were known to be more resilient to both wildfire and drought.

## 1. Introduction

Frequent fire historically shaped the density and structure of many western U. S. forests (Leiberg, 1902; Show and Kotok, 1924). Patchy tree mortality and spatially aggregated regeneration produced a spatially heterogeneous fuel bed, leading to variable fire effects when burned (Weaver, 1943; Cooper, 1960; Larson and Churchill, 2012). In patches of tree mortality with heavier fuels, fire exposed mineral soil and created areas conducive to regeneration (White, 1985). Subsequent fires thinned or locally removed regenerating seedlings and saplings

where fuels had accumulated, but more open patches where fuels were lighter were more likely to escape burning (Show and Kotok, 1924). Seedlings growing in the open and not under the canopy of larger trees also attain a fire resistant size more quickly (Cooper, 1960). This interaction of fire and regeneration dynamics resulted in a fine-scaled matrix of mature trees, gaps, and groups of seedlings and saplings (Larson and Churchill, 2012), which also promoted a diverse herbaceous and shrub understory (Knapp et al., 2013).

Early forest examiners noted the relatively open structure of forest stands and predicted that more trees could be grown if fire were kept

\* Corresponding author.

E-mail addresses: [eknapp@fs.fed.us](mailto:eknapp@fs.fed.us) (E.E. Knapp), [jmlydersen@fs.fed.us](mailto:jmlydersen@fs.fed.us) (J.M. Lydersen), [mnorth@fs.fed.us](mailto:mnorth@fs.fed.us) (M.P. North), [bcollins@berkeley.edu](mailto:bcollins@berkeley.edu) (B.M. Collins).

<http://dx.doi.org/10.1016/j.foreco.2017.08.028>

Received 9 June 2017; Received in revised form 16 August 2017; Accepted 17 August 2017  
0378-1127/ Published by Elsevier B.V.

out (Leiberg, 1902). With the advent of fire exclusion policies, seedlings and saplings once thinned by fire rapidly established, filling gaps and crowding out understory vegetation (Cooper, 1960). Forests that evolved with frequent fire are now commonly much denser than they were historically (Moore et al., 2004; Scholl and Taylor, 2010; Collins et al., 2011; Knapp et al., 2013). In addition, shade-intolerant and fire-resistant species have declined in abundance in many fire-adapted mixed-conifer stands, replaced by more shade-tolerant and fire-sensitive species.

Early timber harvesting removed many of the largest trees (Knapp et al., 2013), and infilling of gaps produced a more homogeneous forest structure, both vertically and horizontally (Larson and Churchill, 2012; Lydersen et al., 2013). Accumulated fuels in the absence of fire along with fuel continuity resulting from increasing forest homogeneity have contributed to a higher probability of stand replacing wildfire. Due to competition for resources, higher tree densities are also associated with reduced tree vigor, increasing the likelihood of loss through bark beetle mortality (Ferrell et al., 1994; Fettig et al., 2007).

While mechanical thinning is one obvious tool for reversing tree densification and mitigating the risk of stand replacing fire or heightened tree mortality, the structural changes associated with thinning can have undesirable impacts on other resources. Maintaining habitat for wildlife species that prefer dense, multi-layered stands is often a competing objective (Lehmkuhl et al., 2007; Scheller et al., 2011). This conflict between thinning to reduce tree densities and conserving closed-canopy habitat for wildlife has been accentuated by conventional thinning approaches adapted for fire hazard reduction (Agee and Skinner, 2005). More nuanced thinning approaches that seek to enhance and restore heterogeneity may be one means of balancing these seemingly competing objectives (North et al., 2009).

Early observers in unharvested or “virgin” forests associated with frequent fire consistently noted that trees were grouped or clustered, as opposed to regularly spaced (Dunning, 1923; Cooper, 1961), and uneven aged, or “at best even-aged by small groups” (Show and Kotok, 1924). Historical data and stand reconstructions indicate that conifer-dominated forests throughout the western US appear to have shared a similar structure, with widely spaced individual trees, groups of trees, and canopy openings organized at 0.1–0.3 ha spatial scales (Larson and Churchill, 2012). This “patchy and broken” structure contributed to the relative immunity of historical forests to crown fire (Show and Kotok, 1924). Because surface fuels are a product of overstory structure and composition (Lydersen et al., 2015), variability in overstory conditions presumably led to surface fuel discontinuity, which likely limited spread of higher intensity fire (Miller and Urban, 2000). Given the environmental stress forest ecosystems are likely to experience under a changing climate, heterogeneity may be particularly important in shaping stand resilience to wildfire and other disturbances (Drever et al., 2006; Stephens et al., 2010).

Conceptual frameworks for managing for greater complexity have been described in different forest types (North et al., 2009; Franklin and Johnson, 2012; Reynolds et al., 2013). Silvicultural prescriptions have been developed for restoring heterogeneity based on historical stand structure data (Harrod et al., 1999; Churchill et al., 2013), or with the goal of simultaneously enhancing forest structural attributes for wildlife species and reducing wildfire hazard (Reynolds et al., 1992; Long and Smith, 2000; Graham and Jain, 2005). However, implementation of forest restoration treatments designed to enhance heterogeneity has been slow (Puettmann et al., 2015). This is partially because contemporary silvicultural approaches are generally still rooted in conventional timber-focused practices, which often seek to maximize individual tree growth (Puettmann et al., 2009). On federally managed forest lands in areas of the western U.S. that historically experienced frequent fire, tree spacing guidelines once employed to maximize growth have to some extent been re-purposed for restoration and fire hazard reduction treatments. Such treatments typically rely on average stand structure metrics (density, basal area) as targets, or employ

uniform crown spacing guidelines, which tend to generate relatively homogenous stand conditions. Most available evidence suggests that such homogeneity did not exist in these forest types historically (Sánchez Meador et al., 2011; Larson and Churchill, 2012; Lydersen et al., 2013; Clyatt et al., 2016).

Notable examples of thinning with the overarching goal of generating heterogeneity applied at experimental or operational scales do exist. In Douglas-fir forests of the Pacific Northwest, Carey (2003) tested a variable thinning on stands divided up into 40 m grid cells, with the goal of multi-resource management and enhancing habitat for a diversity of species. Methods for restoring spatial structure of tree groups, individuals and openings with thinning based on historical reference data, provided in Churchill et al. (2013), are being evaluated in Washington State. In the southwestern U.S., variable thinning prescriptions are now being implemented at landscape scales (Reynolds et al., 2013).

In this study, we compare forest structure (density, basal area, diameter distribution, species composition) and heterogeneity (coefficient of variation for structural variables, variation in canopy closure) of an unthinned control against two thinning approaches – one designed to restore the within stand spatial complexity that historically was generated by frequent fire, and one designed to reduce stand density leaving a relatively regular crown spacing. Half of the units were followed by prescribed burning, allowing an evaluation of the heterogeneity produced by burning alone, as well as thinning and burning. We also compare the structures produced by treatment against a historical reference, obtained from plots stem mapped prior to any logging in 1929 (Knapp et al., 2013).

## 2. Methods

### 2.1. Study area

The approximately 100 ha study area is located within the Stanislaus-Tuolumne Experimental Forest, on the Stanislaus National Forest, near Pinecrest, CA (Fig. 1). The mixed conifer forest at the study elevation (1740 to 1900 m) is composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), and black oak (*Quercus kelloggii*), in order of abundance. Climate is Mediterranean, with the majority of the annual precipitation occurring during fall, winter, and spring. Up to 75% of precipitation fell as snow at this elevation in the past (Kittredge, 1953). Tree growth is rapid due to high site productivity, with deep and well-drained loam to gravelly loam soils (Wintoner-Inville families complex) derived from granite or weathered from tuff breccia. The last fire occurred in 1889 but fire was historically frequent in the study area, with a median return interval of 6 years (Knapp et al., 2013). The study area was selectively logged in 1928 and 1929, removing most of the larger trees. The forest that developed after logging and under fire exclusion contained a greater abundance of white fir and incense cedar, and less pine than the historical forest. At the time our study was initiated the forest density was 240% and basal area 29% greater than historical old-growth forests at this site in the 1920s (Knapp et al., 2013). With the lack of fire, surface fuels were also likely considerably elevated relative to historical conditions. Other than removal of roadside hazard trees, no additional management action had occurred in the decades prior to the study.

### 2.2. Treatments

Two prescribed burning treatments (burned, unburned) were randomly assigned to larger units and three thinning treatments (high variability “HighV” thin, low variability “LowV” thin, and unthinned control) were subsequently randomly assigned to the three units within each burn unit in a nested experimental design. The six total treatments were replicated four times, resulting in 24 units, each approximately

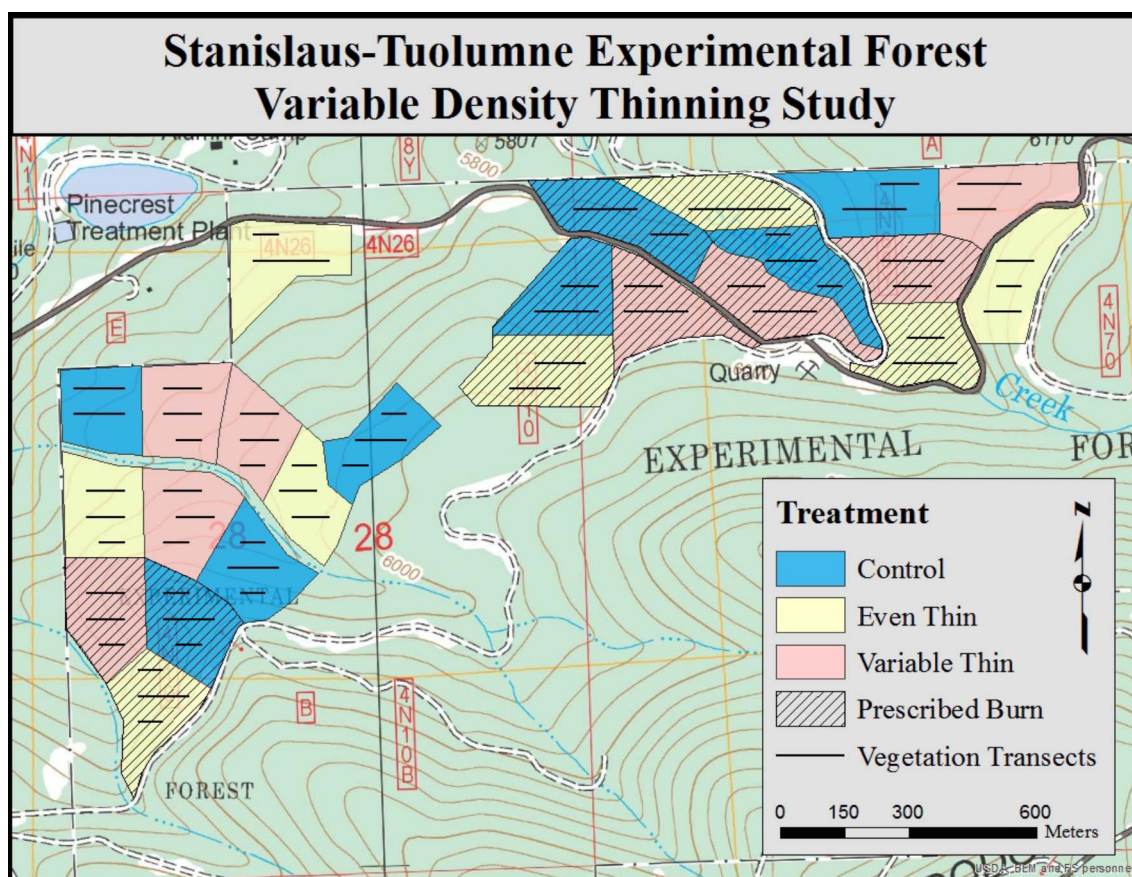


Fig. 1. Location of Variable Density Thinning study units on the Stanislaus-Tuolumne Experimental Forest, Stanislaus National Forest, California.

