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The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments

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ABSTRACT

Disturbance is central to maintaining diversity in forest ecosystems. In the dry forests of the western United States, over a century of fire exclusion has altered the fire regimes of these forests, resulting in high fuel loads and a loss of plant diversity. Mechanical thinning and prescribed fire are widely used to restore structural complexity and species diversity in many western U.S. forests. While studies have shown that the reintroduction of fire into these forests initially promotes plant diversity, there is limited information on the persistence of this effect. We evaluated the effects of thinning and burning treatments on the understory plant community fifteen years after treatment in an old-growth, Sierran mixed-conifer forest. Using a full-factorial design, including three levels of thinning and two levels of burning, we found mechanical thinning and prescribed fire reduced litter depths and increased the availability of bare ground, resulting in an initial increase in herb cover. However, fifteen years after treatment, litter depths and shrub cover increased, resulting in a more homogenous understory community and a loss of herb cover. Overall, our results suggest that while thinning and burning treatments initially promote herbaceous plant cover, these effects are short lived in the absence of a second disturbance.

1. Introduction

Disturbance plays an important role in maintaining species diversity in ecosystems across the globe. Humans have intervened in many cases by altering disturbance frequency and severity. While diversity tends to be highest at intermediate levels of disturbance, intermediate is a function of the productivity of the system (Connell, 1978; Kondoh, 2001). Further, the spatial variability of disturbance can interact with microsite variability, creating fine-scale habitat heterogeneity that is more likely to sustain higher species diversity (Denslow, 1980; Fraterrigo and Rusak, 2008; Roberts and Gilliam, 1995; White and Jentsch, 2001).

Wildfire has played a central role in shaping forest ecosystems across the United States (Agee, 1993; Allen et al., 2002; Baisan and Swetnam, 1990; Bowman et al., 2009). Wildfires burn at different intensities and frequencies, interacting with topographic position, fuel type, edaphic conditions, and weather to produce varying effects across the landscape (Fites-Kauffman, 1997; van Wagtendonk and Fites-Kauffman, 2006). The resulting spatial and structural complexity promotes diversity at the site, stand, and landscape scales. In fire-adapted conifer forests, the majority of this biodiversity is found in the understory plant community (Palik and Engstrom, 1999; Shevock, 1996).

Over a century of fire exclusion has altered the structure and function of frequent-fire forests. High tree densities and surface fuel loads now characterize historically frequent fire forests and with these changes, forest conditions have become more homogenous (Agee and Skinner, 2005; Covington et al., 1997; Gilliam and Platt, 1999). In the absence of disturbance, depauperate plant communities dominated by trees and shade-tolerant species have replaced the once diverse assemblage of herbaceous and woody plants in frequent-fire forest ecosystems (Griffis et al., 2001; Kirkman et al., 2004).

Homogenous forest structure coupled with increasing temperature and longer, drier fire seasons has increased the occurrence of fire and the proportion of wildfires that burn under high-severity in dry forest types (Miller et al., 2009; Westerling, 2016). Large high-severity burn patches trade one homogenous condition for another and the post-fire vegetation community can increase the probability of subsequent high-severity fire (Coppoletta et al., 2016, Guiterman et al., 2017).

Reintroducing fire to drier forests in a manner characteristic of natural fire regimes can promote plant diversity if structural heterogeneity and the accompanying microsite variability are restored (Knapp

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et al., 2007; North et al., 2005a). Prior work in longleaf pine forests of the southeastern US has demonstrated that regular fire events are required to restore forest structural heterogeneity, which supports substantial understory plant diversity (Franklin et al., 2007; Kirkman et al., 2016). In the western US, the area treated by repeat burning has been limited because of a shorter history of prescribed fire use and the scale of the fire hazard problem. However, one study of repeated fire in Sierran mixed-conifer forest found that initial entry burns increased understory plant richness and cover, and that repeated burning could enhance the distributions of species impacted by fire suppression (Webster and Halpern, 2010).

