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Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought

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ABSTRACT

California's high density, fire-excluded forests experienced an extreme drought accompanied by warmer than normal temperatures from 2012 to 2015, resulting in the deaths of millions of trees. We examined tree mortality and growth of mixed-conifer stands that had been experimentally treated between 2011 and 2013 with two different thinning treatments, one with more structural variability (HighV) and one with less structural variability (LowV), applied alone or in combination with prescribed burning. Tree mortality between 2014 and 2018 varied by species ranging from 42% of white fir (*Abies concolor*) to 18% of sugar pine (*Pinus lambertiana*), 12% of incense cedar (*Calocedrus decurrens*) and 10% of yellow pine (*P. ponderosa* and *P. jeffreyi*). Lower overall tree mortality rates at this location relative to drier locations in the southern Sierra Nevada suggested that drought effects may have been ameliorated by lower water deficits due to our site's more northerly location and deep, productive soils in combination with reductions in tree competition following thinning and burning. Averaged across burn treatments, thinning reduced the overall mortality rate between 2014 and 2018 from 34% to 11%. A total of 23% of the basal area was lost in the unthinned control treatments during this time period, while basal area was unchanged in the thinned treatments, with growth offsetting mortality. There was no significant difference in mortality or basal area change between LowV and HighV, suggesting that leaving trees at variable spacing may not compromise growth or resilience of the stand during a drought. Overall tree mortality was greater in the prescribed burn treatments, most pronounced in the smaller tree size classes, and varied by species, with burning having a significant effect on incense cedar and all pines, but not white fir. Trees with greater competition (Hegyi index) were more likely to die, particularly when also burned. Burning, however, consumed surface fuels and lowered fire hazard. With predictions of warmer droughts and greater weather variability, reducing forest density (basal area) and keeping surface fuel loads low will be important for building greater resilience to future drought stress and wildfire.

1. Introduction

Forests in the central and southern Sierra Nevada experienced dramatic mortality following a period of severe drought between 2012 and 2015 (Pile et al., 2019), with over 147 million trees killed on National Forest System lands by 2018 (U.S. Forest Service, 2019). This drought involved both prolonged below average precipitation and anomalously warm temperatures, a combination thought to accentuate tree stress and compound tree mortality (Williams et al., 2013; Allen et al., 2015). In some areas, it was likely the most severe drought in 1,200 years (Griffin and Anchukaitis, 2014). In the Sierra Nevada, deep soil moisture was exhausted in many areas (Goulden and Bales, 2019), weakening tree defenses and leading to an increase in bark beetle populations – the proximal agent of mortality in most instances and for most tree species (Fettig et al., 2019). Tree mortality was most pronounced in climatically drier areas (e.g., at lower elevations and lower latitudes) (Restaino et al., 2019) as well as locations with high tree density (basal area) where competition for water resources was greater (Young et al., 2017). Droughts, particularly ones involving warmer than normal temperatures have resulted in elevated tree mortality in the past (Guarín and Taylor, 2005), but the extent of tree mortality observed in the most recent drought is likely unprecedented in this region (Stephens

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et al., 2018), and the consequences will influence many ecosystem services in the future (Anderegg et al., 2013).

Prior to the drought, forests of the Sierra Nevada were vulnerable to elevated levels of tree mortality in large part due to high densities. By contrast, early foresters noted the relatively open structure of typical old-growth forests in this area, with trees arranged in groups interspersed with numerous small gaps (Show and Kotok, 1924). Forests at that time were thought to be understocked as a result of frequent fires and capable of supporting two or three times more timber if fire could be excluded (Leiberg, 1902; Show and Kotok, 1924). This argument was one of the major reasons fire suppression policies became a central tenet of forest management in the following decades.

Forests in the Sierra Nevada began to change dramatically once indigenous burning was eliminated and most other ignitions – lightning and human caused – were actively suppressed. Ingrowth quickly became established in areas formerly kept open by fire, and gaps filled with saplings and young trees (Fairbanks, 1911; Show and Kotok, 1924; Lydersen et al., 2013). Prior to the 2012–2015 drought, many forests in the Sierra Nevada were two to five times denser than they were historically (Scholl and Taylor, 2010; Collins et al., 2011; Knapp et al., 2013; Stephens et al., 2015). While increases in tree density were likely most strongly associated with alteration of the fire regime (Collins et al., 2011; Knapp et al., 2013), early logging removed the largest and most fire-resilient cohort in many areas, further homogenizing forest conditions. The resulting forest was predisposed to mortality in the event of a bark beetle outbreak or uncharacteristically-severe wildfire.

Bark beetles are natural agents of tree mortality in North American coniferous forests. Eruptions leading to widespread tree mortality occur when constraints keeping them in check are overcome, with climatic warming and reduced habitat heterogeneity among the factors which can lead to thresholds being exceeded (Raffa et al., 2008). Successful colonization of living trees requires bark beetles to overcome tree defenses that consist of anatomical and chemical components (Franceschi et al., 2005). Overcoming tree defenses can only be accomplished once a critical minimum number of beetles are recruited to mass attack the tree (Raffa et al., 1993). The number of beetles required is influenced by host tree vigor (Fettig et al., 2007), which can be improved by forest thinning. In the Sierra Nevada, tree mortality rates during and after the 2012–2015 drought were found to be considerably lower in previously thinned areas (Restaino et al., 2019). Thinning stands and reducing ladder fuels are also effective for moderating wildfire intensity and severity, especially when followed with prescribed fire (Agee and Skinner, 2005; Ritchie et al., 2007; Prichard et al., 2010; Safford et al. 2012). In the short term, prescribed fire may increase the incidence of tree mortality attributed to bark beetles, with fire wounding making some trees more vulnerable to attack (Fettig et al., 2010; Stark et al., 2013). However, in California, rates of tree mortality caused by bark beetles following prescribed fire are generally low (< 5%) under non-outbreak conditions and concentrated in small-diameter trees (Fettig and McKelvey, 2014), which may be of benefit where forests are overly dense (Stark et al., 2013).

Despite its effectiveness at preventing tree losses from bark beetles and wildfires, thinning has been controversial (DellaSala et al., 1995; Six et al., 2014), in part due to concerns about impacting habitat features associated with certain wildlife species (Dodd et al., 2003). High canopy cover is believed to be a key component of optimal habitat for raptors, including spotted owls (*Strix occidentalis*), northern goshawks (*Accipiter gentilis*), and mammals such as the fisher (*Pekania pennanti*) (Purcell et al., 2009; Tempel et al., 2016). However, other recent work suggests that high forest heterogeneity, both horizontally and vertically, may be a better metric (Eyes et al., 2017). Franklin et al. (2000) found spotted owl fitness to be greatest in areas with high complexity and abundant edge environments between older forests and other vegetation types. Nevertheless, standard thinning methods for improving forest health and reducing fire hazard typically utilize individual tree spacing guidelines, which tend not to produce patches with high canopy cover, heterogeneity, or forest edge environments. Stand structures resulting from such spacing guidelines also differ from those found in older forests (Larson and Churchill, 2008; 2012).