4 ha in size (Fig. 1). The HighV treatment units were thinned using a prescription designed to generate a structure similar to that found in historical forests. Historical data that informed the prescription were obtained from three approximately 4 ha “Methods of Cutting” plots installed adjacent to the current study area in 1929. All trees > 10 cm diameter in these historical plots were mapped and tree species and size measurements were collected in 1929 prior to harvesting, providing useful reference information of the historical unlogged forest condition (Knapp et al., 2013; Lydersen et al., 2013). Forty years had transpired since the last fire (1889), so the forest in 1929 was likely already denser than it had been prior to fire exclusion, especially for the smaller size classes of trees that might have established in the absence of fire. For larger trees, which comprise the majority of the basal area, the structure was representative of old-growth, mixed-conifer forest on highly productive soils. The historical data show a forest composed of widely spaced individual trees, clusters (or groups) of trees, and openings (the “individuals, clumps, and openings” (ICO) structure noted in many western conifer forests with a history of frequent mostly lower intensity fire by Larson and Churchill (2012) and others). Trees were relatively even-sized within groups, but had a great range of sizes among groups. Small gaps, ranging in size from 0.025 to 0.2 ha were abundant (> 2 per ha), occupying approximately 15% of the plot area (Lydersen et al., 2013). Because much of the regeneration forming tree groups historically occurred within gaps, tree groups were of similar size to or slightly smaller than gaps.

The goal of the HighV thinning prescription was to produce a spatial structure, density, species composition, and size distribution consistent with the historical patterns once observed on this site. This included creating five gaps 0.04 to 0.2 ha in size in each 4 ha unit, which approximates the density of similarly-sized openings noted on stand maps from 1929 (Lydersen et al., 2013). Gaps were created in areas dominated by white fir and/or cedar where evidence from old stumps

suggested past presence of pine, root disease pockets, areas containing black oak, or by enlarging existing smaller gaps. The remainder of each unit was divided into groups of adjacent, similar size trees. Within groups, the best trees (defined as generally the largest and most vigorous) were retained, regardless of crown spacing. About a third of the groups were thinned more heavily, a third moderately, and a third lightly. Targets for the heavy, moderate, and light thinning were loosely based on basal area and density ranges from the historical plot data, but operationally created more by “feel”, along the lines of the “free selection” silvicultural system proposed by Graham and Jain (2005). No black oaks were cut but all conifers within the drip line of black oaks were removed where damage to the oak could be avoided. Because leave-tree selection was based foremost on size and species and secondarily on crown form, some trees with relatively poor vigor (higher probability of mortality in the short term) and other characteristics such as broken tops thought to be important for wildlife were maintained. All snags larger than 38 cm diameter at breast height (dbh) were retained whenever possible (i.e. when not a safety issue). Additional details about the thinning prescription and how leave trees were marked are provided in Knapp et al. (2012). The LowV treatment was marked for cutting by selecting leave trees spaced approximately 0.5 crown widths from nearest neighbors. We sought to produce approximately the same stem density, basal area, size class distribution and species composition in both thinning treatments, just with a different spatial arrangement of trees. Because of the current lack of pine compared with historical conditions, leave tree priority among conifers for both thinning treatments was sugar pine > ponderosa/Jeffrey pine > incense cedar > white fir.

Thinning was conducted between July and September 2011. Trees larger than about 60 cm dbh were hand felled using chain saws and smaller trees were cut using tracked feller bunchers, with whole trees (and tops of the larger hand-felled trees) moved to landings at the edge

**Table 1**

Fuel moisture values and weather variables (range or standard error in parentheses) averaged over day of the month and thinning treatment for prescribed burns conducted over six days in 2013. Wind speeds were light and averaged  $1.8 \text{ km h}^{-1}$  (range 0 to  $8 \text{ km hr}^{-1}$ ) over the burn period. Live fuel moisture was for white fir needles.

Date	Treatments burned <sup>a</sup>	1 h	10 h	100 h	1000 h	Litter	Duff	Live	Temp C <sup>o</sup>	Relative humidity (%)
		%								
11/11	LowV(part), C(part)	11.2	12.9	13.9	18.2	22.7	26.5	135.9	15 (13–17)	32 (29–38)
11/12	HighV, LowV (part), C (part)	11.1	11.8	14.2	17.9	25.1	31.9	139.4	14 (13–16)	43 (39–48)
11/13	HighV, LowV	13.0	13.5	14.2	22.1	29.4	30.9	145.1	14 (11–16)	49 (44–60)
11/14	HighV, LowV, C	13.6	13.9	15.8	15.8	25.6	43.1	136.1	12 (7 – 1 3)	53 (44–73)
11/17	HighV, C	19.3	19.9	18.1	16.4	36.5	38.1	142.4	11 (7 – 1 3)	48 (37–55)
11/18	LowV, C	17.4	18.1	17.3	18.2	27.6	39.3	138.2	9 (8 – 1 1)	57 (53–68)
	C	16.0 (1.7)	16.2 (1.7)	15.9 (1.0)	18.5 (0.9)	28.3 (2.2)	36.5 (4.9)	141.8 (2.4)	–	–
	HighV	14.3 (1.6)	15.5 (1.6)	15.5 (1.0)	17.2 (0.9)	31.7 (2.4)	39.0 (5.2)	141.1 (2.4)	–	–
	LowV	13.0 (1.4)	13.9 (1.4)	15.3 (1.0)	17.6 (0.9)	24.0 (1.8)	28.8 (3.9)	134.2 (2.2)	–	–
	P	0.430	0.577	0.899	0.564	0.080	0.291	0.084		

<sup>a</sup> HighV = High variability thin, LowV = Low variability thin, C = Unthinned control; units ignited on 11/11 were completed on 11/12.

of roads in the study area using rubber tired skidders. Trees were processed into logs and other forest products at the landings. Small trees and tops of larger trees were chipped and removed as biomass. Designated burn units were treated with prescribed fire Nov. 11–18, 2013, less than two weeks after a three-day precipitation event where 1.7 cm of rain fell. Units were burned using drip torch spot ignition from highest to lowest elevation. Fuel moisture and relative humidity were lowest and air temperature highest during the initial burns, but conditions became less favorable for fuel consumption during the course of the burning period with both relative humidity and fuel moisture rising (Table 1). This resulted in some units burning more completely than others. However, whole burn blocks containing one of each stand structure treatment were generally ignited either the same day or under similar conditions on consecutive days, meaning that each stand structure treatment experienced a similar range of burning conditions.

### 2.3. Data collection: Trees

A 30 m grid was placed over the entire study area and 240 m of belt transect set up within each unit by connecting adjacent gridpoints (Fig. 1). All trees ( $\geq 10 \text{ cm dbh}$ ) with a midpoint growing within 7.5 m on either side of the belt transect (15 m total width) were mapped during the summer of 2009 by measuring location along the transect (X) and perpendicular distance from transect center line (Y). Status (live or dead) was determined, diameter at breast height measured and species noted. The same data were collected during the summer of 2012, a year after logging; in the summer of 2014, a year after prescribed burning; and in the summer of 2016 to capture delayed mortality. All trees remaining in the transect after logging were tagged at breast height with an individually numbered metal tag and diameter at breast height measurements were made directly above the nail.

### 2.4. Data collection: Canopy

Canopy closure was calculated from digital images of the canopy taken during the summer of 2016 with a Sigma 4.5 mm f2.8 EX DC HSM circular fisheye lens mounted on a Nikon D3000 camera. Photographs were taken vertically using a tripod at a height of 1.5 m above each gridpoint along transects where the tree data were collected. The camera was leveled and top of camera registered to true north with a compass. In total, ten or eleven photographs were taken along the 240 m of belt transect in each of the 24 units. Canopy images were taken prior to sunrise, after sunset, or on overcast days to avoid sunlight hitting the canopy. Images were underexposed two f-stops to further reduce glare.

### 2.5. Data collection: Fuels

Fuel loading was quantified using a modified version of the standard Brown's protocol (Brown, 1974). A fuels transect was placed along the centerline of the 15 m wide tree belt transect. The 240 m of transect within each unit was broken into 10 m sections and 1 h ( $< 6 \text{ mm}$ ), 10 h ( $6\text{--}25 \text{ mm}$ ), and 100 h ( $> 25\text{--}76 \text{ mm}$ ) woody fuels bisecting the transect were counted in a 3 m long subsection (between 4 m and 7 m of each 10 m section). Thousand hour woody fuels ( $> 76 \text{ mm}$ ) were quantified over the entire transect length. For these larger fuels, diameter, species, and whether the log was sound or rotten was recorded. Rotten logs were defined as wood soft enough to dent with a kick.

Fuel loading data were collected in all units in 2011, before logging. Because logging had the potential to alter fuel loading, fuels in thinned units scheduled for prescribed burning were evaluated again in 2012, after logging. Winter snows shortly after the prescribed burns precluded an immediate post-burn assessment and the final fuel loading data were therefore collected in the summer of 2014, approximately 8 months after burning.

### 2.6. Analyses

Fuel load was calculated from counts of fuel particle intercepts and forest floor depth, using individual species constants for woody fuels (van Wagtenonk et al., 1996) and fuel beds (van Wagtenonk et al., 1998), weighted by the basal area composition of the forest in the study area. Changes in fuel loading for each treatment between 2011 and 2014 was determined for all fuel loading variables. However, the boundary between litter and duff was not always readily identifiable, and it appeared that different seasonal crews measured the depths of litter and duff in somewhat different ways across years. Therefore, we also estimated fuel changes by analyzing just the 2014 data, comparing treatments against untreated controls to eliminate the confounding caused by the "crew" effect.

The degree of structural heterogeneity generated by each treatment was compared to the contemporary controls (unlogged and unburned treatment) at three spatial scales by dividing each transect into equal segments of varying size (twenty-four 10 m segments (each  $150 \text{ m}^2$ ), sixteen 15 m segments (each  $225 \text{ m}^2$ ), and eight 30 m segments (each  $450 \text{ m}^2$ )). The coefficient of variation (CV) for each treatment unit was calculated for density and basal area at each segment size, in order to quantify the fine-scale variation in stand structure.

To compare the degree of heterogeneity produced by treatments relative to that found in historical old-growth forest, the contemporary data were compared to three permanent "Methods of Cutting" plots installed and stem mapped in 1929, adjacent to the current study (Knapp et al., 2013). Belt transects for the historical data were generated in ArcMap 10.1, using the same sampling grid established across

the Variable Density Thinning units. Within each Methods of Cutting unit, 240 m of 15 m wide transect was created to match the sampling intensity and configuration found in the Variable Density Thinning study. The configuration of the transects within each plot was chosen randomly from all possible combinations of 240 m of consecutive transect, using gridpoints at least 30 m from the plot edge. Tree density and basal area were calculated at three spatial scales by dividing the transect into 10 m, 15 m and 30 m segments, as was done for the Variable Density Thinning study transects. The coefficient of variation was then calculated for these stand structure variables.

Hemispherical canopy images were analyzed using WinScanopy (Regent Instruments Canada Inc.). We attempted to classify the pixels for each photograph as black (canopy) or white (sky) using as close to the same settings as possible to minimize bias. Most photographs were classified using the green channel setting to improve contrast. However, this proved unsatisfactory for a few photographs taken during the day, so the red or blue channels were used instead. Canopy closure (1 – Gap Fraction) was calculated for varying cone widths, ranging from 15° either side of vertical to 60° either side of vertical.