The Sierra Nevada contains over 50% of California's vascular plant species (Davis and Stoms, 1996; Potter, 1998) and the southern Sierra contains the highest species richness and the most endemic and rare species across the range (Shevock, 1996). Historically, shrubs such as ceanothus (*Ceanothus* sp.) and manzanita (*Arctostaphylos* sp.) covered about 22% of the forest understory in mixed-conifer forests of the central Sierra Nevada (Hasel et al., 1934). The patchy distribution of shrubs in the understory was likely associated with a heterogeneous canopy with gaps that allowed for increased light availability on the forest floor (Conard et al., 1985; Cronemiller, 1959; Show and Kotok, 1924). Historically, frequent, low- and mixed-severity fires shaped the structure, function and composition of Sierran mixed-conifer forests (North et al., 2009). The fire season was constrained primarily to the later summer months following snowmelt and a drying of fuels and the typical mean fire return interval for Sierra mixed-conifer was 12–20 years (North et al., 2005b, Van de Water and Safford, 2011). Generally high severity made up 5–10% of total fire area and consisted of many small (< 4 ha), and few large patches (< 100 ha, Collins and Skinner, 2014). The resulting heterogeneity was characterized by a distribution of patch types, including closed-canopy patches, shrub patches and open gaps that promoted substantial understory plant diversity (e.g., Hutchings et al., 2003). Increases in canopy cover as a legacy of fire exclusion have resulted in a less diverse and homogenous understory community (North et al., 2005a). Forest structural and compositional heterogeneity across scales, from the microsite to the landscape, are important for maintaining a range of abiotic conditions that promote a diverse understory plant community (Beatty, 2014).

Management techniques that utilize fire and fire-surrogate (i.e. thinning) treatments can recreate within-stand heterogeneity and promote a diverse herbaceous and shrub understory (Knapp et al., 2013). While fire-surrogate treatments can alter forest structure and light availability, the understory plant community has been found to have a muted response to mechanical-only treatments because fire is required to reduce surface fuels and create establishment opportunities (Collins et al., 2007; Dodson et al., 2008; Wayman and North, 2007; Webster and Halpern, 2010). However, what remains unanswered is if the effects of both mechanical and burning treatments on the understory plant community persist over time.

We used data from the Teakettle Experimental Forest in the Southern Sierra Nevada to answer the question: How do burning and thinning treatments alter plant community composition and structure 15-years after treatment? We hypothesized that: (1) while burning and thinning treatments initially increased understory diversity, 15-years after treatment understory plant diversity would decline as shrub cover and fuel loads increased; (2) herb cover and richness would decrease as shrub cover and fuel loads increased; and (3) shrub cover would increase as live tree density decreased.

2. Material and methods

2.1. Study site

This study was conducted within the 1300 ha reserve of old-growth forest that was established as the Teakettle Experimental Forest in 1938. The Experimental Forest has no prior history of logging or known history of stand replacing disturbance. Teakettle is located 80 km east of Fresno, CA on the north fork of the Kings River with an elevation ranging from 1900 to 2600 m. The climate is Mediterranean, typical of the west side of the Sierra Nevada, with an average annual precipitation of 125 cm that falls predominately as snow between November and April (North et al., 2002). Over the period of this study an extreme drought occurred from 2012 to 2015, with California's driest 12-month period recorded during this event (Swain et al., 2014).

The mixed-conifer forest type at Teakettle is comprised of white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*) and Jeffrey pine (*Pinus jeffreyi*, Rundel et al., 1988). Red fir (*Abies magnifica*) and black oak (*Quercus kelloggii*) are also present in the overstory, but at low densities (North et al., 2007). Other hardwood species include willow (*Salix spp.*), bitter cherry (*Prunus emarginata*) and canyon live oak (*Quercus chrysolepis*). Prior to the last known wildfire in 1865, the mean fire return interval at Teakettle was 17.3 years (North et al., 2005b). The 1865 reconstructed forest structure of this mixed-conifer forest was characterized by a low density (67 trees ha^{-1}) of larger trees (quadratic mean diameter 49.5 cm), with Jeffrey pine and sugar pine accounting for 48.9% of the stems (North et al., 2007). Following fire exclusion, a substantial number of establishment events for white fir and incense-cedar occurred, coincident with years of high precipitation (North et al., 2005b). This resulted in increased tree density (469 stems ha^{-1}), which was dominated by white fir (67.6%, North et al., 2007). Prior to treatment, white fir and red fir comprised approximately 86 percent of the basal area at Teakettle, with sugar pine, Jeffrey pine and incense cedar comprising the remaining 13 percent.