To better balance seemingly competing objectives of forest health, wood production, fire hazard reduction, and habitat/ biodiversity maintenance, silvicultural approaches that emphasize increasing forest heterogeneity have gained interest (O'Hara, 1998; North et al., 2009; Puettmann et al., 2009; Reynolds et al., 2013). Rather than breaking up fuel continuity among individual trees, different structures and habitats from tree clusters to small gaps are created. Leaving some trees in groups may reduce vigor of those trees, with numerous studies having shown a positive relationship between stand density and the probability of tree mortality (Das et al., 2008; Hood et al., 2016), and a negative relationship between stand density and tree growth (Stiell, 1982; Das et al., 2008). While maximizing rates of stand and individual tree growth may no longer be the primary goal in these newer heterogeneity-based approaches to forest management, it is important to examine tradeoffs, including potential tree growth and survival consequences of such prescriptions.

In this study, we evaluated the effects of experimental forest thinning and prescribed fire treatments on tree mortality and growth in a Sierra Nevada mixed-conifer forest following a severe and prolonged drought. We also investigated how tree mortality and growth differed between thinning treatments designed to generate a high degree of heterogeneity, similar to what forests historically shaped by fire once contained, relative to a more standard approach with trees thinned to a more even spacing.

2. Methods

2.1. Study area

The forest in the study area on the Stanislaus-Tuolumne Experimental Forest, near Pinecrest, California is mixed-conifer, composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), and California black oak (*Quercus kelloggii*). Elevation ranges from 1740 to 1900 m. The climate is Mediterranean, with the majority of the annual precipitation occurring during fall, winter, and spring (Cayan and Roads, 1984). Deep and well-drained loam to gravelly loam soils (Wintoner-Inville families complex) derived from granite or weathered from tuff breccia contribute to high-site productivity and rapid tree growth (Knapp et al., 2012). Fire was historically frequent in the study area, with a median return interval of 6 years (Knapp et al., 2013), but the last recorded fire occurred in 1889. The study area was selectively logged in 1928 or 1929, removing most (> 80%) of the larger trees. In the absence of fire, a much denser forest composed of a higher proportion of white fir and incense cedar developed (Knapp et al., 2013). Percentage of white fir, incense cedar, sugar pine, ponderosa/Jeffrey pine, and California black oak by density prior to the study (2009) were 50.0, 40.7, 6.0, 2.9, and 0.4, respectively. It was in this highly altered second-growth forest that the study was established.

2.2. Treatments

Three thinning treatments (high variability thin, low variability thin, and unthinned control) were nested within two prescribed burning treatments (burned and unburned), for a total of six treatments. The 'high variability' (HighV) units were thinned using a prescription designed to create a structure similar to that found in historical forests, with trees singly and in groups of varying size and density, interspersed with numerous small gaps (Knapp et al., 2012; 2017). The 'low variability' (LowV) units were marked for cutting by selecting leave trees spaced approximately 0.5 crown widths from nearest neighbors. Treatments were replicated four times (N = 24) and randomly

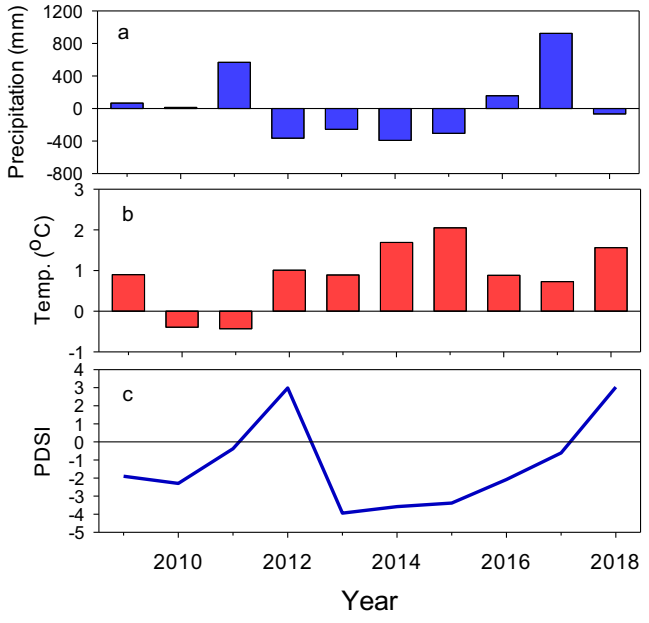

Fig. 1. (a) Precipitation departure relative to the 2000 to 2018 average (mm) at Pinecrest, California (data source: http://cdec.water.ca.gov/), (b) temperature departure from the 1980 to 2010 average (°C) across the Sierra Nevada mountains (data source: https://wrcc.dri.edu/Climate/Tracker/CA/) for water years (Oct 1 – Sept 30), and (c) Palmer Drought Severity Index (PDSI) for the same time period, based on Cook et al. (2010); data source: https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring/drought-variability.

allocated to 4-ha experimental units (*see* Knapp et al., 2017, Fig. 1, p. 230). Thinning was conducted between July and September 2011, and burn units were treated with prescribed fire in mid-November of 2013. Thinning removed ~ 75% of the trees (Table 1) and reduced basal area by > 40%, from an average of 68.0 m^2 ha^{-1} to 37.9 m^2 ha^{-1} (Knapp et al., 2017). Numbers and basal area of trees did not differ between HighV and LowV – the main difference was how the trees were arranged spatially. Density of trees > 25 cm dbh (diameter at breast height, 1.37 m) in the thinned units was similar to what was noted in an old-growth forest adjacent to the study area in 1929, but basal area was less on account of the largest trees being smaller than they were historically (Knapp et al., 2013; 2017). By favoring pines over fir and cedar, thinning moved the species composition closer to what was present historically. Prescribed burns substantially reduced the amount of accumulated surface fuel, killing about 10% of trees in the control treatment and 4% of trees in the thinned treatments. The limited mortality due to burning did not initially significantly change tree density or basal area (Knapp et al., 2017).

Thinning was completed shortly before and burning at the start of a drier and warmer than normal period. The drought intensified thereafter, with far below normal precipitation and far above average temperature in 2014 and 2015 (Fig. 1a,b). The Palmer Drought Severity Index in 2014 was the lowest in recorded history (1895–2017, — the period when instrumental records were widely available (www.ncdc.noaa.gov/cag/)) (Fig. 1c). Tree mortality became extensive throughout the southern and central Sierra Nevada during this time, including in and around the study area. The primary mortality agents were bark beetles. Based on a network of plots on the nearby Eldorado, Stanislaus, Sierra and Sequoia National Forests, Fettig et al. (2019) attributed most mortality in ponderosa and sugar pine to colonization by western pine beetle (*Dendroctonus brevicomis),* and mountain pine beetle (*D. ponderosae*), respectively. Fir engraver (*Scolytus ventralis*) was the primary mortality agent of white fir and an unknown factor (likely carbon starvation or loss of hydraulic conductance) was the primary mortality agent of incense cedar.

2.3. Data collection: Trees

In each unit, tree data were collected within a 240 m long by 15 m wide belt transect, broken into sections depending on the unit shape. Trees (≥10 cm dbh) with a midpoint growing within 7.5 m on either side of the belt transect were mapped by measuring location along the transect (X) and perpendicular distance from the transect center line (Y). Trees retained after thinning in 2011 were tagged at breast height with an individually numbered metal tag and species noted. Status (live or dead) was determined and dbh was measured every two years since thinning (2012 through 2018). This paper utilizes the three years of tree data collection following prescribed burning in 2013 (2014, 2016 and 2018) and includes data for only the trees that were alive at the 2014 measurement.