Significance of differences among treatments for all variables was determined using generalized linear mixed effects models (PROC GLIMMIX in SAS version 9.4). Initial analyses were conducted with all main effects (thinning treatment, burning treatment, and year (when the same data were collected across years)) and interaction terms. Non-significant interaction terms were sequentially removed and the final analyses run using just the significant main and interaction effects. Significance of pairwise comparisons for main and interaction effects was determined with linear contrasts, with level of significance adjusted for the number of observations. Heteroscedasticity was not strong for most variables. Results were not improved when grouped variance was used to account for heteroscedasticity, and therefore final models were run without grouping variables.

While the 2014 data were collected only one year after the prescribed burns and thus likely do not capture the full effect of fire, the years following the burns also coincided with a drought and substantial background bark-beetle caused tree mortality. Thus stand conditions across the entire study area began to be influenced not just by treatments, but by the ongoing drought. Because this paper is focused on stand changes resulting from treatment, we show the 2014 data in the majority of our tables and figures. Some delayed mortality in response to prescribed burning is expected, so we include a description of results of analysis including the 2016 data in cases where the Year x Burning interaction was significant.

### 3. Results

#### 3.1. Fuel loading and consumption with prescribed burning

In the summer of 2014, approximately 8 months after the prescribed burns, significantly less fuel was found for all categories in the burned treatment (Table 2). Values ranged from 54% less for 1 h fuels to 87% less for rotten 1000 h fuels. Fuel loading did not differ among the thinning treatments for all categories except 100 h fuels and litter. Significantly more 100 h fuels were found in the two thinned treatments (3.02 and 2.77 Mg ha<sup>-1</sup> in the LowV and HighV thinning

**Table 2**

Fuel loading (standard error in parenthesis) in different woody and forest floor fuel categories averaged across burned and unburned treatments in 2014, 8 months after prescribed burning. The -S and -R after 1000 h stand for sound and rotten, respectively.

Treatment	1 h	10 h	100 h	1000 h-S	1000 h-R	Litter	Duff	Total
	Mg ha <sup>-1</sup>							
Burned	0.76 (0.07)	3.21 (0.25)	1.59 (0.13)	3.06 (0.49)	0.60 (0.24)	5.23 (0.30)	4.27 (0.82)	18.81 (1.67)
Unburned	1.66 (0.11)	7.54 (0.58)	3.62 (0.29)	8.80 (1.42)	4.58 (1.31)	13.19 (0.74)	26.98 (4.70)	67.74 (6.10)
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	0.002	< 0.001	< 0.001	< 0.001

**Table 3**

Prescribed fire effects in three stand structure treatments – unthinned control, high variability (HighV) thin, and low variability (LowV) thin (standard error in parentheses).

Treatment	Char height (m)	Scorch height (m)	Crown volume scorched (%)
Unthinned control	1.3 (0.5)	6.6 (1.4)	7.7 (5.8)
HighV thin	2.6 (1.3)	10.2 (3.5)	5.1 (3.8)
LowV thin	3.8 (1.6)	15.1 (3.0)	8.1 (6.1)
<i>P</i>	0.225	0.074	0.989

treatments, respectively) than in the unlogged control (1.66 Mg ha<sup>-1</sup>) ( $P = 0.002$  and  $P < 0.001$  for the LowV-Control and HighV-Control contrasts, respectively). Significantly more litter was noted in the unthinned control treatment (9.43 Mg ha<sup>-1</sup>) than in the LowV thin treatment (7.11 Mg ha<sup>-1</sup>) ( $P = 0.010$ ), with the HighV thin treatment intermediate (8.56 Mg ha<sup>-1</sup>) and not significantly different from the other two. The Thinning x Burning interaction was not significant for any fuel category. Except for duff mass, fuel loading differences among treatments in 2014 were similar to estimates of fuel addition (from logging) and consumption (by burning) made by comparing values within the same treatments over time. Changes to duff mass appeared to be confounded with differences in how duff depth was measured over time by different crews. Thus, comparison among treatments using just the 2014 data likely provide a better estimate of the effects of treatment on duff loading.

Average fuel moisture at the time of the prescribed burns did not differ significantly among thinning treatments (Table 1). Average maximum scorch height and average maximum char height were numerically lower in the unthinned control treatment than in the HighV and LowV thinning treatments, but differences were not statistically significant due to the high degree of variation in fire effects (Table 3). Little difference was noted among thinning treatments in the percentage of crown volume scorched.

#### 3.2. Treatment effects on stand structure

In 2014, the first year following completion of the treatments, thinning significantly reduced tree density and basal area and significantly increased the percentage of basal area composed of pine species and the quadratic mean diameter (QMD), compared with pre-treatment conditions (Fig. 2, Appendix A). Thinning removed about three quarters of the trees and reduced basal area by over 40%. Favoring pines over other species and preferential removal of small trees over large trees shifted the stand to a higher proportion of pines and larger average tree size. A significant Thinning x Year interaction was found for tree density, basal area, percentage of basal area composed of pine and QMD (Appendix A). Both thinning treatments resulted in greater change in all four variables over time than occurred in the unthinned control (Table 4). The two thinning treatments differed from each other in change in trees per ha and QMD (Table 4). The LowV treatment showed a lesser degree of change (smaller decrease in trees per ha and smaller increase in QMD from 2009 to 2014) because it, by chance, started out with significantly fewer trees and somewhat larger

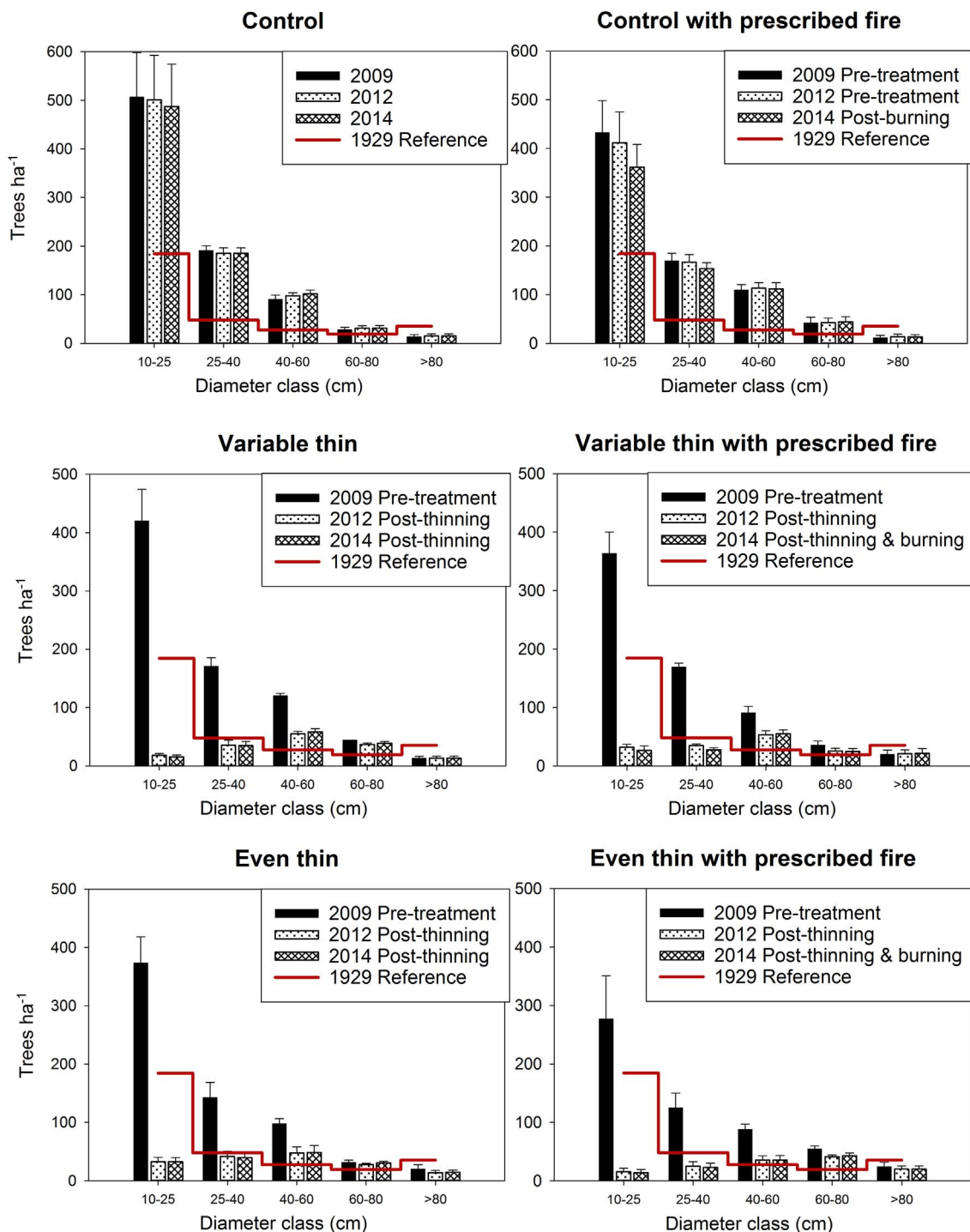


Fig. 2. Tree density by diameter at breast height size class in the six thinning and burning treatment combinations (three thinning treatments (Control, HighV, LowV) and two burning treatments (burned, unburned)) in 2009 (prior to treatment), in 2012 (post-thinning, pre-burning), and in 2014 (post treatment). Historical density of trees in the same size classes, noted in three nearby approximately 4 ha “Methods of Cutting” plots in 1929, is shown for comparison (line).

QMD.

As shown by the lack of significance for the Burning x Year interaction, prescribed burning did not initially (in 2014) significantly affect tree density, basal area, the percentage of basal area composed of pine, or QMD (Appendix A). When 2016 data were included, the Year x Burning interaction became significant for tree density and QMD. The rate of mortality through 2016 was significantly higher in the prescribed burning treatment than in the unburned treatment ( $P = 0.008$ ). Between 2014 and 2016, mortality in burned and unburned units averaged 13.3% and 2.6%, respectively. Even though the Burning x

Thinning x Year interaction was not significant, tree mortality was numerically highest in the unthinned control/burn treatment (7.5% between 2012 and 2014, and 28.6% between 2012 and 2016), resulting in a tree density of 681.7 ha<sup>-1</sup> and 528.1 ha<sup>-1</sup> at the end of the two time periods. Burning also slightly increased the QMD relative to unburned treatments in 2016 (+2.4 cm from 2014, vs. +0.4 cm in the unburned treatments), presumably because delayed mortality was more prevalent among the smaller tree size classes.

**Table 4**

Pre- (2009) and post-treatment (2014) tree density, basal area, percentage of basal area composed of *Pinus* species, and quadratic mean diameter (standard error in parentheses). Significance of slope differences (change from the pre-treatment condition) for each two treatment comparison was calculated with linear contrasts.

