

Longer-term impacts of fuel reduction treatments on forest structure, fuels, and drought resistance in the Lake Tahoe Basin



Kathryn E. Low^{a,*}, Brandon M. Collins^{b,c}, Alexis Bernal^a, John E. Sanders^a, Dylan Pastor^a, Patricia Manley^d, Angela M. White^c, Scott L. Stephens^a

^a Department of Environmental Science, Policy, and Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, CA 94720, USA

^b Center for Fire Research and Outreach, University of California, Berkeley, 130 Mulford Hall, Berkeley, CA 94720, USA

^c USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA

^d USDA Forest Service, Pacific Southwest Research Station, 2480 Carson Road, Placerville, CA 95667, USA

ARTICLE INFO

Keywords:

Mixed-conifer
Thinning
Longer-term impacts
Forest structure
Woody fuels
Drought
Resistance

ABSTRACT

Sierra Nevada mixed-conifer forests have undergone significant changes in structure and composition and are increasingly vulnerable to altered disturbance regimes and climate-related extreme events. Fuel reduction treatments, including thinning and follow-up surface fuel treatments, can reduce this vulnerability by creating forest structural and woody fuel conditions that not only allow forest stands to mitigate wildfire, but also alleviate individual tree stress. However, direct observations that quantify these longer-term effects are lacking. This study compares observed changes in forest structure, tree species composition, and downed woody fuel loads across three distinct time periods: pre-treatment, 1 yr post-treatment, and 10 yr post-treatment. Additionally, using tree ring data, we assessed whether treatments affected individual tree resistance to a severe statewide drought (2012–2015). Thinning treatments were able to effectively reduce tree density and basal area, increase the retention of both larger-sized and shade-intolerant trees, and mitigate tree mortality. Treatments were also associated with significantly lower coarse woody fuel and snag basal area. Snag basal area and time since treatment were related to the accumulation of fine and coarse woody surface fuel loads. Tree ring information indicated that treatments improved drought resistance as well, especially in units with lower residual live basal area. This study complements previous studies on fuel reduction thinning by demonstrating that these treatments have lasting effects on forest structure, which also confers a degree of drought resistance.

1. Introduction

The impacts associated with altered fire regimes, past forest management practices, and more recently changing climatic conditions are common throughout western North American forests (Hessburg et al. 2019). In forests adapted to frequent-fire, historical stand structure consisted of larger trees, lower tree densities, and spatial and structural heterogeneity (Fulé et al., 1997; Brown et al., 2008; Larson and Churchill, 2012; Hagmann et al., 2013; Fry et al., 2014; Collins et al., 2015; Stephens et al., 2015). Contemporary conditions in these forests are characterized by lower proportions of shade-intolerant species and considerably greater tree densities, which have contributed to greater homogeneity (Scholl and Taylor, 2010; Knapp et al., 2013; Collins et al., 2017). These changes are associated with reductions in tree vigor due to increased competition for resources and greater accumulation and continuity of downed woody fuels (Taylor et al. 2014). In addition

to changes in forest demographics, recent accumulated water deficits have led to decreases in forest productivity and increased tree mortality (Allen et al., 2010; Adams et al., 2012; Sohn et al., 2016). As warming continues to influence mortality rates through water deficits and drought stress (van Mantgem et al. 2009), restoring forests to a state that resembles their historic structure and composition or that anticipated in the future may be critical to ensure forest conservation (Stephens et al., 2010; Liang et al., 2018).

Fuel reduction treatments have been applied to millions of hectares of fire-excluded forests throughout the western US (Schoennagel and Nelson, 2011; Vaillant and Reinhardt, 2017). These treatments aim to reduce wildfire hazard by reducing the amount and continuity of surface and ladder fuels (Agee and Skinner 2005). Objectives can be met by either thinning trees using chainsaws or heavy equipment, by using prescribed or managed wildfire, or a combination of the two methods. While designing effective fuel reduction treatments is well understood,

* Corresponding author at: 130 Mulford Hall, University of California, Berkeley, Berkeley, CA 94720, USA.

E-mail address: kathrynelow@berkeley.edu (K.E. Low).

implementation “on-the-ground” is well below what is needed to alter current rates of stand-replacing fire effects (North et al., 2012; Stevens et al., 2017; Vaillant and Reinhardt, 2017; Liang et al., 2018). Furthermore, even when treatments are implemented, several site-specific characteristics can limit the amount and size of material removed. For example, in the Lake Tahoe Basin, mechanical equipment cannot be used on slopes > 30% (Tahoe Regional Planning Agency code 71.4E; TRPA, 2004) and special considerations are recommended for areas near riparian zones or breeding areas of protected species (North et al. 2015). These site-specific restrictions can limit the intensity of treatments, which can impact achievement of objectives (e.g. fire hazard, forest health) (Lydersen et al., 2019; Stephens et al., 2019).

Previous studies have demonstrated that fuel treatments may have a lifespan of approximately 10–15 years, after which time tree ingrowth and accumulation of woody fuels diminish treatment effectiveness (Stephens et al., 2012; Martinson and Omi, 2013; Foster et al., 2020). However, this understanding is based on limited information, i.e., single study sites, reliance on model projections, or retrospective studies that lack longitudinal data. As such, broader inferences about longer-term treatment effects are fairly tenuous. Forest dynamics following fuel reduction treatments can vary considerably even within an individual site depending on treatment type and intensity (Collins et al. 2019). There is additional variability among sites as a function of productivity and species composition. Further investigation into how these factors influence forest stand structure and woody fuels over time is necessary to provide forest managers more robust information on treatment impacts.

Thinning treatments can improve individual tree vigor, thus reducing the impacts of drought on forest stands (Spittlehouse and Stewart, 2003; Chmura et al., 2011; Sohn et al., 2013, 2016; Collins et al., 2014). Although California experiences drought events semi-frequently, the most recent drought from 2012 to 2015 was the most severe drought in the last century (Griffin and Anchukaitis, 2014; Lund et al., 2018). It highlighted just how vulnerable Sierran mixed-conifer forests are to large-scale mortality from natural disturbance agents (Collins et al. 2019). Studies on how thinning treatments affect tree- or stand-level drought stress are typically centered around one stand and/or consider one stand age or thinning regime (Misson et al., 2003; Skov et al., 2004; Brooks and Mitchell, 2011; Chmura et al., 2011; Sohn et al., 2016). Further investigations into the long-term impacts of thinning treatments applied in fire-prone stands can provide meaningful assessments of forests' response to climate-related stress events and the efficacy of management options to preserve forest health (Teets et al. 2018).

This study aims to assess how thinning in forests impacted by long-established fire exclusion and early timber harvesting altered forest structural conditions in the short- and longer-term (~10 yr). The study employs a robust before-after-control impact (BACI) study design to characterize treatment effects, which opportunistically also captured a range of thinning intensities across experimental units. The range of intensities were a product of implementation constraints brought about by forest management resource protection measures (*sensu* Lydersen et al. 2019). We hypothesize that thinning treatments would effectively alter and maintain desired forest stand structure, but not result in a dramatic change in downed woody fuels. We also expect treatments to positively influence a tree's drought resistance, which we anticipate to be more pronounced with greater treatment intensity. We used data from permanently monumented field plots that were established prior to treatment, then re-measured 1-year and approximately 10-years after treatment to test our hypotheses. The main goals of this study were to (1) describe and analyze changes in forest structure and composition; (2) compare downed woody fuel loads across treated and untreated controls and characterize temporal changes in fuel loads as an element of forest structure; (3) understand how thinning treatments impacted overstory tree resistance to the most recent severe drought (2012–2015).