The majority of the plant species diversity in this mixed-conifer forest is in the understory. Prior to treatment, 123 herbaceous species and 14 shrub species were identified within the Experimental Forest. During this period, total shrub cover was 27.2% with the most common species being mountain whitethorn (*Ceanothus cordulatus*), which accounted for almost 30 percent of the total shrub cover (North et al., 2002). Other common shrub species include bush chinquapin (*Chrysolepis sempervirens*), pinemat manzanita (*Arctostaphylos nevadensis*), green leaf manzanita (*A. patula*), snowberry (*Symphoricarpos mollis*), sticky currant (*Ribes viscosissimum*), Sierra gooseberry (*R. roezlii*) and hazelnut (*Corylus cornuta*). The two most abundant shrub species, mountain whitethorn and bush chinquapin, are found throughout the entire forest. The most common herbaceous species prior to treatment was *Monardella odoratissima*. For a complete site description, see North et al. (2002).

2.2. Treatments and data collection

Within the mixed-conifer zone of Teakettle, 18 permanent 4 ha treatment units were established in 1998. Using a full-factorial design, three replicates of each treatment unit were randomly assigned one of two levels of prescribed burning (burn and no burn) and one of three levels of thinning (no thin, understory thin, and overstory thin) for a total of six treatments. For the thin and burn treatments, thinning was implemented in 2000, followed by prescribed burning in 2001. The thin-only treatment units were thinned in 2001. Prescribed burning was applied in late October 2001 after the first major fall rain, resulting in a slow creeping ground fire intended to consume surface fuels while minimizing overstory ignition. Understory thinning removed trees between 25 and 76 cm in diameter while retaining at least 40% canopy cover, following prescription guidelines in Verner et al. (1992). Overstory thinning removed trees greater than 25 cm in diameter, while retaining approximately 22 regularly spaced large diameter (> 100 cm) trees per hectare. The understory thinning treatment reduced stem density from a pre-treatment mean of 469 trees per hectare (TPH) to a post-treatment mean of 239.5 TPH, reducing mean basal area by 15.2 $m^2 ha^{-1}$. The overstory thinning post-treatment mean was 150.3 TPH, with a mean basal area that was reduced by 33.7 $m^2 ha^{-1}$ (North

et al., 2007).

Prior to treatment, all trees were mapped and measured, and sampling gridpoints were established within all 18 treatment units. Gridpoints for two of the three replicates of each treatment were established on a 50 m × 50 m grid (9 points/plot) and one replicate was selected for intensive sampling (49 points/plot) and used a 25 m × 25 m grid, for a total of 402 gridpoints across all treatments. Understory vegetation was sampled at each gridpoint using a 10 m^2 circular plot and visually estimating percent cover by species. Environmental data, including percent cover of bare ground, rock, leaf litter, coarse woody debris (woody pieces > 20 cm diameter) and fine woody debris (woody pieces < 20 cm diameter), were also estimated within the circular plots. Coarse woody debris was separated into two decay categories: decay class 1–3 (relatively intact) and decay class 4–5 (highly decayed). Additionally, three measurements of litter depth (in cm) were taken at each gridpoint, and averaged. Sampling, including overstory measurements, occurred prior to treatment (1998 and 1999), immediately post-treatment (2002 and 2003), and 10 years post-treatment (2011 and 2012). In 2016 and 2017, we conducted the 15-year post-treatment sampling following the same protocol. The only deviation from prior sampling that occurred was Wayman and North (2007) identified all graminoids to species during the 2002 and 2003 sampling period. During the 10- and 15-year post-treatment sampling, graminoids were not identified to species and instead were separated into one of two families: Juncaceae (rushes) or Poaceae (grasses), and this same family grouping was applied to the graminoid species data in the 2002 and 2003 sampling period. For all sampling years, understory herbs and shrubs were identified to species.