Thinning treatment	Year	Trees ha <sup>-1</sup>	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	% <i>Pinus</i> BA	Quadratic mean diameter (cm)
Control	2009	785.0 (57.5)	64.9 (4.1)	18.9 (2.3)	32.5 (1.8)
Control	2014	742.1 (54.4)	66.3 (4.2)	19.2 (2.3)	33.7 (1.9)
HV thin	2009	718.1 (52.6)	68.9 (4.4)	19.3 (2.3)	35.0 (1.9)
HV thin	2014	156.3 (11.4)	38.1 (2.4)	32.6 (3.9)	55.7 (3.1)
LV thin	2009	597.3 (43.7)	67.0 (4.3)	21.5 (2.6)	37.9 (2.1)
LV thin	2014	147.1 (10.8)	37.7 (2.4)	34.2 (4.1)	57.1 (3.1)
C–HV		< 0.001	< 0.001	< 0.001	< 0.001
C–LV		< 0.001	< 0.001	< 0.001	< 0.001
HV–LV		0.044	0.868	0.160	0.002

3.3. Treatment effects on heterogeneity

3.3.1. CV by tree density and basal area

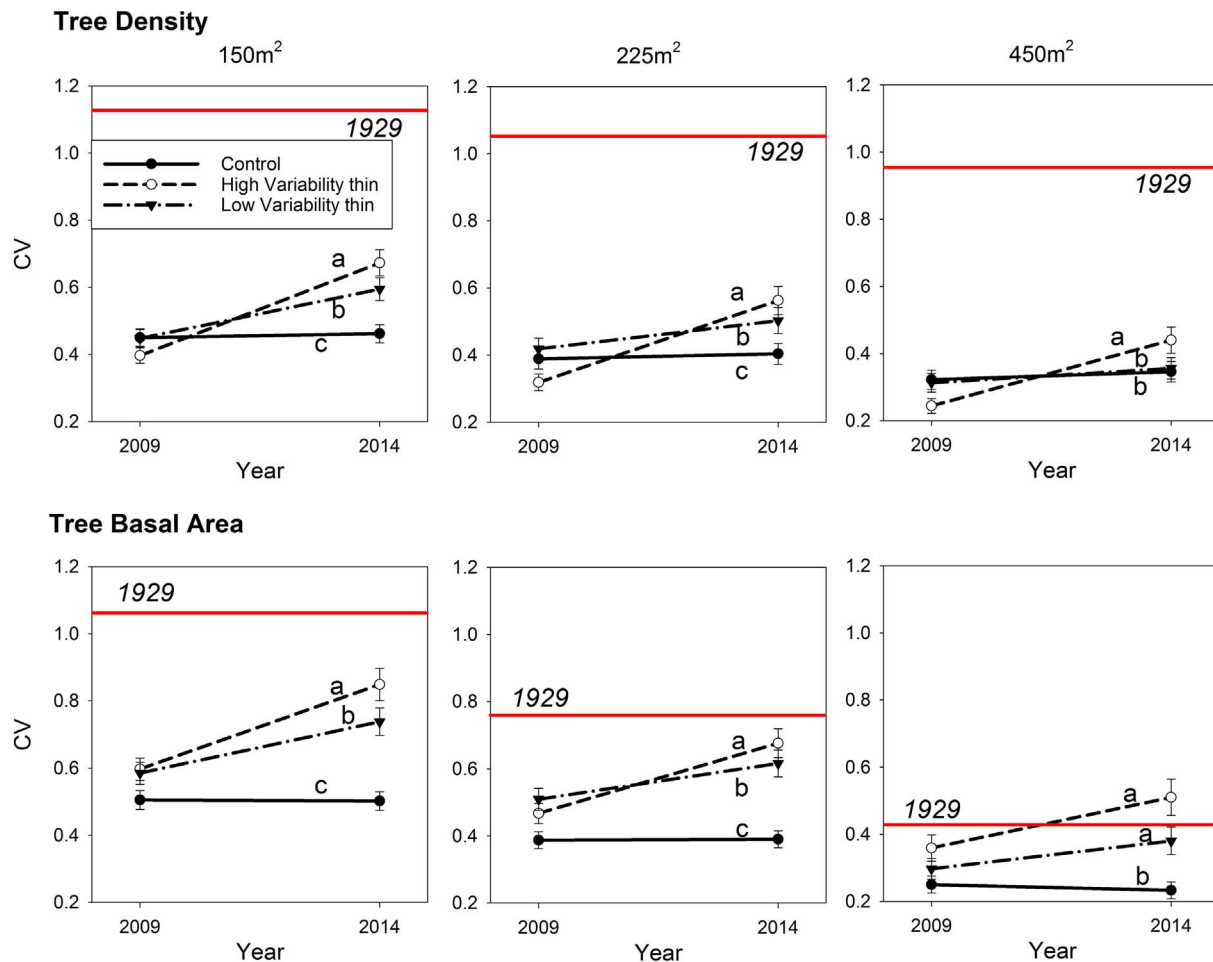
Prior to treatment (2009), the coefficient of variation (CV) for tree density was substantially less than in nearby old-growth forest in 1929 at all three spatial scales analyzed (Fig. 3). Thinning increased the CV for tree density at all three spatial scales, as shown by a significant Thinning x Year interaction (Appendix B). The HighV thinning

treatment resulted in the greatest increase in the CV, relative to the LowV thinning treatment and the unthinned control (Fig. 3). The LowV thinning treatment also increased the CV relative to the unthinned control at the two smallest spatial scales (150m<sup>2</sup> and 225m<sup>2</sup>) but not at the largest. While prescribed burning caused a slight numerical increase in the CV relative to unburned treatments, the Burning x Year interaction was not significant at any of the three spatial scales (Appendix B). CV's did not change appreciably when 2016 data were included in the analysis, with the Burning x Year treatment interaction remaining non-significant, despite some additional tree mortality.

Pre-treatment CV's for basal area were also considerably lower than in 1929 (Fig. 3). As with tree density, the CV for basal area was significantly increased by thinning but not burning (Appendix B). The HighV thinning treatment increased the CV the most at all three spatial scales (Fig. 3). The LowV thinning treatment also increased the CV, relative to the unthinned control, at the two smallest spatial scales but not the largest (Fig. 3). When the 2016 data were included in the analysis, the Burning x Year interaction became significant at the smallest two scales ( $P = 0.009$  and  $P = < 0.001$  at the 150 m<sup>2</sup> and the 225 m<sup>2</sup> scales, respectively). Burning increased the CV's for basal area (+0.036 and +0.020 at the 150 m<sup>2</sup> and the 225 m<sup>2</sup> scales, respectively), while the CV's in the unburned treatment declined slightly (−0.026 at both the 150 m<sup>2</sup> and the 225 m<sup>2</sup> scales).

3.3.2. CV by tree size class

Prior to treatment (2009), the CV for tree density for the 10–25 cm,



**Fig. 3.** Change in the coefficient of variation from 2009 (pre-treatment) to 2014 (post-treatment) for tree density and basal area at three different spatial scales, generated by dividing 240 m × 15 m of belt transect in each unit into 24 (each 10 m × 15 m, or 150 m<sup>2</sup>), 16 (each 15 × 15 m, or 225 m<sup>2</sup>), or 8 sections (each 30 m × 15 m, or 450 m<sup>2</sup>). The 2012 data (post-thinning and pre-burning) are not shown for simplicity. Lines with significantly different slopes are denoted by different letters. Historical reference CV's were calculated at the same spatial scales from three approximately 4 ha “Methods of Cutting” plots that were completely stem-mapped in 1929 prior to logging, and are shown for comparison.

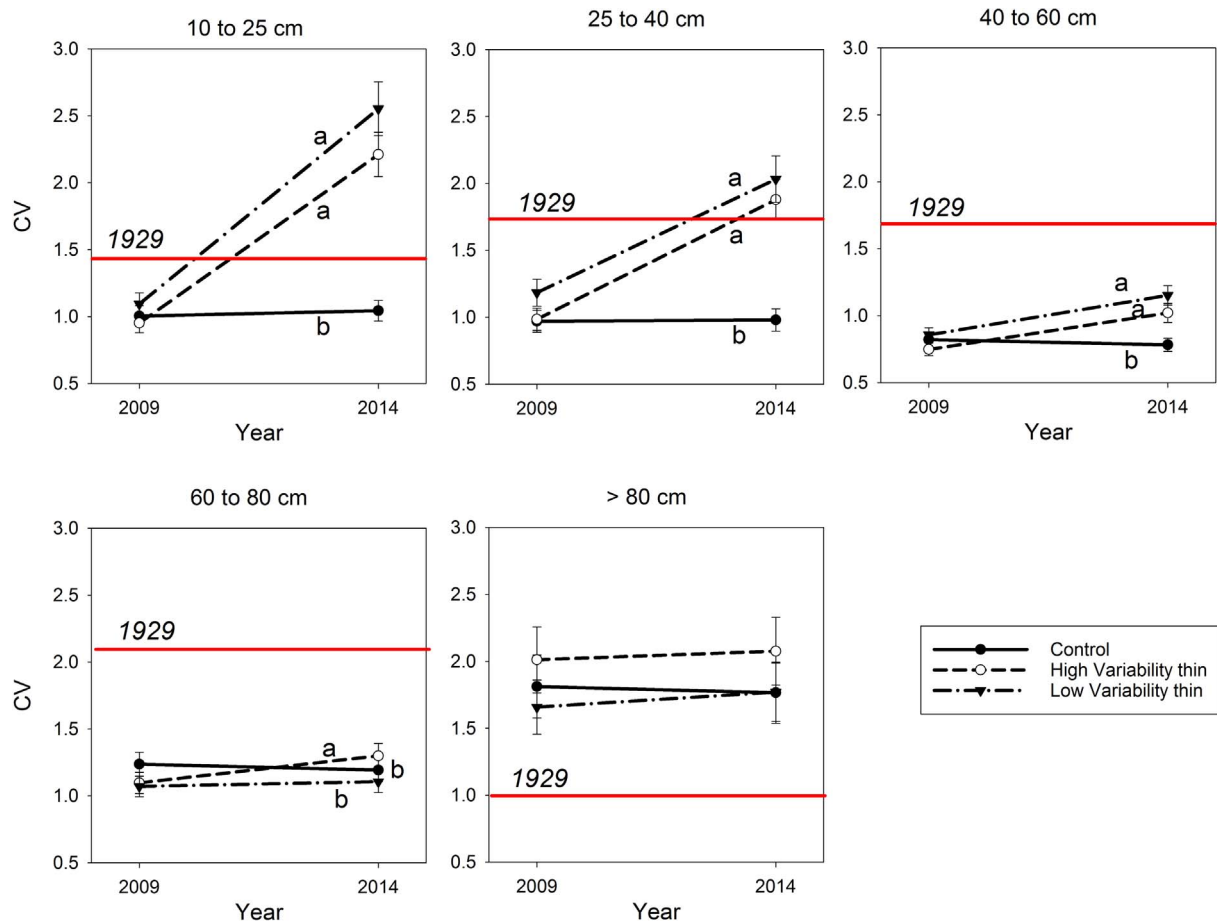


Fig. 4. Change in the coefficient of variation from 2009 (pre-treatment) to 2014 (post-treatment) for tree density in five diameter at breast height size categories. The CV was calculated by dividing 240 m × 15 m of belt transect into sixteen (15 m × 15 m or 225 m<sup>2</sup>) sections per experimental unit. The 2012 data (post-thinning and pre-burning) are not shown for simplicity. Lines with significantly different slopes are denoted by different letters. Historical reference CV's were calculated at the same spatial scales from three approximately 4 ha "Methods of Cutting" plots that were completely stem-mapped in 1929 prior to logging, and are shown for comparison.