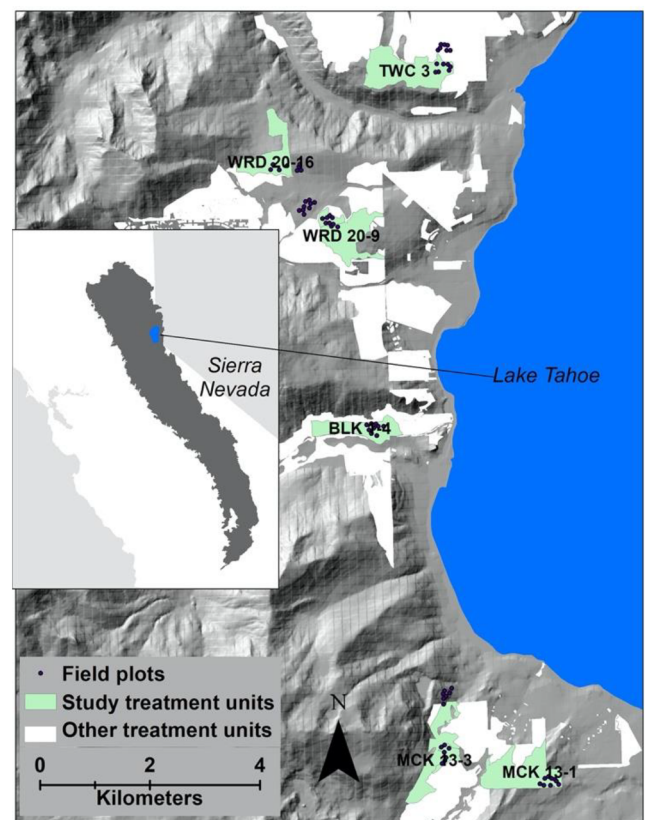


Fig. 1. Map of study sites, which were along the west shore of Lake Tahoe, California U.S.A.

2. Materials and methods

2.1. Study sites

This study took place in six sites along the west shore of Lake Tahoe, California, U.S.A. (Fig. 1). Elevation for these study sites ranged between 1900 and 2200 m with slope gradients varying from 0 to 40%. Vegetation on these sites is characterized as upper elevation mixed-conifer forests, comprised of six dominant canopy species: red fir (*Abies magnifica*), white fir (*A. concolor*), incense-cedar (*Calocedrus decurrens*), lodgepole pine (*Pinus contorta*), Jeffrey pine (*P. jeffreyi*), and sugar pine (*P. lambertiana*). Climate in this area is characterized by cool, wet winters and hot, dry summers. On the northwest shore at Tahoe City, CA, the majority of precipitation falls as snow from December to March with very little falling as rain between May and October. While 30-year averages (1980–2010) in this area showed an average annual temperature of 6.7 °C and average total precipitation of 1060 mm, temperatures during the recent severe drought were 11–25% higher than average (Appendix A) and total precipitation was 21–41% lower than average (PRISM Climate Group 2020). Study sites were chosen based on a shared silvicultural objective to mitigate the impacts of long-established fire exclusion and early timber harvesting. In these forests, fire exclusion and early timber harvesting significantly altered forest structure and composition. The treatments in our study sites (and elsewhere throughout the Sierra Nevada) sought to shift forest structure to better align with forest conditions prior to these major changes (Taylor et al. 2014). This involved the removal of subdominant and understory trees and the retention of large trees. An additional requirement for site selection was that treatments were scheduled to be completed within the same 1–2-year window of time. Plots were located in four watersheds: Blackwood Creek (BLK), McKinney Creek (MCK), Twin Crag (TWC), and Ward Creek (WRD).

Table 1

Generalized treatment descriptions for study units. Upper DBH limit refers to the largest tree sizes available for removal. Treatment intensity refers to the percent of total basal area change immediately following thinning treatments. DBH – diameter at breast height.

Unit	Treatment type	Upper DBH limit (cm)	Activity fuels treatment	Treatment intensity (% BA removed)
WRD 20–16 T, PAC	Hand thin	25.4	Pile/burn	10.0
MCK 13–1 T	Hand thin	35.6	Pile/burn	25.4
TWC 3 T, PAC	Mechanical	60.9	Mastication	33.8
WRD 20–9 T	Mechanical	60.9	Mastication	45.4
BLK 1–4 T, PAC	Mechanical	60.9	Mastication	37.6
MCK 13–3 T	Mechanical	76.2	Mastication	67.9
WRD 20–16C	Control	NA	NA	NA
TWC 3C	Control	NA	NA	NA
WRD 20–9C	Control	NA	NA	NA
MCK 13–3C	Control	NA	NA	NA
MCK 13–1C	Control	NA	NA	NA
BLK 1–4C	Control	NA	NA	NA

2.2. Treatments

From 2007 to 2009, units on the west shore were covered under three different National Environmental Policy Act (NEPA) planning processes, which varied in terms of desired conditions and fuel treatment prescriptions (Table 1). Planned treatments included hand thinning of trees ≤ 25.4 cm diameter with slash piling and mechanical thinning of trees < 76.2 cm in diameter with slash masticated with maximum allowable harvestable tree size ranging from 25.4 to 76.2 cm in diameter (Table 1). In addition to live tree retention guidelines, all treatments specified the retention of 3 snags and 3 downed logs per acre in the largest diameter classes. Treatment prescriptions prioritized the retention of conifer species in this order: (1) *P. lambertiana*, (2) *P. jeffreyi*, (3) *A. concolor*/*A. magnifica*, *C. decurrens*, (5) *P. contorta*. Three of the treated units were located in protected activity centers (PACs) for California Spotted Owl and Northern Goshawk. Treatments within these units were prepared in consultation with wildlife biologists to maintain or enhance habitat conditions while meeting fuel reduction objectives (i.e. retention of larger trees, more snags, two canopy layers and a higher minimum percentage of residual canopy closure).

Treatments were applied within approximately half of each unit so that each treated section of a unit had a paired control. This study included four mechanically-treated units and two hand-treated units, which were dictated by the protection of valuable habitat for species of concern (Table 1). In mechanically treated units, merchantable trees were felled and delimbed with a cut-to-length forwarder while sub-merchantable trees were masticated in place. Activity fuels from thinning were masticated into wood chips < 10 cm in length and to a fuelbed depth of < 15 cm. In hand-treated units, trees were chainsaw felled and hand-piled, with piles burned in the following 6–24 months. Two control units, BLK 1–4 C and MCK 13–1 C were not remeasured in 2018 due to the implementation of unexpected fuels treatments in those units. Units were named using a three-letter code based on geographic location and end with either a “T” or “C” depending on whether the unit was treated (T) or left as a control (C).

2.3. Vegetation and fuels measurements

In 2006, a network of macroplots was established by overlaying a 150×330 m grid over each unit to collect data on fuels and vegetation. The macroplots provided a grid from which 8–10 vegetation plots were randomly selected for each unit. Data for these plots were collected in 2006 (pre-treatment) and remeasured in 2007–2010 (1 yr post-treatment) and in 2018 (10 yr post-treatment). Sampling plots had

a fixed radius of 17.58 m, encompassing 0.1 ha. Within each treated ($n = 45$) and untreated ($n = 26$) plot, all mature trees and snags ≥ 15 cm were tagged with a unique number and had recorded species and DBH (cm). Downed woody surface and ground fuels were sampled along four radial transects using the line intercept method (Brown 1974). Along each transect (17.58 m), individual counts of 1-h (0–0.64 cm) and 10-h (0.64–2.54 cm) fuels were recorded from 15 to 17 m, 100-h (2.54–7.62 cm) fuels from 12 to 17 m, and 1000-h (> 7.62 cm) fuels along the entirety of the transect were sampled. Diameter and decay class were also recorded for coarse woody fuel (1000-h), while duff and litter depth (cm) were measured at 8 and 16 m from plot center.

To characterize forest structure prior to and after treatment, we calculated tree density (trees ha^{-1}), live basal area ($\text{m}^2 \text{ha}^{-1}$), live quadratic mean diameter (QMD, cm), and snag basal area ($\text{m}^2 \text{ha}^{-1}$). Since treatment prescriptions emphasized retention of sugar pine and Jeffrey pine, we also estimated residual basal area of shade tolerant species ($\text{m}^2 \text{ha}^{-1}$). To evaluate changes in fuelbed characteristics before and after treatment, we obtained fuel load (Mg ha^{-1}) estimates of fine woody debris (1–100 h fuels), coarse woody fuel (≥ 1000 h fuels), and ground fuels (litter and duff) from each plot ($n = 71$) using species-weighted formulas derived in *Rfuels* (Foster 2018).