2.4. Analyses

Significant differences among treatments for all tree density, basal area, and growth variables were determined using generalized linear mixed effects models assuming a gamma distribution (PROC GLIMMIX in SAS version 9.4). Block and unit nested within block were considered random effects in the model, the remainder were fixed. Initial analyses were conducted with all fixed main effects (thinning treatment, burning treatment, and year, the latter 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 main and significant interaction effects. Even though the primary bark beetle mortality agent differs among pine species (Fettig, 2016), pines (sugar, ponderosa, and Jeffrey) were combined for some analyses due to small sample sizes for individual species. Numbers of non-conifer tree species (California black oak and Scouler's willow (*Salix scouleriana*)) in the study area were too low to analyze. Heteroscedasticity among treatments and among years 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

Table 1
Average number of live conifer trees per hectare and number of trees per hectare by species in 2014 and 2018 for thinning (HighV, LowV, Control) and prescribed burning (Burn, No burn) treatments. White fir = *Abies concolor*, incense cedar = *Calocedrus decurrens*, sugar pine = *Pinus lambertiana*, ponderosa pine = *P. ponderosa*, and Jeffrey pine = *P. jeffreyi*.

		All conifers		White fir		Incense cedar		Sugar pine		Ponderosa and Jeffrey pine	
Thinning treatment	Burn treatment	2014	2018	2014	2018	2014	2018	2014	2018	2014	2018
Control	Burn	674.0	409.7	328.6	149.0	270.5	223.3	30.0	12.5	19.8	14.2
Control	No burn	800.5	569.2	331.9	160.7	365.5	327.6	40.1	29.5	39.7	36.5
HighV	Burn	155.4	133.5	73.7	60.5	49.4	45.5	13.2	10.0	9.7	8.7
HighV	No burn	154.0	143.0	56.3	50.1	51.2	49.5	31.0	27.7	13.0	13.0
LowV	Burn	134.3	111.4	61.3	45.8	31.3	28.9	19.1	12.1	6.1	6.1
LowV	No burn	160.2	153.2	86.6	80.0	44.7	44.7	19.0	18.4	8.8	8.8

grouping variables. Significance of pairwise comparisons for main and interaction effects was determined with linear contrasts, using the Tukey adjustment for multiple comparisons.

Influence of competition on tree mortality and basal area increment (BAI) growth was evaluated for trees located in the center 5 m of each belt transect. Neighborhood competition was then estimated in radii of 5 m, 7.5 m and 10 m around each of these trees. While the 5 m radius provided a more precise measure of competition, with all circles fully within the 15 m wide belt transect along which trees were mapped, about a third of trees in thinned units did not have neighbors within 5 m. The 7.5 m and 10 m radius circles provided a less precise measure of competition, as portions of the competition circle extended beyond the 15 m wide belt transect (depending on location of the tree relative to the transect midline, between 0 and 11% of the circle and between 14 and 34% of the circle extended beyond the belt transect for the 7.5 and 10 m radii, respectively). Competition within a 7.5 m radius, with only a small portion of area outside the belt, likely provides the best balance between precision and a more accurate representation of competition influencing the variables being tested. Three indices of neighborhood competition were calculated - number of trees, basal area, and the Hegyi Competition Index, which integrates distance and size of the target and competing tree(s) (Hegyi 1974). Initial analyses showed the Hegyi Competition Index to be the strongest predictor of tree mortality and growth, so the other two were dropped. Linear mixed-effects models (PROC GLIMMIX) were used to analyze mortality from 2014 to 2018 of all conifer species combined and of individual conifer species in relation to competition, assuming a binary distribution. BAI growth in relation to competition assumed a normal distribution. For both mortality and BAI growth, thinning treatment, burning treatment, Hegyi Competition Index, thinning treatment × Hegyi Competition Index, and burning treatment × Hegyi Competition Index were fixed predictor variables. Block and unit nested within block were considered random effects. To determine how well the mortality models fit the data, we converted the data to binomial values and saved the predicted probabilities from the output of the SAS PROC GLIMMIX models for use in a logistic regression (PROC LOGISTIC) model, specifying a receiver operating characteristic (ROC) curve output.

3. Results

Between 2014 and 2018, 27% of the trees across all treatments in the study area died. Mortality was most pronounced for white fir (42%), followed by sugar pine (18%), incense cedar (12%), and ponderosa/Jeffrey pine (10%). Incense cedar and pine mortality was generally highest during the 2014–2016 period, while white fir mortality accelerated during the 2016–2018 period (Fig. 2).

3.1. Thinning and tree mortality

Change in tree (conifer) density between 2014 and 2018 was strongly influenced by prior thinning (Table 1), as shown by the significant thinning × year ($P < 0.001$) interaction (Table 2). Thinned treatments experienced less than a third of the mortality found in the unthinned controls (10.6% vs. 34.0%, respectively - both values combined across burning treatments) (Table 1, Fig. 2). The protective effect of thinning treatment on tree mortality was highly significant for all conifers combined, individual species (white fir, incense cedar), and all pines, but especially pronounced for white fir (Table 2). Linear contrasts illustrated that mortality of all conifers, white fir, incense cedar, and all pines in both the HighV and LowV thinning treatments differed significantly ($P < 0.010$) from the control. Mortality differences were not found between the HighV and LowV thinning treatments in these same analyses ($P > 0.49$). When all conifers were broken down by size class, the thinning × year interaction was significant for intermediate (25–60 cm) and larger trees (60–80 cm) trees (Appendix 1). Both the HighV and LowV thinning treatments significantly improved survival of trees in these size classes, relative to the control. Survival of small (10–25 cm) trees did not appear to be influenced by thinning (Appendix 1), while the effect of thinning approached significance for very large (> 80 cm) trees ($P = 0.089$).

3.2. Prescribed fire and delayed tree mortality

Tree mortality differed between burning treatments (Table 1) as shown by the significant burning × year interaction (Table 2). Mortality during the 2014–2018 period for trees that survived the 2013 prescribed burns was higher in the burn treatments, as expected. Mortality rate was about 10% greater with burning regardless of thinning treatment (Table 1, 2). Much of the additional delayed mortality in burn units occurred among smaller trees and in the first two years following the burns (2014–2016) (Fig. 3a, Appendix 1). In the 10–25 cm size class, 31% of trees in burn treatments died during this time, compared with 6% in unburned treatments ($P < 0.001$) (Fig. 3a). In the 25–40 cm size class, 15% of trees in burn treatment died during this time, compared with 2% in unburned treatments ($P = 0.018$) (Fig. 3a). In the 40–60 cm size class, the thinning × burning × year interaction was significant, with a difference between the Burn and No Burn treatment only found in LowV thinning treatment and only for the 2016–2018 time period ($P < 0.001$). Trees < 60 cm that died experienced more crown damage during the burns than those that lived (28% and 7% of crown volume scorched, respectively). Differences in mortality between Burn and No Burn treatments were overall much less pronounced during the 2016–2018 period (Fig. 3b). Tree mortality in the No Burn treatment was initially (2014–2016 period) spread fairly evenly across tree size classes (Fig. 3). By the 2016–2018 period, tree mortality in the No Burn treatment shifted towards the smaller tree size classes (Fig. 3).