25–40 cm, 40–60 cm, and 60–80 cm size classes was much lower than those in the 1929 forest. CV of tree density for the largest (> 80 cm) size category was higher than the 1929 condition. Both thinning treatments increased the CV for tree density in the small (10–25 cm, 25–40 cm) and intermediate (40–60 cm) size classes (Fig. 4). Only the HighV thinning increased the CV for larger intermediates (60–80 cm), while CV's for the largest tree size class (> 80 cm) did not change due to treatment (Fig. 4). Following thinning, the CV for small (10–25 cm) trees now exceeded the 1929 forest, CV for 25–40 cm trees equaled or was slightly higher than values from 1929, while CV's for the 40–60 cm and 60–80 cm sizes remained well below those from 1929, and CV's for the > 80 cm size class remained well above. Prescribed fire did not significantly change the CV in any size class in 2014. When 2016 data were included to reflect delayed mortality (in part), the Burning × Year treatment interaction became significant for the smallest (10–25 cm) size class ( $P = 0.004$ ). CV's in burn treatments increased (+0.41) while CV's in the unburned treatments remained steady (+0.02). Much of the increase was due to delayed mortality reducing the already low number of the smallest trees in the thinned and burned units. While delayed mortality also increased the CV for the 10–25 cm size class in the burn only units (+0.09), it remained below the CV in 1929 (1.22 vs. 1.47 for the 1929 reference).

### 3.3.3. CV by species

Prior to treatment (2009) the CV's of basal area for white fir and incense cedar were much lower and the CV of pine species was somewhat lower relative to 1929 (Fig. 5). Both thinning treatments significantly increased the CV of the basal area for white fir and incense

cedar, relative to the unthinned control, equaling or approaching values found in 1929 (Fig. 5). Thinning did not significantly alter the CV for pine species (Fig. 5). Burning did not initially change the CV significantly for any species. When 2016 data were included, the Burning × Year interaction became significant for pine species ( $P = 0.006$ ), with the burning treatment increasing the CV slightly (+0.11) while the CV for the unburned treatment remained steady (+0.01).

### 3.4. Treatment effects on canopy closure

Canopy closure varied both with the angle from vertical analyzed (Fig. 6) and treatment. Both thinning treatments significantly reduced average canopy closure, but there was no difference in mean closure between the HighV and LowV thinning treatments (Table 5). Burning did not significantly affect canopy closure. The HighV thinning treatment contained a greater range of canopy conditions, with a higher percentage of points with either very low (< 10%) or very high (> 80%) closure (Fig. 7). Twenty-nine percent of gridpoints (and by extension, stand area) contained less than 10% canopy closure, while 14% contained > 70% (compared with 14% and 11%, respectively, in the LowV thinning treatment). The LowV thinning treatment resulted in a normal distribution with higher numbers clustered around the mean, while the unthinned control treatment was skewed overwhelmingly towards the upper end of the range, with over half of gridpoints having > 70% canopy closure. Even though the CV of canopy closure was consistently numerically higher in the HighV treatment, differences among treatments were not statistically significant (Table 5).



**Tree basal area by Species - 225 m<sup>2</sup> scale**

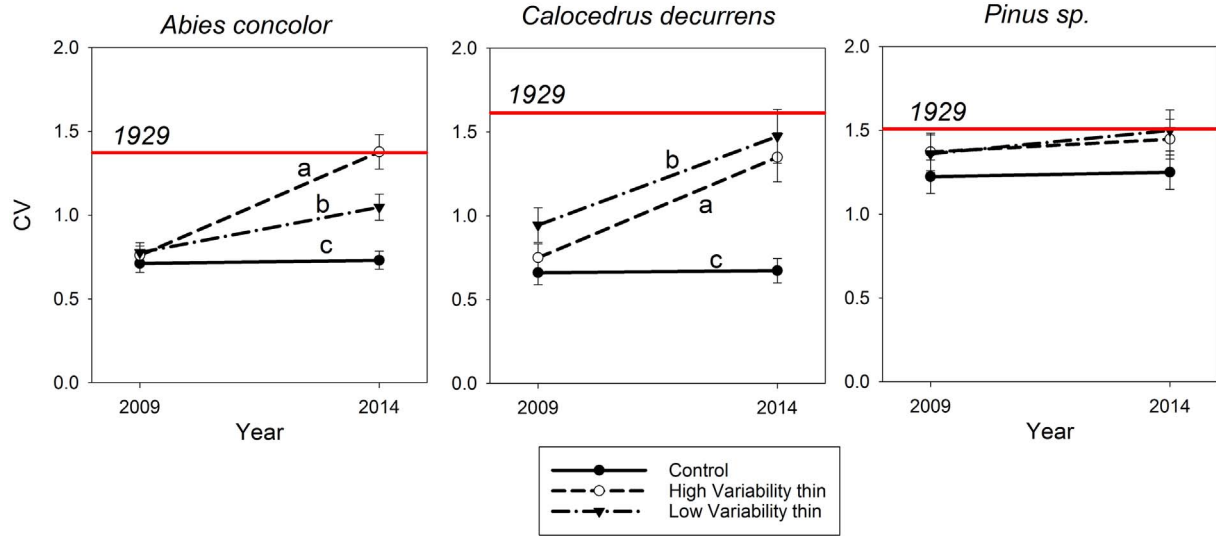


Fig. 5. Change in the coefficient of variation from 2009 (pre-treatment) to 2014 (post-treatment) for tree basal area by species. The CV was calculated by dividing 240 m × 15 m of belt transect into sixteen (15 m × 15 m or 225 m<sup>2</sup>) sections per experimental unit. The 2012 data (post-thinning and pre-burning) are not shown for simplicity. Lines with significantly different slopes are denoted by different letters. Historical reference CV's were calculated at the same spatial scales from three approximately 4 ha “Methods of Cutting” plots that were completely stem-mapped in 1929 prior to logging, and are shown for comparison.

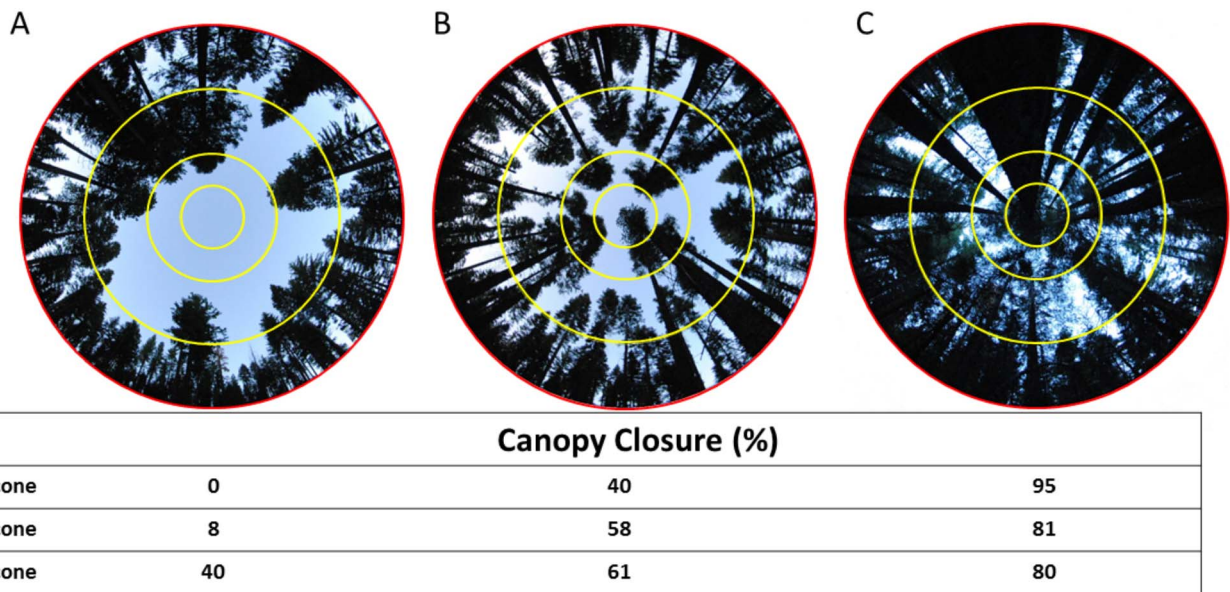


Fig. 6. Hemispherical photographs illustrating the range of canopy closure conditions within the study area, from A) low canopy closure – gridpoint FF8 in a ‘High Variability’ thinned unit; B) moderate canopy closure – gridpoint DD20 in a ‘Low Variability’ thinned unit, and C) high canopy closure – gridpoint T4 in an unthinned control unit. Yellow concentric circles from smallest to largest show the amount of canopy captured in a cone 15°, 30°, and 60° on either side of vertical, respectively, with percentages listed in the table below.

**4. Discussion**

**4.1. Effect of treatments on average stand metrics**

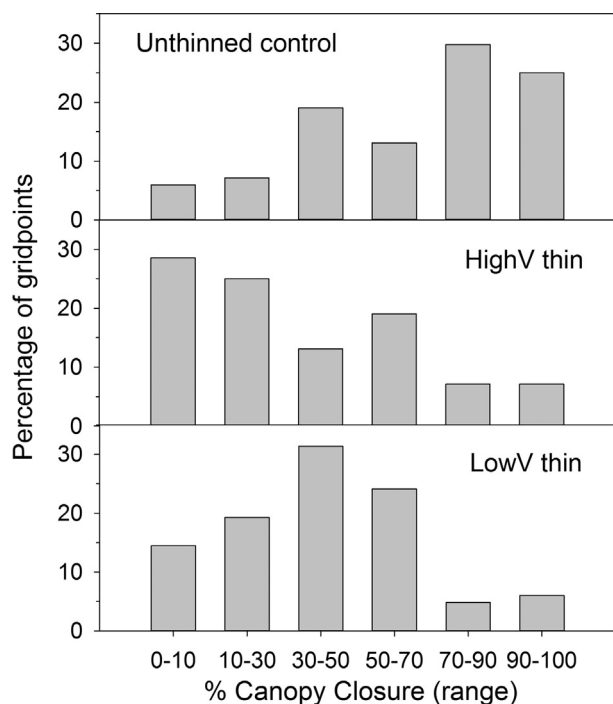
Thinning treatments significantly altered stand structure by reducing density, increasing average tree diameter, and increasing the percentage of pine. In contrast the prescribed burning treatment had only a minor effect on live tree conditions but did significantly reduce surface fuels – a critical step in providing resilience to wildfire burning under extreme conditions. The majority of tree mortality in the prescribed fire only treatment occurred in the smallest 10–25 cm dbh size class. While the level of tree mortality was higher than would have been expected given the low direct fire damage observed, post-fire mortality was likely exacerbated by a severe drought following the burns (van

Mantgem et al., 2013b). Despite this drought-related mortality, reductions were still insufficient to restore historical tree densities. Prior to treatment, the greatest deviation in tree density compared to a 1929 historical old-growth reference stand occurred in the intermediate size classes (25–60 cm dbh). Mechanical thinning was able to reduce numbers of intermediate-sized and larger trees closer to the reference condition. Density of trees > 25 cm dbh in the prescribed fire only treatment was 287.5 ha<sup>-1</sup> three years after the burns, whereas thinning reduced the density to a level nearly identical to the 1929 reference plots (average of HighV and LowV = 131.9 ha<sup>-1</sup>, vs. 130.0 ha<sup>-1</sup> in the 1929 reference). All treatments still contained a deficit of trees in the largest (> 80 cm dbh) size class, but with time, some of the intermediate-sized trees should grow and fill this void. Mechanical thinning did lead to a deficit of trees in the smallest (10–25 cm dbh) category,

**Table 5**  
Canopy closure based on the analysis of circular digital canopy photographs taken with a 180° fisheye lens. Closure was calculated using WinScanopy for different cones from vertical, ranging from 15° to 60° degrees. The 15° cone approximates canopy cover or the vertical projection of the canopy as would be determined using a densitometer, while the 60° cone captures a radius similar to that measured by a densitometer. Photos were taken in the summer of 2016.