2.4. Tree ring measurements

In 2018, trees were cored to determine how thinning treatments impacted an individual tree's resistance to California's most recent severe drought period. One core was collected from up to three dominant or co-dominant live trees per species per plot at approximately DBH. A total of 389 cores were collected, 55 of these had labeling errors making it impossible to pair them with their associated data, therefore 334 cores were used in the analysis. Analyzed cores ($n = 334$) contained at least the last 25 years of annual growth rings. Cores were collected from both treated ($n = 216$) and untreated ($n = 118$) plots. All samples were prepared using standard dendrochronological methods (Speer 2010). Cores were mounted and sanded using progressive grits from 150 up to 600. Ring widths were counted and measured for each core using a dissecting microscope and digital sliding stage micrometer with a precision of 0.01 mm (Velmet Measuring System, Bloomfield, NY; Acurite encoder Heidenhain 178 Corp, Schaumburg, IL). Cores from each plot, species, and unit were cross-dated by comparing narrow rings across multiple samples to detect the presence of false and missing rings. Visual cross-dating of the six species-specific chronologies were validated using COFECHA software (Holmes 1983). Series intercorrelation by species ranged from 0.32 to 0.59 with a mean of 0.47.

Total tree ring measurements were converted to basal area increments (BAI) using the *dplrR* package (Bunn 2008) in R (R Core Team 2018). BAI is a commonly used proxy for tree vigor and removes the need to detrend data, as the metric is less dependent on tree age compared to raw ring widths (Biondi and Qeadan, 2008; Lloret et al., 2011; Valor et al., 2020). From BAI measurements, tree resistance indices were calculated using methods described in Lloret et al. (2011) and Valor et al. (2020). Resistance was calculated using the equation:

$$\text{Resistance} = \text{BAI}_{\text{Stress}} / \text{BAI}_{\text{PreStress}}$$

where $\text{BAI}_{\text{Stress}}$ is the average BAI during California's most recent severe drought (2012–2015) and $\text{BAI}_{\text{PreStress}}$ is the average BAI of the four years preceding the drought (2008–2011). Resistance was calculated for individual trees across all units whether or not they were subject to treatment or were part of the control.

2.5. Statistical analysis

2.5.1. Stand structure

To assess the effects of treatment and time on overstory composition, we conducted linear mixed-effects models using the *lme4* package

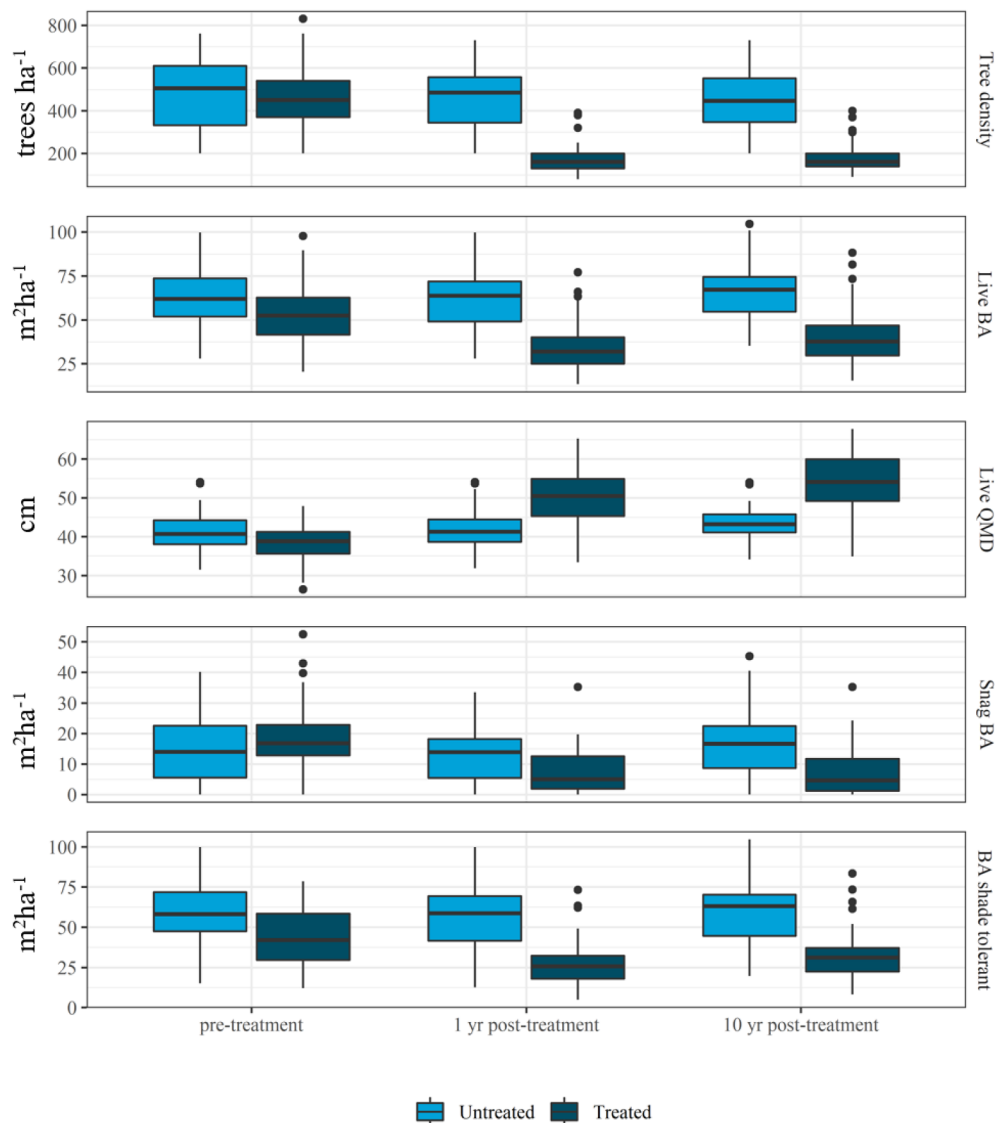


Fig. 2. Measured characteristics of forest structure across time, including (from top to bottom) live tree density, live basal area (BA), live quadratic mean diameter (QMD), cumulative snag basal area, and basal area of shade tolerant species.

(Bates et al. 2015) in R. Preliminary analysis of diagnostic plots (Kassambara 2020) suggested that our residuals met the assumptions of a linear model with outliers removed and the application of square root or log transformations (for basal area of shade tolerant species and live quadratic mean diameter, respectively). Using tree density, residual live basal area, live quadratic mean diameter, cumulative snag basal area, and basal area of shade tolerant species as our response variables, we started with a null model that included time period (pre-treatment, 1 yr post-treatment, and 10 yr post-treatment) as a covariate and treatment unit as our random effect. We tested for the effect of treatment (treated or untreated) by creating a second model that included treatment as a fixed effect in addition to time period, as well as evaluating a third model with an interaction term between treatment and time period. We compared all three models using Akaike information criterion (AIC), choosing a final model based on the lowest AIC value. If models were within 2 AIC points from the model with the lowest AIC value, we compared those models using a likelihood ratio test to determine if model performance significantly improved with additional terms. Models with the lowest AIC values which contained terms that significantly improved model performance were then used to evaluate the efficacy of treatment and time on forest structure.

2.5.2. Fuels

When evaluating the influence of overstory composition and time on fuels, preliminary analysis of diagnostic plots suggested our models predicting fine woody fuels (1–100 h fuels) and coarse woody fuel (≥ 1000 h fuels) complied with the assumptions of linear models when outliers were removed and square root transformations (coarse woody fuel) were applied. Since transformations and removal of outliers from ground fuel (litter and duff) estimates still did not comply with normality and homoscedasticity, we used generalized linear mixed-effects models with a gamma distribution and a log link function to account for skewed, positive, and continuous data. Using loads of fine woody fuels, coarse woody fuel, and ground fuels as our response variables, we started with a null model that included time period (pre-treatment, 1 yr post-treatment, 10 yr post-treatment) as a covariate and treatment unit as our random effect. We evaluated the effect of treatment (treated or untreated) on woody fuel loads by adding it as a fixed effect in combination with time, as well as a separate model that included an interaction term between treatment and time. Similar to our forest structure analysis, we used AIC values and likelihood ratio tests to determine our top model. We then tested for the effect of overstory characteristics on woody fuel loads by creating six models that included each characteristic (tree density, live basal area, QMD, snag basal area,

Table 2

Model outputs from top linear mixed-effect models predicting fuel loads across treatments and time. Model outputs include which fixed effects were included in a given model, their coefficient estimates, standard error, p-value, and variance inflation factor estimating multi-collinearity. Values in bold indicate significance based on an alpha level of 0.05. Fine woody fuels include 1–100 h, coarse woody fuels include 1000 h, and ground fuels include duff and litter.