3.3. Basal area change

Difference in live basal area between 2014 and 2018 was a function of both tree mortality and growth of surviving trees. The thinning treatment influenced basal area change for conifers overall, with the thinning × year interaction significant at $P < 0.001$ (Table 3). Basal area in the unthinned control treatments (burned and unburned) dropped by 23.4% (65.7 $m^2\ ha^{-1}$ to 50.3 $m^2\ ha^{-1}$), while basal area in the thinned units (burned and unburned) exhibited very little change (37.9 $m^2\ ha^{-1}$ to 37.8 $m^2\ ha^{-1}$, or −0.2%), with mortality essentially balanced by growth (Fig. 4a). Prior thinning prevented or reduced basal area losses for all species, but the protective effect of thinning was especially pronounced in white fir (Fig. 4b). For incense cedar and pines, thinning treatments actually gained basal area (both HighV and LowV for incense cedar, HighV for pines), compared with losses in the Control (Fig. 4 c,d). With pines, much of the basal area loss in the Control occurred during the height of the drought (2014–2016), while white fir basal area loss in all treatments was delayed, accelerating near the end or after the drought (2016–2018). There was no difference in basal area change between the HighV and LowV treatments for all conifer species combined or for individual species (Fig. 4a-d).

The burning × year interaction was significant for all conifers (Table 3), with basal area declining 12.3% across the burned treatments and 4.9% across the unburned treatments between 2014 and 2018 (Fig. 4e). The difference between the two values provides a measure of change likely caused by delayed mortality associated with fire damage, which further predisposed trees to bark beetle attack. Still, the effect of the burning treatment on basal area change was substantially less than that of thinning (Table 3, Fig. 4). Burning did not significantly influence basal area change for white fir (Table 3), as basal area declined sharply in both the Burn and No Burn treatments (Fig. 4f). Burning slightly, but significantly, reduced basal area change relative to the No Burn treatment in incense cedar and pines combined (Fig. 4 g, h).

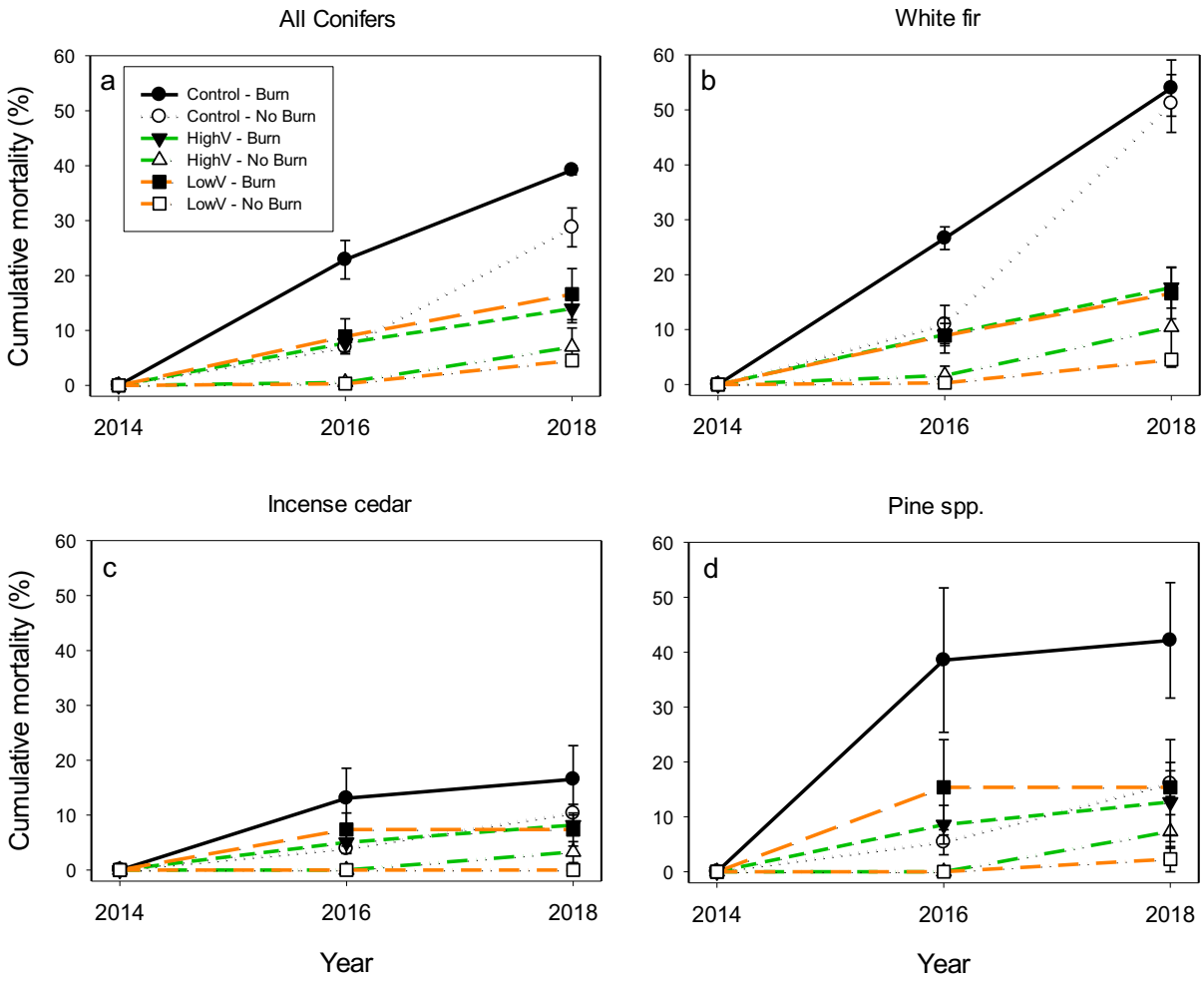

Fig. 2. Cumulative mortality for all conifers (a), white fir (*Abies concolor*) (b), incense cedar (*Calocedrus decurrens*) (c), and all pines – sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and Jeffrey pine (*P. jeffreyi*), in order of abundance) (d) in thinning (Control, HighV, LowV) and burning (Burn, No Burn) treatments from 2014 to 2018. Thinning and burning occurred in 2011 and 2013, respectively. Error bars display the standard error.

3.4. Stand and individual tree growth

Annualized basal area growth (i.e., basal area increment (BAI) summed across all trees) between 2014 and 2018 did not differ between thinning treatments ($P = 0.924$), averaging 0.615 $m^2\ ha^{-1}\ yr^{-1}$ in the control, 0.628 $m^2\ ha^{-1}\ yr^{-1}$ in HighV, and 0.615 $m^2\ ha^{-1}\ yr^{-1}$ in LowV. Basal area growth was significantly less in burned treatments compared to unburned treatments ($P = 0.036$). When growth rate of individual trees for the period from 2014 to 2018 was investigated, the thinning × burning interaction for periodic BAI was significant ($P = 0.011$). Trees in both thinning treatments (Burn and No Burn combined) had a higher average BAI than the control (Table 4). Trees in the HighV Burn treatment grew slower than trees in the HighV No Burn treatment, although this difference was marginal ($P = 0.051$) when adjusted for multiple comparisons (Table 4). A similar outcome was found for BAI of just the largest trees (> 50 cm dbh), with faster growth occurring in the two thinning treatments than in the Control (Thinning effect, $P < 0.001$). There was no difference between HighV and LowV for all basal area growth and BAI comparisons (Table 4).

Table 2
Generalized linear mixed model ANOVA results (DF = degrees of freedom for numerator, denominator) for conifer mortality (density change) and mortality by species and species groups between 2014 and 2018 following thinning (HighV, LowV, Control) and prescribed burning (Burn, No Burn) treatments. Ingrowth was not included and change is for trees that were alive in 2014. White fir = *Abies concolor*, incense cedar = *Calocedrus decurrens*, and Pine spp. includes sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and Jeffrey pine (*P. jeffreyi*). The Thin × Burn and Thin × Burn × Year interactions were not significant for all analyses and therefore not included in the final model. DF are for the model including Thin × Year and Burn × Year interactions and the dominator DF was greater if interactions were removed in the final model.