Thinning treatment	Canopy closure – 15°		Canopy closure – 30°		Canopy Closure – 60°	
	%	CV	%	CV	%	CV
Control	65.1 <sup>a</sup> (4.0)	8.7 (0.9)	67.6 <sup>a</sup> (3.3)	5.6 (0.6)	74.9 <sup>a</sup> (2.0)	2.9 (0.4)
HV thin	35.0 <sup>b</sup> (2.2)	9.2 (0.9)	42.5 <sup>b</sup> (2.1)	6.2 (0.7)	54.6 <sup>b</sup> (1.4)	3.4 (0.5)
LV thin	40.5 <sup>b</sup> (2.5)	8.1 (0.8)	44.6 <sup>b</sup> (2.2)	5.3 (0.6)	57.0 <sup>b</sup> (1.5)	2.7 (0.4)

<sup>a,b</sup> Significant differences among treatments are denoted with different letters.



**Fig. 7.** Percentage of gridpoints within different percentage canopy closure categories in the unthinned control treatment and two thinning treatments – High Variability (HighV) and Low Variability (LowV). Canopy closure (1 – canopy openness) was estimated for a cone 15° on either side of vertical using the program WinScanopy.

relative to the historical reference. The “reference” condition for trees of this size might have been inflated somewhat because 40 years had transpired between the last fire (1889) and when the stand was measured in 1929. Some regeneration likely would have grown to > 10 cm dbh from establishment during this time. Still, it is likely that fewer small trees remained following thinning than would have occurred in the average historic high productivity mixed conifer forest stand.

A lack of small trees following thinning is typical for many projects that include a fuel reduction objective. Trees too small to cut into lumber (approximately 25 cm dbh and smaller) are generally not marked in USFS timber sales and logging contracts commonly call for their removal. Thus the only small trees retained are often in stream exclusion zones, on steep slopes, or other areas where access for mechanical equipment is restricted. While “black and white” contracting language makes the job of a logging operator easier, the lack of middle ground restricts opportunities to generate additional structural variability. If ending up with a broader range of tree size classes, including saplings, is a restoration goal, improvement may be possible by writing

contracts in a way that retains more small trees, or marking some for retention – i.e. individuals not growing directly under the canopy of other trees, where they may present a ladder-fuel concern. However, in many areas this young cohort is currently dominated by white fir and cedar, which establish more readily in shaded environments than pine (Levine et al., 2016). If regenerating a broader mix of species, including pine, is desired, cutting white fir and cedar saplings to produce gaps more favorable to pine regeneration may actually yield a long-term benefit (York et al., 2012), even if it results in a temporary deficit of small trees.

Lower intensity prescribed fire has been shown to be insufficient to restore structure to long-unburned forest in other studies as well (e.g. Sackett et al., 1996; Schmidt et al., 2006; North et al., 2007; Battaglia et al., 2009; Collins et al., 2011; Roccaforte et al., 2015). Lack of substantial overstory change can be attributed to trees too large to easily kill with prescribed burns or burns of insufficient intensity. For many reasons, including high fuel loads after decades without fire, reducing the risk of losing control of a prescribed burn, and lack of available crews during wildfire season, prescribed burns in conifer forests of California are frequently done only when fuel moisture is relatively high and air temperature low, either in the spring before wildfire season or in the fall, after some rainfall (Knapp et al., 2009; Ryan et al., 2013). Such burns under benign fire weather conditions tend to produce less ecological change than fire during the dry summer season when fuels are drier and temperatures are hotter.

Fires at this study location were likely historically of relatively low intensity, given a median fire return interval of only six years (Knapp et al., 2013), which would have limited fuel accumulation. Such fires would not be expected to cause substantial thinning of larger trees, except perhaps through gradual attrition as basal fire scars burned out, leading to mechanical failure (Show and Kotok, 1924). Frequent predominantly low-intensity fire is believed to have historically shaped tree density primarily by curtailing establishment, killing or thinning seedlings and saplings before they reached a fire resistant size (Show and Kotok, 1924; Sackett et al., 1996; van Wagtenonk and Fites-Kaufman, 2006). The exception might have been in the vicinity of single large trees or groups of trees that died and subsequently created fuel “jackpots”, increasing the probability of localized torching and other higher severity effects. In the contemporary second-growth forest, the long-term absence of fire allowed regenerating trees to achieve considerable size and grow thicker bark, making them much more fire resistant and difficult to kill with single-entry prescribed fire. This does not mean that stand density cannot be restored with fire alone in other forests with different representation among tree size classes. Some of the better examples of fire-only approaches being successfully used for reducing stand densities to within historic ranges come from old-growth settings containing a greater range of pre-fire tree sizes (e.g. Keifer et al., 2000; Becker and Lutz, 2016). In such forests, larger more fire-resistant trees are still present and ingrowth is generally smaller and less fire resistant as a result of growing under this canopy (Lydersen and North, 2012; Knapp et al., 2013). Where ingrowth has attained larger sizes, higher intensity prescribed burns (Fulé et al., 2004; Schmidt et al., 2006; van Mantgem et al., 2011) or managed wildfire, and perhaps multiple such fires may be required (Collins et al., 2011).

Mechanical thinning resulted in a significant shift in forest species composition because marking guidelines favored pines for retention over fir and cedar. The forest composition following thinning was similar to the 1929 historical reference. In contrast, prescribed fire did not alter the species composition, presumably at least in part because changing the relative basal area of species requires sufficient tree mortality, particularly in larger size classes, to affect change. In addition, even though pines are assumed to be more fire resistant than white fir or incense cedar, differences in susceptibility to fire-caused tree mortality among species of the mixed-conifer forest tend to be relatively weak beyond the seedling to sapling stages (van Mantgem and Schwartz, 2003; van Mantgem et al., 2013a), even in higher-intensity

prescribed fires (van Mantgem et al., 2011). The relationship between bark thickness and fire resistance may also be diluted by other factors. For example, consumption of sloughing bark accumulated at the base of large pines in the long-term absence of fire can put these trees at greater risk of mortality than smaller pines (Kolb et al., 2007) or species that do not shed bark, such as white fir and incense cedar. Historically, when fire was frequent, it likely shaped forest species composition at younger tree ages. Show and Kotok (1924) noted that surface fires killed a higher proportion of white fir and incense cedar than pine seedlings by torching, because of the tendency of seedlings of the former to have denser foliage and grow in thicker clusters.

#### 4.2. Effect of treatments on within-stand heterogeneity

The very low CV's of tree density prior to treatment compared to the historical condition illustrates how homogenous these forests had become over time, similar to findings from other frequent fire forest ecosystems (Larson and Churchill, 2012). The shade-tolerant tree species at our site are heavy seed producers that readily establish under the canopy of mature trees and in gaps in the forest in the absence of fire (Zald et al., 2008; Levine et al., 2016). This infilling of shade-tolerant trees leads to a homogeneous forest structure with very few gaps of any size (Lydersen et al., 2013). While the HighV thinning prescription increased the CV of tree density at all spatial scales, values were well below the 1929 historical reference because thinned units lacked the dense groups of small trees found in historical stands. As noted previously, the CV's from 1929 may be higher than would have been the case with the historical fire regime because 40 years had transpired between the last fire (1889) (Knapp et al., 2013) and when the stands were measured – enough time for at least some seedlings to become small trees.

As with CV's for tree density, CV's for basal area were below the historical 1929 reference prior to treatment. HighV thinning left the CV just under the 1929 reference at the 225 m<sup>2</sup> scale and exceeded the 1929 reference at the 450 m<sup>2</sup> scale. This suggests that the group and gap structure of historical forests was on average organized at scales less than 450 m<sup>2</sup> and additional variation not fully restored by thinning once existed at the 150 m<sup>2</sup> scale. When marking the stands in HighV units for cutting, crews tended to focus on producing tree group and gap variation at the 400 m<sup>2</sup> to 2000 m<sup>2</sup> scales, with variation at smaller scales mainly a byproduct of selecting the best trees to leave, regardless of crown spacing. Extending the range of tree group and gap sizes on the smaller end would likely reduce this deviation from the historical reference. While prescribed burning increased the CV's slightly when delayed mortality was accounted for, the magnitude of the change was small relative to the changes caused by thinning. CV's increased the most in the burn only unit experiencing the most intense fire, indicating that hotter prescribed burns would have produced greater change. Over time, CV's for both density and basal area should move closer to the historical reference as existing trees grow and regeneration establishes in some of the gaps while other gaps are maintained or new ones are created. This process of gap creation and maintenance will likely require fire or additional mechanical treatments having a similar effect.

The greater heterogeneity produced by the HighV thinning prescription, relative to the LowV thinning prescription is also seen in the canopy closure data. Even though average canopy closure did not differ significantly between the two thinning treatments, the HighV thinning treatment contained a broader range of canopy closure values, with a somewhat greater percentage of area containing very high (> 70%) canopy closure, and more area with open canopy (< 10% canopy closure) (Fig. 7). Conversely, the frequency histogram of the LowV thinning treatment showed the majority of locations had average canopy closure values.

Spatial complexity, whether fire created (Roberts et al., 2008) or generated through mechanical thinning (Carey, 2000), has been shown to be associated with abundance of some small mammal species,

possibly through diversifying food sources and stabilizing food availability. Assuming sufficient canopy cover remains, treatments that increase spatial complexity should also be beneficial for species like the Northern goshawk (*Accipiter gentilis*) and spotted owl (*Strix occidentalis*), which prefer high canopy closure areas for nesting and roosting but may use more open and diverse areas for foraging (Reynolds et al., 1992; Tempel et al., 2016; Eyes et al., 2017). Northern flying squirrels (*Glaucomys sabrinus*) are a key component of the diet for spotted owls (Gutiérrez, 1996), and a recent paper from our study area showed that while Northern flying squirrel density was lower in thinned units, the total population size did not change pre- to post-thinning, presumably due to the heterogeneity in canopy conditions present (Sollman et al., 2015). Benefits of heterogeneity to the spotted owl are also suggested by documented higher fecundity in landscapes with more forest edge (Franklin et al., 2000).

The greater abundance of low canopy closure areas within the HighV units may also provide better environments for natural regeneration of pines. Bigelow et al. (2011) found that the tipping point favoring shade-intolerant ponderosa pine over shade-tolerant white fir was when the understory received more than 41% of the direct above canopy radiation. Gaps may also play an important role in moderating fire behavior and increasing resilience to wildfire. Areas lacking a canopy will accumulate surface fuels more slowly, potentially impeding or altering fire spread. Even thinning, on the other hand, would be expected to result in greater surface fuel continuity into the future.

The wider the angle of view, the greater the difference between canopy closure and the vertical projection of the canopy, or canopy cover (Jennings et al., 1999). At angles < 30° from vertical, measurements of canopy closure approach canopy cover (Paletto and Tosi, 2009). Our estimates of canopy closure in a 15° cone from vertical should therefore approximate canopy cover. Indeed, mean canopy closure (15° cone from vertical) of the pre-treatment forest calculated from hemispherical canopy photographs (65%) was very close to canopy cover values calculated by Lydersen et al. (2013) for adjacent forest using stand maps and canopy radius allometric equations based on species and tree diameter (62%). The average for the thinned units (38%) was slightly less than what canopy cover in adjacent old-growth forest was estimated to have been in 1929 (45%) (Lydersen et al., 2013). This deviation from historical is likely due to the relative lack of small (< 25 cm) trees following thinning. When trees < 25 cm were excluded in the historical forest canopy cover estimate, a value of 35% was obtained (Lydersen et al., 2013), which is very similar to that found in the thinned units. When trees are aggregated, canopy cover for a given forest density is expected to be somewhat less than when trees are evenly spaced (Battaglia et al., 2002), and such a trend was noted in this study. Although the differences were not significant, the HighV treatment had slightly lower canopy closure despite slightly higher tree density. In the absence of tree mortality, canopy closure in thinned units should over time approach the 1929 reference values, as crowns thicken and expand in response to more light and a new cohort of small trees is recruited.