Response variable	Fixed effect	Estimate	Standard error	P-value	VIF
Fine woody fuels	Treated	0.084	0.902	0.926	1.000
	1 yr post-treatment	0.051	0.648	0.938	1.000
	10 yr post-treatment	3.690	0.648	< 0.001	–
Coarse woody fuels	Treated	0.974	0.820	0.235	1.349
	1 yr post-treatment	0.441	0.749	0.556	1.630
	10 yr post-treatment	3.216	0.749	< 0.001	–
	Treated*1yr Post	–2.969	0.953	0.002	1.751
	Treated*10 yr Post	–2.446	0.950	0.010	–
Ground fuels	Treated	0.035	0.173	0.840	1.000
	1 yr post-treatment	0.312	0.065	< 0.001	1.000
	10 yr post-treatment	0.149	0.065	0.022	–

and basal area of shade-tolerant species) separately as a fixed effect in addition to time period, as well as an additional six models that included interaction terms between each overstory characteristic and time period. We avoided combinations of overstory metrics within the same model due to highly correlated variables (Harrell 2019; Appendix B) that would potentially influence coefficient estimates and detection of significant relationships. Again, we used AIC values and likelihood ratio tests to determine our top model.

2.5.3. Resistance

Individual tree resistance to the 2012–2015 drought was assessed using generalized linear mixed-effects models. Since initial analysis of diagnostic plots inferred that residuals failed to meet the assumptions of a linear model, we created models using a gamma distribution and log link function. Using resistance as our response variable, we created a null model which included treatment units as a random effect. Additional models were constructed using treatment type, post-treatment live residual basal area, and shade tolerance groupings (tolerant or intolerant) as independent fixed terms, in combination with each other, and with interaction terms. We intended to test if drought resistance varied by species, but given the limited sample size, individual resistance values were aggregated by shade tolerance. Shade-tolerant species included *A. concolor*, *A. magnifica*, and *C. decurrens* and shade-intolerant species included *P. contorta*, *P. jeffreyi*, and *P. lambertiana*. Model selection was based off a combination of AIC values and likelihood ratio tests similar to those used in the forest structure and fuel analysis.

3. Results

3.1. Stand structure

Results from our top linear mixed-effects models suggest that treatments were effective at reducing stand density and basal area, shifting tree size to larger diameter trees, mitigating tree mortality, and reducing shade-tolerant species, with the effects of treatment persisting even 10 years after treatments were implemented (Fig. 2). All top models evaluating stand structure included interaction terms (Appendix C), with each model consistently finding a significant interaction between treatment and time. The effects of treatment on tree density were immediately apparent during 1 yr post-treatment, reducing density 61% relative to pre-treatment levels and showing 63% lower tree density than untreated stands during the same time period ($p < 0.001$). Lower tree density was maintained 10 years following treatment, with treated units still exhibiting 61% lower density than controls ($p < 0.001$). These reductions were also accompanied by immediate reductions in basal area during 1 yr post-treatment, with treated stands containing 34% less basal area than pre-treatment levels and 44% lower basal area than untreated units during the same time

period ($p < 0.001$). Although treated units still maintained 40% lower basal area than untreated stands 10 years after treatment ($p = 0.002$), increases in residual live basal area between 1 yr post-treatment and 10 yr post-treatment was 57% greater in treated stands than controls. This increase corresponded to increases in average tree size, with treated stands exhibiting a 22% increase in QMD during 1 yr post-treatment and 16% higher QMD than untreated units during the same time period ($p < 0.001$). This greater abundance of larger-sized trees was maintained during the entire sampling period, with treated stands still exhibiting 19% higher QMD than controls ($p < 0.001$) during 10 yr post-treatment. Prior to treatment, 25% of total basal area in treated units were composed of snags while untreated units only exhibited 17%. Removal of dead trees immediately reduced snag basal area by 55% in treated units, with stands exhibiting 38% lower levels than controls during 1 yr post-treatment ($p < 0.001$). Not only did treated stands maintain 53% lower snag basal area than controls 10 years after treatment ($p < 0.001$), controls showed a 24% increase in snag basal area from 1 yr post-treatment to 10 yr post-treatment, while treated units showed no change in snag basal area during that same time period. Preferential retention of pine species immediately reduced the basal area of shade tolerant species in treated stands by 37% during 1 yr post-treatment, with treated units showing 53% lower basal area of shade-tolerant species than controls during the same time period ($p = 0.005$). The effects of treatment persisted 10 years later, with treated units still exhibiting 48% lower basal area of shade-tolerant species than controls ($p < 0.001$) during 10 yr post-treatment.

3.2. Fuels

Results from our top linear mixed-effects models indicate that coarse woody fuels were the only fuel class to be effectively reduced following thinning in both the short term and long term (Table 2). Stands that were thinned showed similar coarse woody fuel loads across both activity fuel treatments (Appendix D), with loads immediately reduced 44–63% 1 yr post-treatment and 20–58% lower than controls during that same time period ($p = 0.002$). That effect persisted even 10 years after treatments were applied ($p = 0.010$), with treated stands still showing 15–29% lower coarse woody fuel loads than pre-treatment levels and 36–55% lower fuel loads than controls ($p = 0.010$). While fine woody fuels were similar to pre-treatment levels 1 yr post-treatment across all stands ($p = 0.938$), we also found that fine woody fuels were 31–39% higher 10 yr post-treatment whether the stand was thinned or not ($p = 0.001$). Accumulation of ground fuels was consistent throughout the entire sampling period, showing higher levels 1 yr and 10 yr post-treatment across all stands ($p < 0.001$ and $p = 0.022$, respectively).

Our top mixed-effects models suggested that dead trees were the most important overstory characteristic driving accumulation of fine woody fuels and coarse woody fuel (Appendix E). For both fuel classes,

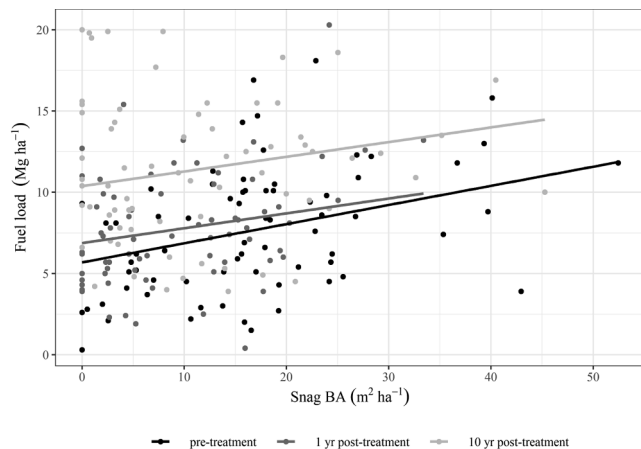


Fig. 3. Model response curves from top linear mixed effects model predicting fine woody fuel (1–100 h fuels) loads as function of time period and snag basal area (BA). Dots represent actual observations from both treated and untreated plots combined.

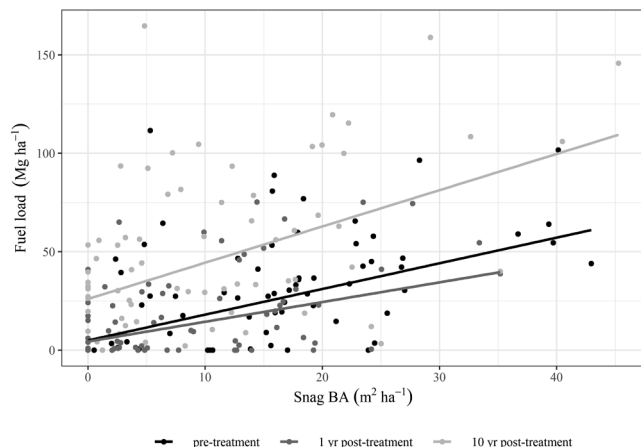


Fig. 4. Model response curves from top linear mixed effects model predicting coarse woody fuel (≥ 1000 h fuels) loads as function of measurement period and snag basal area (BA). Predictions are back-transformed from square root transformation, with dots representing actual observations from treated and untreated plots combined.

total snag basal area was associated with 7% higher fine woody fuel loads (Fig. 3; $p < 0.001$) and 24% higher coarse woody fuel loads (Fig. 4; $p < 0.001$). Although interaction terms did not improve model performance, models indicated that 10 yr post-treatment had a positive association with fine and coarse woody fuels ($p < 0.001$), increasing 30–33% relative to pre-treatment levels by that time period. Despite trends observed for fine and coarse woody fuels, our models did not detect a significant effect of any overstory characteristic on ground fuel accumulation. Rather, time was the only variable to show an effect on woody fuel dynamics (Appendix E), with 1 yr post-treatment and 10 yr post-treatment associated with higher fuel loads relative to pre-treatment levels ($p < 0.001$ and $p = 0.021$, respectively).