Variable	DF	All conifers		White fir		Incense cedar		Pine spp.	
		— F	*P*	F	*P*	F	*P*	F	*P*
Thin (T)	2, 14	402.29	< **0.001**	56.79	< **0.001**	39.20	< **0.001**	5.73	**0.015**
Burn (B)	1, 6	3.05	0.131	0.74	0.423	1.16	0.323	7.81	**0.031**
Year (Y)	2, 40	123.70	< **0.001**	68.16	< **0.001**	24.36	< **0.001**	15.82	< **0.001**
T × Y	4, 40	27.50	< **0.001**	19.69	< **0.001**	4.28	**0.006**	3.81	**0.010**
B × Y	2, 40	13.06	< **0.001**	–	–	6.60	**0.003**	7.13	**0.002**

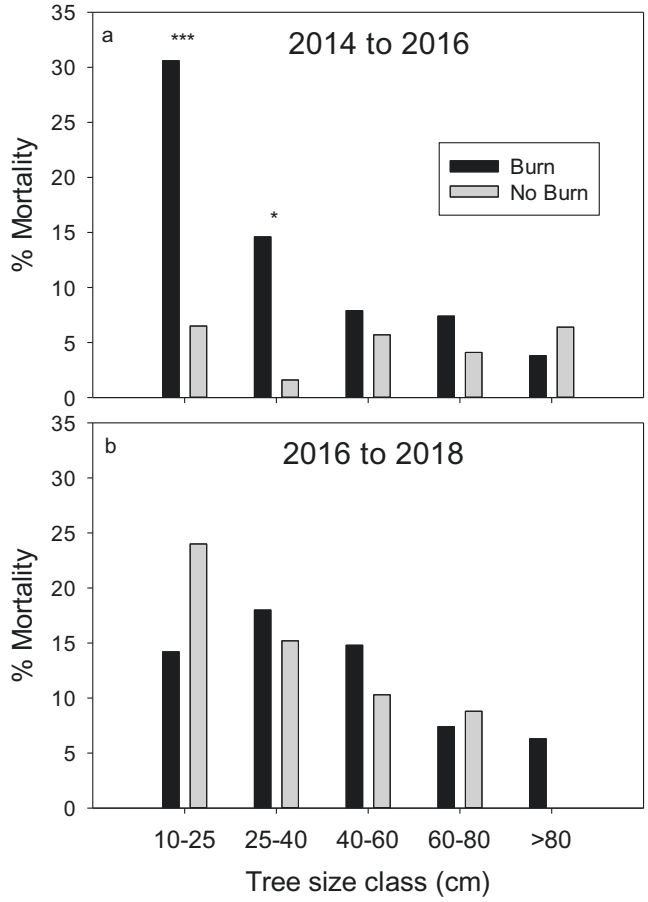

Fig. 3. Conifer mortality by tree size class (dbh) in Burn and No Burn units between 2014 and 2016 (a), and between 2016 and 2018 (b). Significant differences between burning treatments in each time period are denoted by * ($P < 0.05$) and *** ($P < 0.001$).

3.5. Mortality, growth and inter-tree competition

Results of tree mortality and growth analyses including the Hegyi Competition Index as a covariate were very similar for all neighborhood sizes (radii) investigated. The 7.5 m radius results likely best captures the competitive effects given the limitations of the relatively narrow 15 m wide belt along which trees were mapped, and these are therefore the data presented.

For all conifer species combined, probability of mortality within treatments increased with neighborhood competition, with significant Hegyi Competition Index × thinning ($P = 0.007$) (Fig. 5a) and Hegyi Competition Index × burning ($P = 0.005$) interactions (Fig. 5b). Tree mortality was highest in areas with more competition within the controls, but areas with more competition within thinned units also exhibited higher tree mortality. Mortality was especially pronounced when trees with more competition were also burned. When the data were broken down by individual species and all pines, a relationship between competition and mortality existed just for white fir (Hegyi Competition Index × thinning and Hegyi Competition Index × burning interactions significant at $P = 0.029$ and $P = 0.003$, respectively). No Hegyi Competition Index main or interaction effect was found for incense cedar or for all pines combined. The ROC statistic was 0.73, 0.77, 0.84, and 0.75 for the all conifer, white fir, incense cedar, and all pines combined models.

Trees with more competition also experienced slower BAI growth, with variation in response among thinning treatments, as shown by a significant Hegyi Competition Index × thinning interaction ($P < 0.001$) and a significant Hegyi Competition Index main effect ($P < 0.001$) for all conifer species combined. Graphing out the interaction demonstrated that the unthinned control had a greater range of Hegyi Competition Index values and the resulting slope of the BAI response differed from both thinning treatments (Fig. 6). When broken down by individual species and species groups, the negative effect of competition on BAI was most pronounced for white fir and incense cedar (Hegyi Competition Index × thinning interaction and Hegyi Competition Index main effect significant at $P = 0.001$ and $P < 0.001$, respectively for white fir and Hegyi Competition Index × thinning interaction and Hegyi Competition Index main effect both significant at $P < 0.001$, for incense cedar). The Hegyi Competition Index main effect was significant ($P = 0.015$) for all pines combined. The Hegyi Competition Index × burning interaction was not significant for any variable - all conifers combined and individual species.

4. Discussion

4.1. Influence of stand thinning on tree mortality and growth

Tree mortality during the 2012–2015 drought was substantially reduced by thinning implemented in 2011, a finding in line with expectations and other reports (e.g. Restaino et al., 2019). All tree species (white fir, incense cedar, and pines combined) benefited from thinning, but the effect was most pronounced for white fir - the most abundant tree species on our experimental units. Previous research has shown drought-associated white fir mortality to be strongly associated with stand basal area (Ferrell et al., 1994). The test in our study is strengthened by an experimental design with adjacent replicated units, which allows the magnitude of the effect of treatments on tree mortality and growth to be determined without the influence of confounding factors such as variation on drought severity, productivity, and bark beetle pressure. The difference between thinned and unthinned treatments was even starker for change in basal area, a metric that combines

Table 3
Generalized linear mixed model ANOVA results (DF = degrees of freedom for numerator, denominator) for conifer basal area change and basal area change by species between 2014 and 2018 for thinning (HighV, LowV, Control) and burning (Burn, No Burn) treatments. Ingrowth was not included and change is therefore a function of mortality and growth of trees alive in 2014. White fir = *Abies concolor*, incense cedar = *Calocedrus decurrens*, and Pine spp. includes sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and Jeffrey pine (*P. jeffreyi*). The Thin × Burn and Thin × Burn × Year interactions were not significant for all analyses and therefore not included in the final model. DF are for the model including Thin × Year and Burn × Year interactions and the dominator DF was greater if interactions were removed in the final model.