#### 4.3. Fuels and fire behavior

We did not find a significant increase of activity fuels from thinning, probably due to the logging method used. Smaller and intermediate trees were harvested whole then de-limbed and topped at the landing rather than directly on site. Larger trees were hand-felled and cut into sections, but these sections, including the tops, were similarly processed at landings. Lack of a logging effect on fine fuel loading has been observed with other whole tree harvest operations (Stephens et al., 2009). The only woody fuel component that was significantly more abundant in the thinned units was the 100 h (2.5–7.6 cm diameter) fuel, which may have been added as dead branches along the bole broke off during hand felling or skidding. Had logging added substantial surface fuel, we might have expected significantly greater fire effects to trees (char

height, scorch height) in the thinned units. While char and scorch height were numerically (but not statistically) higher in the thinned units, observations from the fire line suggested that minor differences in fuel moisture may have had a stronger influence on fire behavior than any added fuel loading. A heavy canopy can slow the rate at which fine fuels dry after a precipitation event (Estes et al., 2012), particularly in the fall when the sun angle is low. Thus, by aiding the drying process immediately post-precipitation, thinning may expand the window during which prescribed burns can be completed. However, while fine fuel moisture values were often numerically higher in unthinned controls than adjacent thinned units, statistically significant differences among treatments were not found because of the large amount of variation.

#### 4.4. Management implications

With variable density thinning, we were able to create a forest structure with a density of large trees and species composition similar to that found prior to logging and long-term fire exclusion. This variably-thinned forest also was more heterogeneous in density and basal area than forests thinned with the more standard individual tree crown spacing guides and contained greater variation in canopy closure, which more closely approximated the heterogeneity found in historical forests. While such structural restoration might also be accomplished with multiple cycles of prescribed fire, mechanical thinning produced more rapid change. Furthermore, the mechanical thinning produced saw logs as well as wood chips for bioenergy production, creating a positive socio-economic impact not observed in the prescribed fire only treatment. The value of mechanical thinning as a tool for rapidly reducing stand densities and generating heterogeneity is likely especially pronounced where ingrowth due to fire exclusion has reached large, more fire resistant sizes, such as sites with productive soils, previously logged forest where growth was faster due to high light conditions, or forest with the longest fire-free intervals.

Even though prescribed fire alone produced much less change to overstory conditions in this study, this does not reflect the potential value of prescribed fire (or any predominantly low- to moderate-intensity fire) for long-term forest resilience. Reduction of accumulated surface fuels with prescribed fire or low-moderate intensity managed wildfire has been shown to protect both thinned (Ritchie et al., 2007, Prichard et al., 2010, Safford et al., 2012) and unthinned (Lydersen et al., 2014) forests from stand replacing wildfire. Prescribed fire following thinning in our study caused relatively minor changes to stand structure because many of the smaller-sized trees that would have been most susceptible to fire had already been removed by thinning. The HighV thinning treatment with follow-up burning produced the best outcome in terms of structure most similar to those once created by frequent fire, combined with low surface fuel loads for greater protection from future high-severity wildfire. While thinning alone has generally been shown to moderate fire behavior, without prescribed fire, thinned stands with heavy surface fuel loads and high fuel continuity may still be susceptible to considerable fire-caused mortality (Ritchie et al., 2007). In stands where a restored canopy structure has been created by thinning, some form of low- to moderate-intensity fire may be vital for maintaining this structure by preventing ingrowth from homogenizing the stand. Fire will need to be frequent enough to shape the species composition through differentially selecting pines over

species with more shade tolerant and fire-sensitive seedlings and saplings.

In this study we used historical structure as a guide to thinning and compared our treatment results to this historical reference. While valid questions have been raised about such an approach in a time of changing climate (Millar et al., 2007, Stephens et al., 2010), our intent was not to doggedly adhere to these historical conditions but rather to provide a general framework for restoring heterogeneity. Frequent fire forests across a range of climatic conditions were historically structured at similar within-stand spatial scales, presumably because of the common process – fire – doing much of the shaping (Larson and Churchill, 2012). Historical forest variability has been associated with attributes that current forests often lack. Tree clusters with high levels of local canopy closure may provide critical habitat for some sensitive species, such as the California spotted owl and fisher, or their prey, that are often associated with high canopy cover forest (Sweizer et al., 2016, Tempel et al., 2014, 2016) or forest edge environments (Franklin et al., 2000, Tempel et al., 2014, Eyes et al., 2017). At the same time, canopy gaps break up crown fuel continuity and would be expected to produce a patchier distribution of surface fuels over time, both of which may slow or impede fire spread. Among the challenges facing managers is how to create resilient and diverse forests containing a broad range of habitats as climate and disturbance regimes continue to change. In the absence of information on how a changing climate might alter the scale at which within-stand variation in frequent fire forests is structured, the historical range of variation still provides a useful reference (Keane et al., 2009). Treatments that increase forest heterogeneity likely possess a greater capacity to adapt to new climates and uncertain stressors (Churchill et al., 2013). Heterogeneity is thus a key feature of resilient forest stands, with different structures and species combinations improving the chance that at least some will be suitably adapted to future stressors. The merits of greater forest heterogeneity are highlighted by recent widespread drought and bark beetle-caused tree mortality in the Sierra Nevada (Young et al., 2017). Because bark beetles are in many cases specific to single species or size class host trees, heterogeneous forests with a broad range of species and tree size classes are likely to be less vulnerable to excessive mortality than more simplified stands (Fettig, 2012). Going forward, selective forces will continue to act on this variability, particularly if processes such as the fire regime are also restored, either retaining the existing basic elements of structural heterogeneity or perhaps reshaping the forest so it one day looks quite different than historical ‘reference’ conditions.

#### Acknowledgements

We thank the Stanislaus National Forest for their crucial role in carrying out the thinning and burning treatments, Sierra Resource Management (logging contractor) for their diligence in implementing the thinning treatments, Bob Carlson for oversight of treatment implementation and data collection, Nels Johnson for assistance with statistical analyses, Celeste Abbott for analyzing the canopy photographs, Terrie Alves for database development, and the many seasonal USFS employees who have helped collect the data. The paper also benefitted from suggestions by two anonymous reviewers. This work was supported in part by the USDA, National Institute of Food and Agriculture (NIFA) program, grant number 11-03859.

#### Appendix A

Generalized linear mixed model ANOVA results (DF = Degrees of Freedom for numerator, denominator) for tree density, basal area, percentage of basal area composed of *Pinus* species, and quadratic mean diameter for thinning (HighV, LowV, Control) and burning (prescribed fire, no prescribed fire) treatments across three measurement years – 2009 (pretreatment), 2012 (post-thinning, pre-burning, and 2014 (posttreatment). Thinning treatments were nested within burning treatments in a split-plot design. The F statistic is the ratio of mean square of the variable and the mean square error and P is the probability of a value greater than F.

Variable	DF	Trees ha <sup>-1</sup>		Basal area (m <sup>2</sup> ha <sup>-1</sup> )		% <i>Pinus</i> BA		Quadratic mean diameter (cm)	
		F	P	F	P	F	P	F	P
Thin (T)	2, 12	144.19	< 0.001	11.16	0.002	7.56	0.008	21.47	< 0.001
Burn (B)	1, 6	0.94	0.369	0.26	0.629	6.64	0.042	0.85	0.391
T × B	2, 12	0.56	0.585	0.26	0.773	1.55	0.252	0.61	0.562
Year (Y)	2, 36	1077.81	< 0.001	417.71	< 0.001	271.05	< 0.001	989.91	< 0.001
Y × T	4, 36	252.25	< 0.001	119.92	< 0.001	66.31	< 0.001	201.22	< 0.001
Y × B	2, 36	0.85	0.434	0.75	0.478	2.50	0.096	0.49	0.614
Y × T × B	4, 36	0.99	0.427	0.69	0.604	1.68	0.176	0.80	0.535

## Appendix B

Generalized linear mixed model ANOVA results (DF = Degrees of Freedom for numerator, denominator) for the coefficient of variation of tree density and basal area among three stand structure treatments (unthinned control, HighV thin, and LowV thin) at three within-stand scales – 10 × 15 m, 15 × 15 m, and 30 × 15 m, in three years – 2009 (pretreatment), 2012 (post-thinning and pre-burning), and 2014 (post-treatment). Thinning treatments were nested within burning treatments in a split-plot design. The F statistic is the ratio of mean square of the variable and the mean square error and P is the probability of a value greater than F.

Variable	DF	CV Trees ha <sup>-1</sup>						CV Basal area (m <sup>2</sup> ha <sup>-1</sup> )					
		10 m		15 m		30 m		10 m		15 m		30 m	
		F	P	F	P	F	P	F	P	F	P	F	P
Thinning (T)	2, 18	11.29	0.002	3.58	0.060	0.49	0.622	18.44	< 0.001	41.62	< 0.001	16.33	< 0.001
Burning (B)	1, 18	0.83	0.398	0.98	0.360	0.43	0.538	0.50	0.507	0.01	0.916	0.41	0.548
T × B	2, 18	0.07	0.931	0.46	0.642	0.14	0.872	1.34	0.299	1.63	0.237	2.14	0.160
Year (Y)	2, 36	47.21	< 0.001	32.45	< 0.001	21.62	< 0.001	77.70	< 0.001	98.22	< 0.001	20.12	< 0.001
Y × T	4, 36	15.65	< 0.001	14.20	< 0.001	10.33	< 0.001	24.66	< 0.001	30.72	< 0.001	8.68	< 0.001
Y × B	2, 36	0.41	0.665	1.08	0.350	0.22	0.800	0.41	0.664	1.74	0.190	0.16	0.855
Y × T × B	4, 36	0.70	0.595	1.71	0.170	1.29	0.292	0.20	0.936	0.17	0.952	0.10	0.983