3.3. Tree resistance

Results indicate that thinning treatments were effective at increasing individual tree resistance to drought (Fig. 5). Although the addition of an interaction term did not improve top model performance, our top model indicated that a combination of unit treatment type (treated or untreated) and post treatment live residual basal area were associated with higher levels of resistance (Appendix F). Greater and more variable resistance values were detected in individual trees

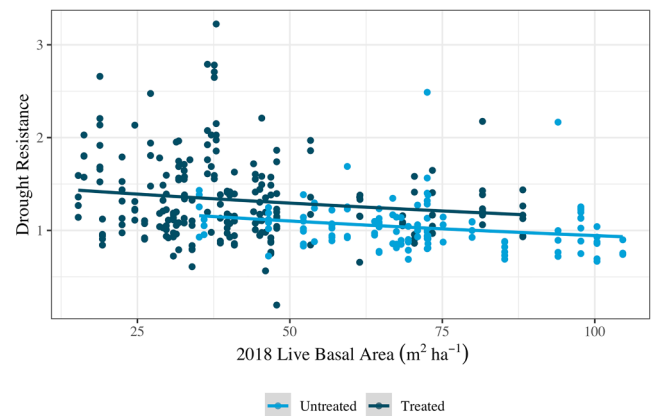


Fig. 5. Response curves showing the relationship between 2018 live basal area (BA) and drought resistance. Model response curves are back-transformed from a log transformation and points represent actual individual tree resistance values. Points are colored based on treatment status. There were 334 analyzed cores, 216 from treated units and 118 from untreated units.

sampled in units that were subject to treatment ($p < 0.001$) and had lower residual basal area post treatment ($p = 0.001$). The average resistance values for trees in treated units was 1.33 while the average resistance for those in untreated units was 1.04. Mean resistance for trees in treated units was 28% greater than those in untreated units. Resistance also tended to decline as residual basal area increased.

4. Discussion

Our findings indicate that thinning treatments can substantially alter forest structure and be accompanied by changes in fuel loads and drought resistance that persist long after treatments are implemented. Even 10-years after treatment, we found that stands still had lower tree density, live and dead basal area, and basal area of shade-tolerant species, as well as greater relative abundance of larger-sized trees relative to their untreated counterparts. Two of the most interesting by-products of using treatments to reduce live and dead basal area is the potential to lower the accumulation of downed woody fuels and promote higher drought resistance relative to unmanaged stands – a trend we consistently found across time. While these changes are not surprising given the fuel reduction and forest restoration objectives of the treatments, it is interesting that the range of thinning prescriptions implemented (Table 1) resulted in such distinct and persistent effects relative to the untreated control areas. The designation of PACs that dictated this range of prescriptions (Table 1) was apparently not so restrictive that it resulted in ineffective treatments, as was the case in the southern Sierra Nevada (Lydersen et al. 2019).

While we observed general decreases in tree density over time, significant reductions in density were immediately evident in treated units one-year-post-treatment. This is different from using prescribed fire alone, in that it may take multiple applications of fire to effectively kill and consume small- and mid-sized trees (North et al., 2007; Collins et al., 2019). In addition to these size classes being targeted to mitigate fire behavior, the higher abundance of larger-diameter trees we observed in the treated units may ultimately render these stands more resistant to high intensity fires (Agee and Skinner 2005). Although treatments had lower live basal area than untreated stands, the amount of residual live basal area in both post-treatment periods (35.0 – 40.5 $\text{m}^2 \text{ha}^{-1}$) were still relatively high but closer to reconstructed historic reference conditions of forests in the Lake Tahoe Basin (29.4 $\text{m}^2 \text{ha}^{-1}$) (Taylor et al. 2014).

Similar to other restoration projects (Hood et al. 2018), we found positive longer-term effects on tree growth following treatment. Although treated units exhibited lower basal area than untreated stands a

decade after treatments were applied, residual live basal area increased nearly 2.5 times in treated units despite drought conditions. This suggests that restoration treatments may have the additional benefit of maintaining forest health under changing environmental conditions. Since prescriptions explicitly stated marking guidelines that favored the retention of pines, lower basal area of shade-tolerant species in treated units would facilitate transitions towards the more pine-dominated forests that existed historically in this area (Beaty and Taylor, 2008; Taylor et al., 2014). Furthermore, a shift in dominance of overstory pines may also be self-reinforcing in that it can allow for greater pine regeneration (Zald et al. 2008).

The accumulation of downed woody fuels over time is a product of deposition from both live and dead trees (Keane 2008). At our study sites there was a direct connection with dead trees, indicating that as dead trees decompose and drop foliage, branches, and ultimately boles, their rates of deposition exceed decomposition on the forest floor over time. This reinforces previous findings demonstrating the influence of overstory composition and structure on woody fuel loads (Lydersen et al., 2015; Knapp et al., 2017). However, we also found that the effect of time was much stronger on woody fuel accumulation than snag basal area. A possible interpretation of this positive temporal effect is that it is driven by a combination of increased individual tree growth, which was more pronounced in treated sites (Fig. 5), and greater recruitment of snags, which was only evident in untreated sites (Fig. 2). Although we did not detect a relationship between any overstory metric and the ground fuels we observed, litter and duff deposition may be related to overstory characteristics that we did not measure such as canopy cover (Lydersen et al., 2015; Fry et al., 2018).

We also found that lower levels of residual live basal area were associated with higher individual tree drought resistance even though treatments occurred 4–6 years prior to the severe drought. While thinning can increase tree resistance to drought (Sohn et al., 2013; Navarro-Cerrillo et al., 2019), the persistent effects of treatment suggest that current applications of thinning may be beneficial for anticipating future climate scenarios. Despite drought and drought-related disturbances being a primary driver of increased mortality in forests (van Mantgem et al., 2009; Fettig et al., 2019), benefits of treatment-related density reductions in improving tree growth (Coomes and Allen, 2007; Collins et al., 2014) may be the reason we observed lower trends of tree mortality in thinned stands even under severe drought conditions. Since drier sites with dense vegetation are some of the most vulnerable to tree mortality (Young et al. 2017), treatments may mitigate future mortality events by increasing soil moisture (Wayman and North 2007) and improving the physiological performance of residual trees (Skov et al., 2004; Kolb et al., 2008). Although our initial goal was to assess potential differences in drought resistance among six conifer species, insufficient sample sizes amongst species limited our statistical analyses. When species were aggregated by shade tolerance, our inability to detect differences ($p = 0.75$) was likely due to only sampling dominant and co-dominant trees that may have been less affected by above-ground competition. Undetectable differences in resistance values among tolerance groups might also be attributed to species interactions affecting local water availability during a drought (Forrester 2014). Facilitation or niche partitioning in heterogeneous forest stands can lead to greater water availability and water-uptake efficiency, mitigating water stress (Forrester and Bauhus 2016). However, the relationship between species, thinning regimes, and drought resistance warrants further investigation as it can provide critical information regarding the responses of trees to drought in relation to thinning treatment intensity (Sohn et al. 2016).

Calculating resistance values by using trends in radial growth allowed us to use drought resistance as a proxy for tree vigor. Despite experiencing the most severe drought in the last 1200-years (Griffin and Anchukaitis, 2014; Lund et al., 2018), average drought resistance

values for trees in treated and untreated units remained above 1, indicating that average radial growth was not severely impacted by the combination of reduced precipitation and record high temperatures (Griffin and Anchukaitis 2014; Appendix A). Although annual precipitation is related to drought vulnerability, this can vary across latitudinal gradients (Restaino et al. 2019). Due to the location of our study, precipitation may still have been sufficient to maintain growth regardless of temperature and competitive environment. While drought periods typically result in decreased annual growth (Fritts, 1974; Littell et al., 2008; Williams et al., 2010), extension of the growing season may present opportunities for continued growth in higher latitude forests that may not be as sensitive to drought. However, this interpretation should be met with caution as climatic effects on tree growth depend on the magnitude and duration of drought, particularly over multiple years of severe drought (Restaino et al. 2016).