Variable	DF	All conifers		White fir		Incense cedar		Pine spp.	
		F	*P*	F	*P*	F	*P*	F	*P*
Thin (T)	2, 12	10.93	**0.001**	5.08	**0.022**	14.88	< **0.001**	0.25	0.785
Burn (B)	1, 6	0.01	0.925	1.00	0.355	0.14	0.726	6.07	**0.049**
Year (Y)	2, 40	42.57	< **0.001**	36.85	< **0.001**	8.37	< **0.001**	2.38	0.106
T × Y	4, 40	38.70	< **0.001**	17.87	< **0.001**	6.05	< **0.001**	2.92	**0.033**
B × Y	2, 40	8.08	**0.001**	–	–	3.61	**0.036**	3.25	**0.049**

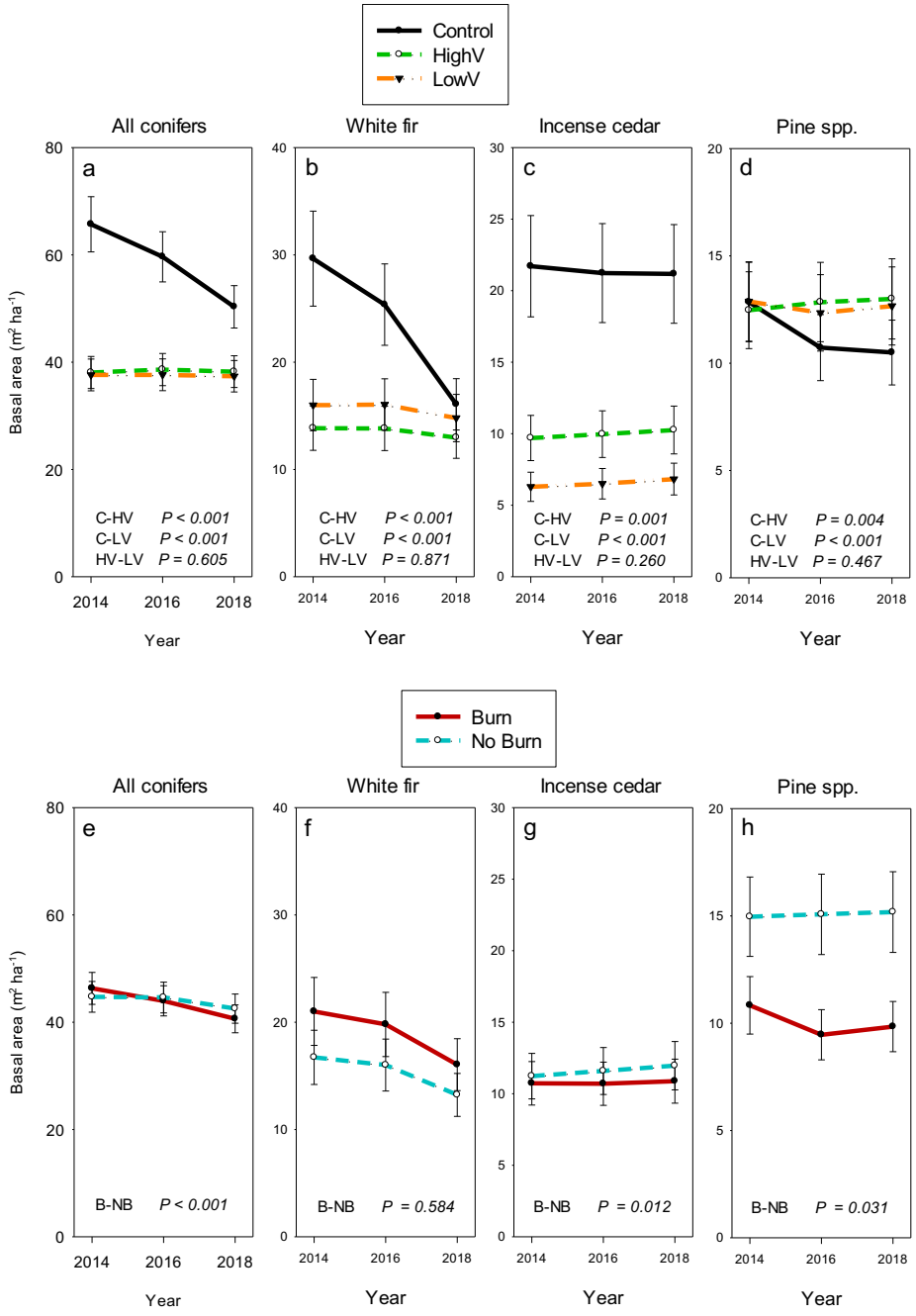

Fig. 4. Basal area by species in 2014, 2016, and 2018 among thinning treatments (Control, HighV, LowV) (a-d) and between burning treatments (Burn, No Burn) (e-h). Error bars display the standard error, and *P* values are for two-way contrasts testing differences in the rate of change between 2014 and 2018. Note that species have different y-axis scales.

both mortality and growth. A 34% mortality rate between 2014 and 2018 in the unthinned controls translated into a 23% drop in basal area over time, while an 11% mortality rate in the thinned treatments resulted in no basal area change over the same time period. The lack of basal area change in thinned units was partly due to mortality concentrated in smaller tree size categories, with small trees contributing little to stand basal area. Mortality in the thinned units was also balanced by faster growth of residual trees (Table 4, Fig. 4). While individual trees in thinned units grew faster, the unthinned controls contained far more trees. Somewhat surprisingly, stand basal area growth (i.e. amount of live basal area ha^{-1} gained over time) did not differ between treatments. It often requires years for basal area growth in thinned units to approach growth of unthinned stands as it takes time for tree canopies to grow and fill the empty space (Oliver and Larson, 1996). In this case, growth did not differ, likely in large part because of the higher tree mortality in the controls.

Substantial research has been devoted to mechanisms by which thinning reduces bark beetle-caused tree mortality. Skov et al. (2004) found that thinning increased predawn water potential relative to unthinned control trees, with the greatest difference in drought years. Reducing stand basal area through thinning generally increases the BAI (Kolb et al., 2007) and resin duct area (Hood et al., 2016) of the retained trees. Resin production has been shown, at least in some forests, to be strongly positively correlated with BAI (McDowell et al., 2007) and negatively correlated with stand basal area (Kolb et al., 2007). Resin production is the main means by which conifers resist bark beetle attack. Allocation to growth of phloem and xylem elements may also lead to more resin ducts being produced, while resource limitation

Table 4
Periodic annual basal area increment (BAI) for the period between 2014 and 2018 by treatment for all trees and for the largest trees (> 50 cm dbh) following thinning in 2011 and burning in 2013. Means (standard error in parentheses) are averaged across burning treatments when the thinning × burning treatment interaction was not significant. Different letters denote significant differences among treatments.

Thin treatment	Burn treatment	BAI	BAI - trees > 50 cm
		$cm^2\ yr^{-1}$	
Control	Burn	14.15[b] (1.24)	33.71[b] (2.42)
Control	No burn	12.08[b] (1.06)	
HighV	Burn	37.50[a] (3.29)	58.86[a] (4.23)
HighV	No burn	55.86[a] (4.91)	
LowV	Burn	46.79[a] (4.11)	62.88[a] (4.52)
LowV	No Burn	48.45[a] (4.26)	