## References

- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96.
- Battaglia, M., Smith, F.W., Sheppard, W.D., 2009. Predicting mortality of ponderosa pine regeneration after prescribed fire in the Black Hills, South Dakota, USA. *Int. J. Wildland Fire* 18, 176–190.
- Battaglia, M.A., Mou, P., Palik, B., Mitchell, R.J., 2002. The effect of spatially variable overstory on the understory light environment of an open-canopied longleaf pine forest. *Can. J. For. Res.* 32, 1984–1991.
- Becker, K.M.L., Lutz, J.A., 2016. Can low-severity fire reverse compositional change in montane forests of the Sierra Nevada, California, USA? *Ecosphere* 7, 1484.
- Bigelow, S.W., North, M.P., Salk, C.F., 2011. Using light to predict fuels-reduction and group-selection effects on succession in Sierran mixed-conifer forest. *Can. J. For. Res.* 41, 2051–2063.
- Brown, J.K., 1974. Handbook for inventorying downed woody material. Intermountain Forest and Range Experiment Station, Ogden UT.
- Carey, A.B., 2000. Effects of new forest management strategies on squirrel populations. *Ecol. Appl.* 10, 248–257.
- Carey, A.B., 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing heterogeneity with variable-density thinning. *Forestry* 76.
- Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *For. Ecol. Manage.* 291, 442–457.
- Clyatt, K.A., Crotteau, J.S., Schaedel, M.S., Wiggins, H.L., Kelley, H., Churchill, D.J., Larson, A.J., 2016. Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. *For. Ecol. Manage.* 361, 23–37.
- Collins, B.M., Everett, R.G., Stephens, S.L., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2 Article 51.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* 30, 129–164.
- Cooper, C.F., 1961. Pattern in ponderosa pine forests. *Ecology* 42, 493–499.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* 36, 2285–2299.
- Dunning, D., 1923. Some results of cutting in the Sierra forests of California. U.S. Department of Agriculture, Department Bulletin No. 1176.
- Estes, B.L., Knapp, E.E., Skinner, C.N., Uzoh, F.C.C., 2012. Seasonal variation in surface fuel moisture between unthinned and thinned mixed conifer forest, northern California, USA. *Int. J. Wildland Fire* 21, 428–435.
- Eyes, S.A., Roberts, S.L., Johnson, M.D., 2017. California Spotted Owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape. *The Condor* 119, 375–388.
- Ferrell, G.T., Orosina, W.J., Demars Jr., C.J., 1994. Predicting susceptibility of white fir during a drought-associated outbreak of fir engraver, *Scolytis ventralis*, in California. *Can. J. For. Res.* 24, 302–305.
- Fettig, C.J., 2012. Forest health and bark beetles. In *Managing Sierra Nevada Forests*, USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-237, Pages 13–22.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebaker, T.E., Negron, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For. Ecol. Manage.* 238, 24–53.
- Franklin, A.B., Anderson, D.R., Gutierrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol. Monogr.* 70, 539–590.
- Franklin, J.F., Johnson, K.N., 2012. A restoration framework for federal forests of the Pacific Northwest. *J. Forest.* 110, 429–439.
- Fulé, P.Z., Cocke, A.E., Heinlein, T.A., Covington, W.W., 2004. Effects of an intense prescribed forest fire: is it ecological restoration? *Restor. Ecol.* 12, 220–230.
- Graham, R.T., Jain, T.B., 2005. Application of free selection in mixed forest of the inland northwestern United States. *For. Ecol. Manage.* 209, 131–145.
- Gutiérrez, R.J., 1996. Biology and distribution of the Northern spotted owl. *Studies in Avian Biology* 17, 2–5.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *For. Ecol. Manage.* 114, 433–446.
- Jennings, S.B., Brown, N.D., Sheil, D., 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover, and other measures. *Forestry* 72, 59–73.
- Keane, R.E., Hessburg, P.F., Landres, P.B., Swanson, F.J., 2009. The use of historical range and variability (HRV) in landscape management. *For. Ecol. Manage.* 258, 1025–1037.
- Keifer, M., Stephenson, N.L., Manley, J., 2000. Prescribed fire as the minimum tool for wilderness forest and fire regime restoration: a case study from the Sierra Nevada, CA. In: *Proceedings: Wilderness science in a time of change*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, RMRS-P-15, vol. 5, Pages 266–269.
- Kittredge, J., 1953. Influences of forests on snow in the ponderosa-sugar pine-fir zone of the central Sierra Nevada. *Hilgardia* 22, 1–96.

- Knapp, E., North, M., Benech, M., Estes, B., 2012. The Variable Density Thinning study at Stanislaus-Tuolumne Experimental Forest. In: Managing Sierra Nevada Forests, USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-237, Pages 127–139.
- Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. U.S. Department of Agriculture, Pacific Southwest Research Station, General Technical Report PSW-GTR-224.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstorey and understorey change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecol. Manage.* 310, 903–914.
- Kolb, T.E., Agee, J.K., Fulé, P.Z., McDowell, N.G., Pearson, K., Sala, A., Waring, R.H., 2007. Perpetuating old ponderosa pine. *For. Ecol. Manage.* 249, 141–157.
- Larson, A.J., Churchill, D.C., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manage.* 267, 74–92.
- Lehmkuhl, J.F., Kennedy, M., Ford, P.L., Singleton, P.H., Gaines, W.L., Lind, R.L., 2007. Seeing the forest for the fuel: integrating ecological values and fuels management. *For. Ecol. Manage.* 246, 73–80.
- Leiberg, J. B. 1902. Forest conditions in the northern Sierra Nevada, California. U.S. Department of the Interior, U.S. Geological Survey, Professional paper No. 8, Series H, Forestry 5. Washington, D.C.
- Levine, C.R., Krivak-Tedley, F., van Doorn, N.S., Ansley, J.S., Battles, J.J., 2016. Long-term demographic trends in a fire-suppressed mixed conifer forest. *Can. J. For. Res.* 46, 745–752.
- Long, J.N., Smith, F.W., 2000. Restructuring the forest: goshawks and the restoration of southwestern ponderosa pine. *J. Forest.* 98, 25–30.
- Lyderson, J., North, M., 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15, 1134–1146.
- Lyderson, J.M., Collins, B.M., Knapp, E.E., Roller, G.B., Stephens, S., 2015. Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. *Int. J. Wildland Fire* 24, 484–494.
- Lyderson, J.M., North, M.P., Collins, B.M., 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *For. Ecol. Manage.* 328, 326–334.
- Lyderson, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. *For. Ecol. Manage.* 304, 370–382.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Miller, C., Urban, D.L., 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecol.* 15, 145–154.
- Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *For. Sci.* 50, 162–176.
- North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. *Can. J. For. Res.* 37, 331–342.
- North, M., Stine, P., O'Hara, K., Zielinski, W., Stephens, S., 2009. An ecosystem management strategy for Sierran mixed-conifer forests. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-220.
- Paletto, A., Tosi, V., 2009. Forest canopy cover and closure: comparison of assessment techniques. *Eur. J. Forest Res.* 128, 265–272.
- Prichard, S.J., Peterson, D.L., Jacobson, K., 2010. Fuel treatments reduce the severity of wildfire effects in dry mixed conifer forest, Washington, USA. *Can. J. For. Res.* 40, 1615–1626.
- Puettmann, K.J., Coates, K.D., Messier, C., 2009. A Critique of Silviculture: Managing for Complexity. Island Press, Covelo, CA.
- Puettmann, K.J., McG Wilson, S., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged management – what limits global adoption? *For. Ecosyst.* 2:8, 10.1186/s40663-015-0031-x.
- Reynolds, R.T., Graham, R.T., Reiser, M.H., 1992. Management recommendations for the northern goshawk in the southwestern United States. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-217.
- Reynolds, R.T., Sánchez Meador, A.J., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P. L., DeLorenzo, D.G., Graves, A.D., 2013. Restoring composition and structure in southwestern frequent fire forests: a science-based framework for improving ecosystem resiliency. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, General Technical Report RM-GTR-310.
- Ritchie, M.W., Skinner, C.N., Hamilton, T.A., 2007. Probability of tree survival after wildfire in an interior pine forest of northern California: effects of thinning and prescribed fire. *For. Ecol. Manage.* 247, 200–208.
- Roberts, S.L., van Wagtenonk, J.W., Miles, A.K., Kelt, D.A., Lutz, J.A., 2008. Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. *Fire Ecology* 4, 83–104.
- Roccaforte, J.P., Huffman, D.W., Fulé, P.Z., Covington, W.W., Chancellor, W.W., Stoddard, M.T., Crouse, J.E., 2015. Forest structure and fuels dynamics following ponderosa pine restoration treatments, White Mountains, Arizona, USA. *For. Ecol. Manage.* 337, 174–185.
- Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Front. Ecol. Environ.* 11 (Online Issue 1):e15–e24.
- Sackett, S. S., S. M. Haase, and M. G. Harrington. 1996. Lessons learned from fire use for restoring southwestern ponderosa pine ecosystems. In: Adaptive ecosystem restoration and management: restoration of Cordilleran conifer landscapes of North America. U.S.D.A. Forest Service, General Technical Report RM-GTR-278, Pages 53–60.
- Safford, H.D., Stevens, J.T., Merriam, K., Meyer, M.D., Latimer, A.M., 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *For. Ecol. Manage.* 274, 17–28.
- Sánchez Meador, A.J., Parysow, P.F., Moore, M.M., 2011. A new method for delineating tree patches and assessing spatial reference conditions of ponderosa pine forests in Northern Arizona. *Restor. Ecol.* 19, 490–499.
- Scheller, R.M., Spencer, W.D., Rustigan-Romsos, H., Syphard, A.D., Ward, B.C., Strittholt, J.R., 2011. Using stochastic simulation to evaluate competing risks of wildfires and fuels management on an isolated forest carnivore. *Landscape Ecol.* 26, 1491–1504.
- Schmidt, L., Hille, M.G., Stephens, S.L., 2006. Restoring northern Sierra Nevada mixed conifer forest composition and structure with prescribed fires of varying intensities. *Fire Ecol.* 2, 204–217.
- Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecol. Appl.* 20, 362–380.
- Show, S.B., Kotok, E.I., 1924. The role of fire in the California pine forests. USDA, Bulletin No, pp. 1294.
- Sollman, R., White, A.M., Gardner, B., Manley, P.N., 2015. Investigating the effects of forest structure on the small mammal community in frequent-fire forests using capture-recapture models for stratified populations. *Mammalian Biol.* 80, 247–254.
- Stephens, S.L., Millar, C.I., Collins, B.M., 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. *Environ. Res. Lett.* 5, 024003.
- Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecol. Appl.* 19, 305–320.
- Sweizer, R.A., Furnas, B.J., Barrett, R.H., Purcell, K., Thompson, C., 2016. Landscape fuel reduction, forest fire, and biophysical linkages to local habitat use and local persistence of fishers (*Pekania pennanti*) in Sierra Nevada mixed conifer forests. *For. Ecol. Manage.* 361, 208–225.
- Tempel, D.J., Gutierrez, R.J., Whitmore, S.A., Reetz, M.J., Stoelting, R.E., Berigan, W.J., Seamans, M.E., Peery, M.Z., 2014. Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests. *Ecol. Appl.* 24, 2089–2106.
- Tempel, D.J., Keane, J.J., Gutierrez, R.J., Wolfe, J.D., Jones, G.M., Koltunov, A., Ramirez, C.M., Berigan, W.J., Gallagher, C.V., Munton, T.E., Shaklee, P.A., Whitmore, S.A., Peery, M.Z., 2016. Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management. *Condor* 118, 747–765.
- van Mantgem, P., Schwartz, M., 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *For. Ecol. Manage.* 178, 341–352.
- van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Brooks, M., 2013a. Tree mortality patterns following prescribed fire for *Pinus* and *Abies* across the southwestern United States. *For. Ecol. Manage.* 289, 463–469.
- Van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Knapp, E.E., Flint, A., Flint, L., 2013b. Climatic stress increases forest fire severity across the western United States. *Ecol. Lett.* 16, 1151–1156.
- van Mantgem, P.J., Stephenson, N.L., Knapp, E., Battles, J., Keeley, J.E., 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. *For. Ecol. Manage.* 261, 989–994.
- van Wagtenonk, J.W., Benedict, J.M., Sydorak, W.M., 1996. Physical properties of woody fuel particles of Sierra Nevada conifers. *Int. J. Wildland Fire* 6, 117–123.
- van Wagtenonk, J.W., Benedict, J.M., Sydorak, W.M., 1998. Fuel bed characteristics of Sierra Nevada conifers. *Western J. Appl. For.* 13, 73–84.
- van Wagtenonk, J.W., Fites-Kaufman, J., 2006. Sierra Nevada bioregion. In: Sugihara, N.G., van Wagtenonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley and Los Angeles, CA, pp. 264–294.
- Weaver, H., 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. *J. For.* 41, 7–15.
- White, A.S., 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66, 589–594.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecol. Lett.* 20, 78–86. <http://dx.doi.org/10.1111/ele.12711>.
- York, R.A., Battles, J.J., Wenk, R.C., Saah, D., 2012. A gap-based approach for regenerating pine species and reducing surface fuels in multi-aged mixed conifer stands in the Sierra Nevada, California. *Forestry* 85, 203–213.
- Zald, H.S.J., Gray, A.N., North, M., Kern, R.A., 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed conifer forest, USA. *For. Ecol. Manage.* 256, 168–179.