5. Management implications

Thinning treatments can effectively improve resistance to drought and restore stand structure closer to historic conditions. Thinning treatments are widely implemented across western US forests and are considered a viable management tool for future forest restoration initiatives (USDA-FS, 2011; Collins et al., 2014). Based on our observations, future applications of appropriate thinning treatments (Stephens et al. 2009) can be more extensive and intense to meet structural objectives and increase stand resistance to ecological stressors. Identifying known hazards and explicitly stating both short- and long-term management goals is critical to maximizing the efficacy of treatments (Stephens and Moghaddas, 2005a). While coarse woody fuel and fine fuels are critical components of mixed-conifer forest structure, untreated activity fuels can produce undesired fire behavior and effects (Stephens and Moghaddas, 2005a, 2005b). This particular study was part of a larger regional restoration initiative that included multiple collaborative agencies and management objectives. The overall objectives of this project were to reduce the amount of activity fuels and improve forest health and ecosystem function. Although thinning treatments may increase activity fuels in the short-term, we found beneficial improvements to preserving tree vigor in the long term.

Our findings highlight the importance of understanding how thinning treatments can impact forest structure and whether this translates into resistance to multiple disturbances. Although public forest management emphasizes promoting forest resilience (USDA-FS, 2011; Franklin and Johnson, 2012; Collins et al., 2014), incorporating resistance-based objectives into management plans provides the benefit of forestalling impacts associated with disturbances and climate change (Parker et al., 2000; Stephens et al., 2010). Treatments that aim to improve tree resistance to drought and stand resistance to wildfire are critical for maintaining the ecological integrity of forests and the ecosystem services they provide (e.g. wildlife habitat, soil stability, and carbon sequestration) (Collins et al., 2014; Stephens et al., 2020). Stands with decreased vigor and higher rates of mortality can not only reduce commercial values for timber, but also impair visual aesthetics associated with recreation (Stephens and Moghaddas, 2005a), a critical enterprise in the Lake Tahoe area and other regions in the Sierra Nevada mixed-conifer zone. With climate change already associated with larger wildfires (Williams et al. 2019), future climate projections also indicate an increased frequency and severity of droughts (Griffin and Anchukaitis 2014). Left unmanaged except for continued fire suppression, forests may be particularly vulnerable to novel structural changes, possibly diminishing future restoration treatments. We conclude that appropriately designed thinning treatments provide managers the opportunity to enhance resistance to projected stressors and mitigate future loss to amplified disturbances.

CRediT authorship contribution statement

Kathryn E. Low: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Brandon M. Collins:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Alexis Bernal:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing. **John E. Sanders:** Data curation, Writing - original draft, Writing - review & editing. **Dylan Pastor:** Methodology, Formal analysis, Investigation, Data curation, Writing - review & editing. **Patricia Manley:** Conceptualization, Methodology, Investigation, Resources, Supervision, Project administration, Funding acquisition. **Angela M. White:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Scott L. Stephens:** Writing - review & editing, Supervision, Funding acquisition.

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.

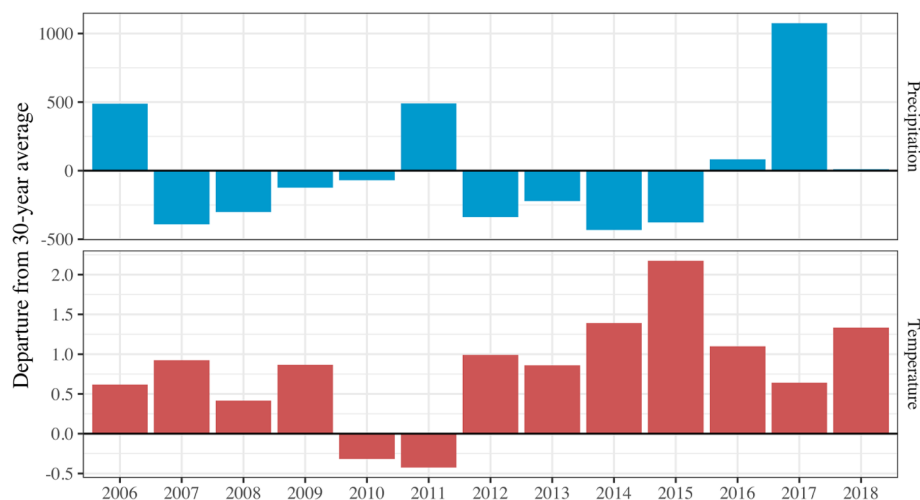
Acknowledgements

We would like to thank Allison Stanton, Hannah Etchells, and Natalia Rico for helping with field data collection. Hannah Etchells and Samuel Phillips also helped with tree core preparation.

Funding Sources

Funding for the duration of the project was provided by the Bureau of Land Management through the Southern Nevada Public Lands Management Act administered by U.S. Forest Service Lake Tahoe Basin Management Unit (project nos. R9-26: P033 and R16-8: P001), by the Nevada Division of State Lands through the Lake Tahoe License Plate Program (project nos. LTLP-09-2, LTLP 07-01, and LTLP 08-10), and by added support from the Lake Tahoe West Partnership agencies and stakeholders. This current work was also supported by a research partnership between the U.S. Forest Service Pacific Southwest Research Station and UC Berkeley College of Natural Resources (project no. 16-JV-11272167-063).

Appendix A. Departure of total precipitation (mm) and mean temperature (°C) from 30-year averages (1980–2010) during our study period (2006–2018). Estimates of total precipitation were obtained using precipitation year (July–June), while estimates of mean temperature were obtained using wet year (October – September).



Appendix B. Spearman's rank-order correlation coefficients (p-value) amongst forest structure metrics, including tree density (TPH), live basal area (live BA), live quadratic mean diameter (live QMD), cumulative snag basal area (snag BA), and basal area of shade tolerant species (BA shade tolerant). Values in bold indicate significant correlation based on an alpha level of 0.05.

	Live TPH	Live BA	Live QMD	Snag BA	BA shade tolerant
Live TPH	1 (NA)	0.748 (< 0.001)	-0.641 (< 0.001)	0.417 (< 0.001)	0.665 (< 0.001)
Live BA	0.748 (< 0.001)	1 (NA)	-0.047 (0.495)	0.337 (< 0.001)	0.909 (< 0.001)
Live QMD	-0.641 (< 0.001)	-0.047 (0.495)	1 (NA)	-0.276 (< 0.001)	0.06 (0.598)
Snag BA	0.417 (< 0.001)	0.337 (< 0.001)	-0.276 (< 0.001)	1 (NA)	0.349 (< 0.001)
BA shade tolerant	0.665 (< 0.001)	0.909 (< 0.001)	0.036 (0.598)	0.349 (< 0.001)	1 (NA)

Appendix C. Model outputs from top linear mixed-effect models predicting overstory characteristics. Overstory characteristics included tree density (TPH), residual live basal area (live BA), live quadratic mean diameter (live QMD), cumulative snag basal area (snag BA) and basal area of shade tolerant species (BA shade tolerant). Model outputs include which fixed effects were included in a given model, their coefficient estimates, standard error, p-value, and variance inflation factor estimating multi-collinearity. Values in bold indicate significance based on an alpha level of 0.05.

Response variable	Fixed effect	Estimate	Standard error	P-value	VIF
TPH	Treated	-48.750	31.088	0.117	1.469
	1 yr post-treatment	-19.231	31.496	0.541	1.620
	10 yr post-treatment	-39.231	31.496	0.213	-
	Treated*1yr Post	-261.785	39.926	< 0.001	1.768
	Treated*10 yr Post	-242.672	40.022	< 0.001	-
Live BA	Treated	-12.069	6.899	0.080	1.120
	1 yr post-treatment	-1.293	3.784	0.733	1.700
	10 yr post-treatment	1.462	3.823	0.702	-
	Treated*1yr Post	-17.496	4.816	< 0.001	1.651
	Treated*10 yr Post	-14.815	4.829	0.002	-
Live QMD	Treated	-0.037	0.046	0.418	1.199
	1 yr post-treatment	0.006	0.036	0.872	1.699
	10 yr post-treatment	0.056	0.036	0.118	-
	Treated*1yr Post	0.249	0.044	< 0.001	1.762
	Treated*10 yr Post	0.266	0.044	< 0.001	-
Snag BA	Treated	-1.078	0.667	0.106	1.176
	1 yr post-treatment	-0.059	0.279	0.833	1.640
	10 yr post-treatment	0.188	0.279	0.500	-
	Treated*1yr Post	-1.420	0.354	< 0.001	1.697
	Treated*10 yr Post	-1.260	0.355	< 0.001	-
BA shade tolerant	Treated	1.157	3.019	0.702	1.047
	1 yr post-treatment	-1.375	2.158	0.524	1.616
	10 yr post-treatment	1.698	2.180	0.436	-
	Treated*1yr Post	-7.741	2.735	0.005	1.629
	Treated*10 yr Post	-10.892	2.752	< 0.001	-

Appendix D. Average (± 2 SE) forest conditions over time within each thinning treatment. Forest conditions include live tree density (trees ha⁻¹), live basal area (BA; m² ha⁻¹), and downed woody fuel loads (Mg ha⁻¹). Downed woody fuel loads include fine woody fuels (FWD; 1–100 h fuels), coarse woody fuels (CWD; ≥ 1000 h fuels), and ground fuels (litter and duff). To treat activity fuels following thinning, hand thin treatments were followed up with pile and burn, while mechanical treatments were followed up with mastication.