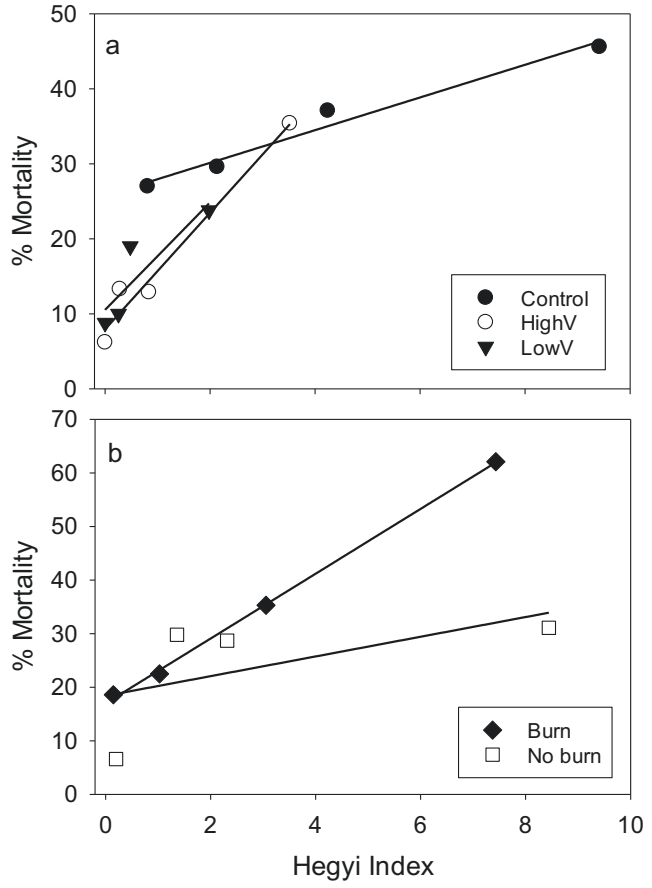

Fig. 5. Percentage tree mortality among thinning treatments (Control, HighV, LowV) (a) and between burning treatments (Burn, No Burn) (b) at different levels of competition. Competition was for trees growing < 7.5 m from the target tree and competition levels are the average Hegyi Competition Index for quartiles of the dataset sorted from small to large.

could mean carbohydrates are used for non-defense mechanisms instead. While increased tree vigor and growth are generally tied to decreased mortality risk (Fettig et al., 2007), the link between growth and resin duct formation is not universal (Christiansen et al., 1987) and therefore the mechanisms may vary. Lower tree densities also influence microclimate within stands that affect bark beetle phenology and voltinism as well as fecundity and fitness of predators, parasites and competitors (Fettig et al., 2007). Thinning can disrupt pheromone plumes used for recruiting conspecific bark beetles during initial phases of host tree colonization (e.g. Thistle et al., 2004). Thinning also

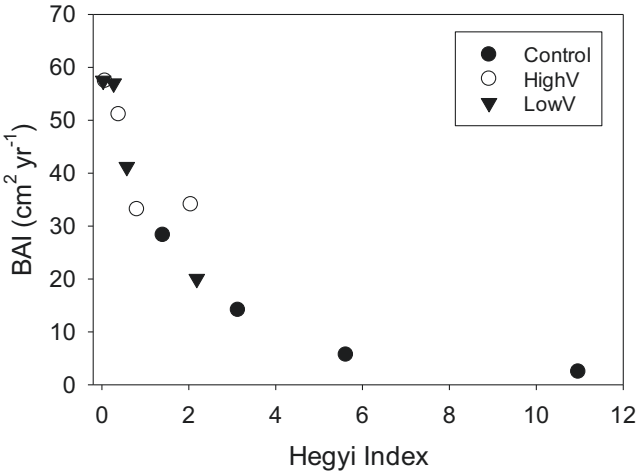

Fig. 6. Basal area Increment (BAI) growth among thinning treatments (Control, HighV, LowV) at different levels of competition. Competition was for trees growing < 7.5 m from the target tree and competition levels are the average Hegyi Competition Index for quartiles of the dataset sorted from small to large.

increases the distance between hosts, thus negatively impacting host finding and colonization successes (Fettig et al., 2014). Because thinning impacts both host vigor and bark beetle dispersal dynamics, the ultimate mechanism may be a challenge to decipher, but all may play a role to some degree.

4.2. Tree mortality among species and over time

During our study period, mortality was most pronounced in white fir, and while mortality of pines was elevated above background levels, rates were considerably lower than those reported in other areas of the central and southern Sierra Nevada. Both Fettig et al. (2019) and Restaino et al. (2019) noted that of all mixed conifer forest tree species, ponderosa pine had the highest mortality rate, followed by sugar pine, white fir and incense cedar. Fettig et al. (2019) reported 89.6% of ponderosa pine in their plots died between 2014 and 2017. Restaino et al. (2019) reported pine mortality was positively associated with conspecific tree density and the relative abundance of ponderosa pine in our study area was low compared with sites sampled by Fettig et al. (2019) and Restaino et al. (2019). It is possible that insufficient hosts (numbers of ponderosa pine) existed to allow populations of western pine beetle to rapidly increase to epidemic levels. The modest mortality of ponderosa pine in our study illustrates the possible benefits of maintaining a diversity of tree species, thereby reducing the dominance of any one bark beetle host. On the other hand, mortality of white fir, the most common species in the study area and at well above historical densities on account of fire exclusion (Knapp et al., 2013), was considerable (Fig. 2).

While the drought substantially increased mortality of all conifer species, peak mortality of white fir was delayed until 2016 and 2018 (Fig. 2), after normal to above normal precipitation returned (Fig. 1). One possible explanation was that despite the slightly above average precipitation, the winter of 2016 was still warmer than normal and PDSI didn't fully recover until 2018. Thus, trees remained somewhat drought stressed. In addition, peak mortality is often delayed because of the time needed for bark beetle populations to build up to outbreak levels. Once numbers are high, even less stressed trees may be colonized and killed. Lagged mortality with this drought, especially for white fir has been noted by others (Pile et al., 2019). In northern Arizona, Kane et al. (2014) reported relationships between most climatic variables (e.g., temperature, precipitation, and PDSI) and tree mortality were lagged by one to four years.

Another interesting feature of the tree mortality episode was the

tree size classes most impacted and how this changed with time. Mortality in unburned treatments was initially (2014–2016) dispersed across all tree size classes, but later (2016–2018) became more concentrated in the smaller size classes (Fig. 3). Smaller trees were typically growing in the shade of larger trees and therefore with elevated competition for light and water. Poor health may have reduced their capacity to respond quickly to improving growing conditions, leaving them vulnerable to bark beetle attack. Our 2018 field crews noted unusually abundant fresh pitch streaming from entrance holes present on nearly every white fir across the range of tree sizes. It is therefore also possible that the smaller diameter trees were simply the ones more likely to be girdled and killed by gallery formation.

When compared to other nearby locations affected by the 2012–2015 drought, the lower levels of tree mortality and smaller tree size classes impacted in our study may be due to differences in drought intensity. Farther south in the Sierra Nevada, where the drought was even more severe, levels of tree mortality were higher, and highest for moderate to large trees (Fettig et al., 2019; Restaino et al., 2019). Though still extraordinarily dry, the central Sierra Nevada received more precipitation and experienced a lesser forest water deficit – an index incorporating climatic water deficit and forest basal area/competition (Young et al., 2017), and a less pronounced cumulative precipitation – evapotranspiration overdraft (Goulden and Bales, 2019). Both metrics showed a strong positive relationship with tree mortality across the Sierra Nevada (Young et al., 2017; Goulden and Bales, 2019). Deep, productive soils at our site may have also buffered against more severe drought stress.

4.3. Influence of prescribed fire on tree mortality and growth

Tree mortality from prescribed fire can be immediate or it can be delayed, as a result of fire injuries to the crown, bole, or roots, which may increase susceptibility to climate stressors, bark beetles, and other factors (Hood et al., 2018). Some delayed mortality is normal and may be beneficial if the goal is to reduce stand density or detrimental if stand density targets have already been reached. In this study, it was a bit of both, depending on treatment (control vs. thinning), which can complicate interpretation. Much of the delayed tree mortality appeared to be relatively transient, occurring in the first two years, and mostly in the smaller tree size classes (Fig. 3). While van Mantgem et al. (2011) noted elevated mortality up to six years post-burning, we could not detect significant differences in mortality rate between the Burn and No Burn treatments beyond the first two full seasons following prescribed burns.