	Pre-treatment		1 yr post-treatment		10 yr post-treatment	
	Hand thin	Mechanical	Hand thin	Mechanical	Hand thin	Mechanical
Tree density	435 (91)	460 (47)	228 (50)	154 (15)	232 (45)	156 (17)
Live BA	47.2 (10.2)	54.9 (5.9)	39.7 (10.7)	33.1 (4.4)	46.8 (11.5)	37.9 (5.1)
FWD	7.8 (3.2)	8.3 (1.5)	10.0 (3.2)	7.6 (1.0)	12.7 (4.3)	12.0 (1.8)
CWD	49.3 (20.9)	41.2 (11.6)	28.3 (18.3)	14.9 (7.6)	35.2 (13.4)	50.3 (14.3)
Ground fuels	83.4 (13.3)	87.1 (12.4)	84.0 (14.0)	140.3 (25.6)	99.0 (26.5)	106.5 (13.1)

Appendix E. Model outputs from top mixed-effect models predicting woody fuel load estimates. Fuel load estimates included fine woody fuels (1–100 h fuels), coarse woody fuel (≥ 1000 h fuels), and ground fuels (litter and duff). Model outputs include which fixed effects were included in a given model, their coefficient estimates, standard error, p-value, and variance inflation factor estimating multi-collinearity. Values in bold indicate significance based on an alpha level of 0.05.

Response variable	Fixed effect	Estimate	Standard error	P-value	VIF
Fine woody fuel	Snag BA	1.068	0.286	< 0.001	1.057
	1 yr post-treatment	0.819	0.662	0.216	1.028
	10 yr post-treatment	4.278	0.648	< 0.001	-
Coarse woody fuel	Snag BA	1.235	0.191	< 0.001	1.044
	1 yr post-treatment	-0.567	0.461	0.219	1.022
	10 yr post-treatment	2.351	0.452	< 0.001	-
Ground fuels	1 yr post-treatment	0.312	0.065	< 0.001	-
	10 yr post-treatment	0.150	0.065	0.021	-

Appendix F. Various model outputs from top mixed-effect models predicting drought resistance. All models include drought resistance as their response variable and contain unit (1|Unit) as a random effect. Treatment refers to unit treatment type, BA refers to post-treatment live residual basal area, and tolerance refers to shade tolerance groupings (tolerant or intolerant). Model outputs include fixed effects included in a given model, their coefficient estimates, standard error, p-value, and variance inflation factor estimating multi-collinearity. Values in bold indicate significance based on an alpha level of 0.05.

Model inputs	Fixed effect	Estimate	Standard Error	P-Value	VIF
Treatment + BA	Treatment	0.170	0.044	< 0.001	1.664
	BA	-0.066	0.020	0.001	1.664
Treatment + BA + Treatment*BA	Treatment	0.180	0.047	< 0.001	1.884
	BA	-0.050	0.034	0.138	4.639
	Treatment * BA	-0.024	0.043	0.575	3.173
Treatment + BA + Tolerance	Treatment	0.171	0.044	< 0.001	1.694
	BA	-0.066	0.020	0.001	1.666
	Tolerance	0.004	0.035	0.921	1.023
Treatment	Treatment	0.262	0.035	< 0.001	-
Treatment + Tolerance	Treatment	0.263	0.036	< 0.001	1.021
	Tolerance	0.006	0.036	0.858	1.021

References

- Adams, H.D., Luce, C.H., Breshears, D.D., Allen, C.D., Weiler, M., Hale, V.C., Smith, A.M.S., Huxman, T.E., 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology* 5, 145–159.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using *lme4*. *J. Stat. Softw.* 67, 1–48.
- Beaty, R.M., Taylor, A.H., 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. *For. Ecol. Manage.* 255, 707–719.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree Ring Res.* 64, 81–96.
- Brooks, J.R., Mitchell, A.K., 2011. Interpreting tree responses to thinning and fertilization using tree-ring stable isotopes. *New Phytol.* 190, 770–782.
- Brown, J.K., 1974. Handbook for Inventorying Downed Woody Material. USDA For. Serv. Gen. Tech. Rep. 24. < <https://www.fs.usda.gov/treesearch/pubs/28647> > .
- Brown, P.M., Wienk, C.L., Symstad, A.J., 2008. Fire and forest history at Mount Rushmore. *Ecol. Appl.* 18, 1984–1999.
- Bunn, A.G., 2008. A dendrochronology program library in R (*dplR*). *Dendrochronologia* 26, 115–124.
- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C., St. B., Clair, J., 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. *For. Ecol. Manage.* 261, 1121–1142.
- Collins, B.M., Das, A.J., Battles, J.J., Fry, D.L., Krasnow, K.D., Stephens, S.L., 2014. Beyond reducing fire hazard: fuel treatment impacts on overstory tree survival. *Ecol. Appl.* 24, 1879–1886.
- Collins, B.M., Lydersen, J.M., Everett, R.G., Fry, D.L., Stephens, S.L., 2015. Novel characterization of landscape-level variability in historical vegetation structure. *Ecol. Appl.* 25, 1167–1174.
- Collins, B.M., Fry, D.L., Lydersen, J.M., Everett, R., Stephens, S.L., 2017. Impacts of different land management histories on forest change. *Ecol. Appl.* 27, 2475–2486.
- Collins, B.M., Stephens, S.L., York, R.A., 2019. Perspectives from a long-term study of fuel reduction and forest restoration in the Sierra Nevada. *Tree Rings* 29, 7–9.
- Coomes, D.A., Allen, R.B., 2007. Effects of size, competition, and altitude on tree growth. *J. Ecol.* 95, 1084–1097.
- Fettig, C.J., Mortenson, L.A., Buloin, B.M., Foulk, P.A., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For. Ecol. Manage.* 432, 164–178.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292.
- Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. *Curr. For. Res.* 2, 45–61.
- Foster, D.E., 2018. *Rfuels: Estimate Fuel Loads from Brown's Transects for Sierra Nevada Conifers*. R package version 0.1.0.
- Foster, D.E., Battles, J.J., Collins, B.M., York, R.A., Stephens, S.L., 2020. Potential wildfire and carbon stability in frequent-fire forests in the Sierra Nevada: tradeoffs from a long-term study. *Ecosphere* in press.
- Franklin, J.F., Johnson, K.N., 2012. A restoration framework for federal forests in the Pacific Northwest. *J. Forest.* 110, 429–439.
- Fritts, H.C., 1974. Relationships of ring widths in arid-site conifers to variations in monthly temperature and precipitation. *Ecol. Monogr.* 44, 411–440.
- Fry, D.L., Stephens, S.L., Collins, B.M., North, M., Franco-Vizcaino, E., Gill, S.J., 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. *PLoS ONE* 9, e88985.
- Fry, D.L., Stevens, J.T., Potter, A.T., Collins, B.M., Stephens, S.L., 2018. Surface fuel accumulation and decomposition in old-growth pine-mixed conifer forests, northwestern Mexico. *Fire Ecol.* 14, 6–21.
- Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* 7, 895–908.
- Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought? *Geophys. Res. Lett.* 41, 9017–9023.
- Hagmann, R.K., Franklin, J.F., Johnson, K.N., 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. *For. Ecol. Manage.* 304, 492–504.
- Harrell, F.E., 2019. *Hmisc: Harrell miscellaneous*. R package version 4.2-0.
- Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z.E., Gray, R.W., Kane, V.R., Churchill, D.J., Hagmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Salter, R.B., 2019. Climate, environment, and disturbance history govern resilience of Western North American forests. *Front. Ecol. Evolut.* 7, 239.
- Hood, S.M., Cluck, D.R., Jones, B.E., Pinnell, S., 2018. Radial and stand-level thinning treatments: 15-year growth response of legacy ponderosa and Jeffrey pine trees. *Restor. Ecol.* 26, 813–819.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43, 69–78.
- Kassambara, A., 2020. *ggpubr: ggplot2 based publication ready plots*. R package version 0.2.5.
- Keane, R.E., 2008. Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. *Can. J. For. Res.* 39, 1431–1445.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 310, 903–914.
- Knapp, E.E., Lydersen, J.M., North, M.P., Collins, B.M., 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *For. Ecol. Manage.* 406, 228–241.
- Kolb, T.E., Holmberg, K.M., Wagner, M.R., Stone, J.E., 2008. Regulation of ponderosa pine physiology and insect resistance mechanisms by basal area treatments. *Tree Physiol.* 18, 375–381.
- Larson, A.J., Churchill, D., 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.
- Liang, S., Hurteau, M.D., Westerling, A.L., 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. *Front. Ecol. Environ.* 16, 207–212.
- Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecol. Monogr.* 78, 349–368.
- Lloret, F., Keeling, F.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Okios* 120, 1909–1920.
- Lund, J., Medellín-Azuara, J., Durand, J., Stone, K., 2018. Lessons from California's 2012–2016 drought. *J. Water Resour. Plann. Manage.* 144.
- Lydersen, J.M., Collins, B.M., Knapp, E.E., Roller, G.B., Stephens, S., 2015. Relating fuel loads to overstory structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. *Int. J. Wildland Fire* 24, 484–494.
- Lydersen, J.M., Collins, B.M., Hunsaker, C.T., 2019. Implementation constraints limit benefits of restoration treatments in mixed-conifer forests. *Int. J. Wildland Fire* 28, 495–511.
- Martinson, E.J., Omi, P.J., 2013. Fuel treatments and fire severity: a meta-analysis. USDA

- Forest Service Research Paper RMRS-RP-103WWW. Fort Collins, Colorado, USA: USDA Forest Service, Rocky Mountain Research Station 38.
- Misson, L., Antoine, N., Joel, G., 2003. Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). *For. Ecol. Manage.* 183, 47–60.
- Navarro-Cerrillo, R.M., Sánchez-Salguero, R., Rodríguez, C., Lazo, J.D., Moreno-Rojas, J.M., Palacios-Rodríguez, G., Camarero, J.J., 2019. Is thinning an alternative when trees could die in response to drought? The case of planted *Pinus nigra* and *P. Sylvestris* stands in southern Spain. *For. Ecol. Manage.* 433, 313–324.
- 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.P., Collins, B.M., Stephens, S.L., 2012. Using fire to increase the scale, benefits and future maintenance of fuels treatments. *J. Forest.* 110, 392–401.
- North, M., Brough, A., Long, J., Collins, B., Bowden, P., Yasuda, D., Miller, J., Sugihara, N., 2015. Constraints on mechanized treatment significantly limit mechanical fuels reduction extent in Sierra Nevada. *J. Forest.* 113, 40–48.
- Parker, W.C., Colombo, S.J., Cherry, M.L., Flannigan, M.D., Greifenhagen, S., McAlpine, R.S., Papadopol, C., Scarr, T., 2000. Third Millennium Forestry: what climate change might mean to forests and forest management in Ontario. *Forestry Chronicle* 76, 445–463.
- PRISM Climate Group, 2020. Time Series Values for Individual Locations. Accessed 19 May 2020. <http://www.prism.oregonstate.edu>.
- R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Restaino, C.M., Peterson, D.L., Littell, J., 2016. Increased water deficit decreases Douglas fir growth throughout western US forests. *PNAS* 113, 9557–9562.
- Restaino, C., Young, D.J.N., Estes, B., Gross, S., Wuenschel, A., Meyer, M., Safford, H., 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecol. Appl.* 29, 4.
- Schoennagel, T., Nelson, C.R., 2011. Restoration relevance of recent National Fire Plan treatments in forests of the western United States. *Front. Ecol. Environ.* 9, 271–277.
- 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.
- Skov, K.R., Kolb, T.E., Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *For. Sci.* 50, 81–91.
- Sohn, J.A., Gebhardt, T., Ammer, C., Bauhus, J., Häberle, K.H., Matyssek, R., Grams, T.E.E., 2013. Mitigation of drought by thinning: short-term and long-term effects of growth and physiological performance of Norway spruce (*Picea abies*). *For. Ecol. Manage.* 308, 188–197.
- Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecol. Appl.* 26, 2190–2205.
- Speer, J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson, AZ, Tucson.
- Spittlehouse, D.L., Stewart, R.B., 2003. Adaptation to climate change in forest management. *BC J. Ecosyst. Manage.* 4, 1.
- Stephens, S.L., Moghaddas, J.J., 2005a. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *For. Ecol. Manage.* 215, 21–36.
- Stephens, S.L., Moghaddas, J.J., 2005b. Fuel treatment effects on snags and coarse woody debris in a Sierra Nevada mixed conifer forest. *For. Ecol. Manage.* 214, 53–64.
- 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.
- 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., Collins, B.M., Roller, G.B., 2012. Fuel treatment longevity in a Sierra Nevada mixed conifer forest. *For. Ecol. Manage.* 285, 204–212.
- Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., Meyer, M.D., 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere* 6, 79.
- Stephens, S.L., Kobziar, L.N., Collins, B.M., Davis, R., Fulé, P.Z., Gaines, W., Ganey, J., Guldin, J.M., Hessburg, P., Hiers, K., Hoagland, S., Keane, J.J., Masters, R.E., McKellar, A.E., Montague, W., North, M., Spies, T.A., 2019. Is fire for the birds? How two rare species influence fire management across the United States. *Front. Ecol. Environ.* 17, 391–399.
- Stephens, S.L., Westerling, A.L., Hurteau, M.D., Peery, M.Z., Schultz, C.A., Thompson, S., 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Front. Ecol. Environ.* 18, 354–360.
- Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017. Changing spatial patterns of stand-replacing fire in California mixed-conifer forests. *For. Ecol. Manage.* 406, 28–36.
- Taylor, A.H., Vandervlugt, A.M., Maxwell, R.S., Beaty, R.M., Airey, C., Skinner, C.N., 2014. Changes in forest structure, fuels and potential fire behavior since 1873 in the Lake Tahoe Basin, USA. *Appl. Veg. Sci.* 17, 17–31.
- Teets, A., Fraver, S., Weiskeittel, A.R., Hollinger, D.Y., 2018. Quantifying climate-growth relationships at the stand level in a mature mixed-species conifer forest. *Glob. Change Biol.* 24, 3587–3602.
- USDA-FS, 2011. Region Five ecological restoration: leadership intent. March 2011. U.S. Forest Service, Pacific Southwest Region, Albany, California, USA.
- Vaillant, N.M., Reinhardt, E.D., 2017. An evaluation of the Forest Service hazardous fuels treatment program—are we treating enough to promote resiliency or reduce hazard? *J. Forest.* 115, 300–308.
- Valor, T., Battipaglia, G., Piqué, M., Altieri, S., González-Olabarria, J.R., Casals, P., 2020. The effect of prescribed burning on the drought resilience of *Pinus nigra* ssp. *salzmannii* Dunal (Franco) and *P. sylvestris* L. *Ann. For. Sci.* 77, 13.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323, 521–524.
- Wayman, R.B., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *For. Ecol. Manage.* 239, 32–44.
- Williams, A.P., Allen, C.D., Millar, C.I., Swetnam, T.W., Michaelsen, J., Still, C.J., Leavitt, S.W., 2010. Forest responses to increasing aridity and warmth in the southwestern United States. *PNAS* 107, 21289–21294.
- Williams, A.P., Abatzoglou, J.T., Gershunov, A., Guzman-Morales, J., Bishop, D.A., Balch, J.K., Lettenmaier, D.P., 2019. Observed impacts of anthropogenic climate change on wildfire in California. *Earth's Future*. <https://doi.org/10.1029/2019EF001210>.
- Young, D.J.N., Stevens, J.T., Mason Earles, J., 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.
- Zald, 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 forests, USA. *For. Ecol. Manage.* 256, 168–179.