Even though pines are generally thought to be more fire resistant than white fir and incense cedar (Agee and Skinner, 2005), delayed mortality following prescribed burning was greatest for pines and not significant for white fir. Incense cedar was intermediate. Once mature, the bark of all species at our study site is relatively thick, but a long fire-free period may have left the pines more vulnerable to fire because of bark fragments that dehisce and accumulate at the base of the tree over time. Bark of white fir and incense cedar, on the other hand, stays on the tree bole. Thus the heat pulse experienced at the base of pines may have been elevated over that of white fir and incense cedar and unprecedented compared with historical conditions when fire occurred at median intervals of ~ 6 years (Knapp et al., 2013). Elevated levels of delayed mortality of large (e.g., > 50 cm dbh) pines following re-introduction of fire after a long absence has been noted by others (Swezy and Agee, 1991; Kolb et al., 2007; Fettig and McKelvey, 2014), both under drought and non-drought conditions.

Delayed mortality following prescribed burning was especially pronounced for trees with the greatest neighborhood competition, which were predominantly located in unthinned control units (Figs. 2, 5). Pines, but sugar pine in particular, fared poorly in the unthinned control following burning, with mortality from the combined stressors far exceeding mortality found in treatments with just the stress of excess density (unburned controls) or just the stress of prescribed fire damage (thinned treatments) (Table 1, Fig. 2). Multiple stressors including competition and drought have been found to compound delayed mortality from fire injury in other studies (van Mantgem et al., 2013, 2018). It should be noted that the sequence of stressors differs, with the fire the most proximal stressor in the van Mantgem et al. (2013, 2018) studies and drought the most proximal stressor in our study. Based on our data, thinning prior to reintroducing fire may reduce mortality of desired trees during droughts, especially for pines.

Most studies of burning have reported minor to no long-term negative effects on tree growth (Peterson et al., 1994; Busse et al., 2000; Scherer et al., 2016, but see Fajardo et al., 2007). Where burning reduces the density of competing trees, growth rates may increase (van Mantgem et al. 2016). In our study, direct mortality due to fire did not reduce stand basal area significantly and evidence for reduction in growth due to fire injury was weak. For one, many of the trees most affected by prescribed fire (i.e. highest percentage of crown scorch) died during the drought and are therefore not included in the growth measurements. In addition, the trend towards lower BAI in the burned versus the unburned HighV treatments (marginally non-significant when *P* values were corrected for the number of observations), might be explained by somewhat higher levels of bark char in this treatment compared to the others. Two of the three thinned and burned units that experienced the highest bark char were in the HighV treatment. This bark char can slough off over time, reducing outer bark tree diameter without necessarily impacting wood accretion. Preliminary analyses of increment cores taken from a subset of trees indicated no difference in wood growth between the HighV burned and HighV unburned treatments (A. Bernal, unpublished data).

4.4. Management implications

While the 2012–2015 drought was exceptional, excess tree density relative to historical conditions greatly elevated the impacts of drought on forests of the region. Our study suggests that if forests had been closer to their historic densities, tree mortality would likely not have been nearly as severe. With warmer droughts and greater variability in weather conditions increasing in our warming climate, reducing forest basal area may be critical for decreasing the severity of such mortality episodes in the future (Bradford and Bell, 2017; Vose et al., 2018). Mechanical thinning is the tool of choice for reducing basal area on most National Forest System lands, but the challenge is in balancing forest health and growth benefits with other forest management goals such as maintaining or creating habitat for a diverse array of non-tree species. This focus on multi-species management has elevated interest in thinning approaches designed to generate a higher degree of heterogeneity, not only in the Sierra Nevada (North et al., 2009), but in many other forest types adapted to frequent fire (Reynolds et al., 2013; Addington et al., 2018).

Our findings show that both thinning treatments – LowV and HighV – reduced tree mortality substantially. Importantly, HighV did not sacrifice tree survival or growth relative to the more standard even crown spacing treatment – a concern of stakeholders with a forest-products focus. While neighborhood density (Hegyi Competition Index) was positively associated with tree mortality and negatively associated with growth in all treatments, the effect of trees left in groups in HighV on mean treatment mortality and growth may have been limited because less than a third of the area within HighV stands (~32%) contained medium (4–9) and large (≥10) groups of trees, while 41% of the area contained small clumps of 2–3 trees and 27% of the area was in gaps or occupied by individual widely spaced trees (A. Bernal, unpublished data). Elevated mortality and reduced growth of trees left in groups may have also been balanced by the lower than average mortality and higher than average growth of trees left at wider than standard spacing. Some mechanical thinning occurred even within tree groups and groups were generally surrounded by more open areas including gaps. Even

trees in groups therefore had less competition and greater access to light and soil moisture compared to trees prior to thinning. Proximity to gaps increased the growth of residual trees in a moist coastal Washington (USA) forest (Roberts and Harrington, 2008). York and Battles (2008) found that a thinning-induced growth release extended to trees up to 10 m from gap edge. The size and shape of gaps therefore likely plays a role, with fine scale heterogeneity increasing the proportion of trees that may benefit. Our results illustrate the possibility that HighV can provide a greater diversity of habitat conditions without sacrificing carbon sequestration and/or wood production, at least in the short-term.

While prescribed burning increased tree mortality somewhat, thinned and burned treatments still experienced much lower mortality relative to the untreated controls. Reducing a century or more of accumulated surface fuel with prescribed fire is critical for enhancing forest resilience to wildfire – another increasing threat. Without prescribed fire, heavy surface fuels can leave even thinned stands vulnerable to wildfire burning under extreme conditions (Agee and Skinner, 2005; Ritchie et al., 2007; Safford et al., 2012; Fernandes 2015). Fire also shapes the spatial dynamics of regeneration which is key to maintaining forest pattern and the eventual development of old-growth characteristics (Binkley et al., 2007). Another potential benefit of prescribed fire is that burning may stimulate resin production, increasing the capacity of trees to resist bark beetle attack (Perrakis and Agee, 2006).

The effectiveness of prescribed fire for treating surface and ladder fuels to reduce the incidence of passive crown fire is well supported by modeling of predicted fire behaviors (Stephens et al., 2009) and by empirical research (Ritchie et al., 2007). The combination of mechanical thinning and prescribed fire has been shown in numerous studies to most rapidly restore ecological processes (McIver et al., 2013). Thinning designed to increase structural heterogeneity, prior to burning, adds another wrinkle to habitat enhancement, potentially benefiting a broader array of forest species. With climatic variation, including extreme droughts, predicted to increase (Swain et al., 2018), retaining and enhancing a variety of stand structures and species assemblages may allow forests to adapt to a greater range of uncertain future conditions (Millar et al., 2007; O'Hara and Ramage, 2013) and improve resilience to wildfire (Koontz et al., 2020).

CRediT authorship contribution statement

Eric E. Knapp: Conceptualization, Methodology, Project administration, Funding acquisition, Formal analysis, Writing - original draft. **Alexis A. Bernal:** Formal analysis, Funding acquisition, Writing - original draft. **Jeffrey M. Kane:** Writing - original draft. **Christopher J. Fettig:** Writing - original draft. **Malcolm P. North:** Conceptualization, Funding acquisition, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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