2.3. Analyses

All statistical analyses were conducted in R version 3.3.2 (R Core Team, 2016). We divided the data collected at each of the 402 gridpoints into two categories: plant cover and environmental variables. We conducted a nonmetric multidimensional scaling (NMS) using the Vegan package (Oksanen et al., 2017) to determine if plant diversity would decline as shrub cover and surface fuels increased over time for each of the six treatments. To be consistent with the NMS performed in Wayman and North (2007), we created a vegetation matrix using the species that occurred at eight or more gridpoints in each of the four sampling periods. Rare species were excluded (those present on < 2% of gridpoints), leaving 19 species for analysis. We totaled the cover values for each of these 19 species for each treatment and year for a total of 24 "treatment-years". We then log-transformed ($\log_{10}(x + 1)$) the plant cover values to account for the highly skewed distribution and the large number of cells containing zero values. The ordination used relativized Euclidean distance measures with a random starting configuration and a maximum of 100 iterations. Two convergent solutions were reached after 20 iterations. We used the same vegetation matrix to create a hierarchical agglomerative cluster analysis to group treatments and sampling years with similar understory vegetation communities, using a Euclidean distance measure and complete-linkage clustering.

Due to the non-normal distribution of both the plant cover and environmental data, we used non-parametric analyses to investigate the relationship between plant cover and environmental variables, and to identify treatment differences. Using the plant cover data for each plot, we calculated richness (mean richness per gridpoint) for each of the six treatments for all four sampling years (1999, 2003, 2011 and 2017). To assess differences in vegetation cover between treatments at the same point in time, we compared mean richness, shrub cover, herb cover, and total plant cover using the Kruskal-Wallis test and Dunn's post hoc test for all four sampling years. To test for changes in plant cover over time, we used the Friedman Test to compare shrub cover, herb cover, total plant cover and mean richness for all treatments using repeated measures. Pre-treatment (1999) values were compared to each post-treatment sampling period (2003, 2011, and 2017) using gridpoint averages per plot.

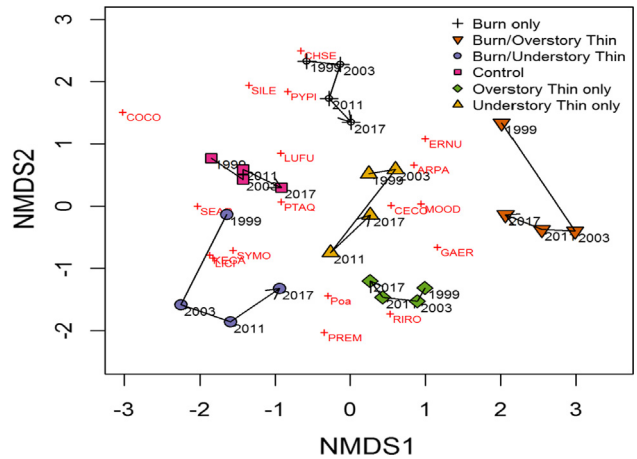

Fig. 1. Nonmetric multidimensional scaling ordination of the treatments through time. Cover values for the 19 species that occurred at eight or more gridpoints in every sampling year were totaled by treatment/year combination. The four letter codes for each of the 19 species are: ARPA = *Arctostaphylos patula*, CAUM = *Calyptridium umbellatum*, CECO = *Ceanothus cordulatus*, CHSE = *Chrysolepis sempervirens*, COCO = *Corylus cornuta*, ERNU = *Eriogonum nudum*, GAER = *Gayophytum eriospermum*, KEGA = *Kelloggia galioides*, LICI = *Linanthus ciliatus*, LUFU = *Lupinus fulcratus*, MOOD = *Monardella odoratissima*, Poa = *Poaceae family*, PREM = *Prunus emarginata*, PTAQ = *Pteridium aquilinum*, PYPI = *Pyrola picta*, RIRO = *Ribes roezlii*, SEAR = *Senecio aronicoides*, SILE = *Silene lemmonii* and SYMO = *Symphoricarpus mollis*.

We used Spearman's rho to identify the most significant associations between the plant cover and environmental variables using the 2017 dataset. The selected plant diversity and cover measures were percent shrub cover, percent herb cover, total plant cover, and mean richness. We compared these measures with the corresponding gridpoint data for bare ground, litter and course woody debris. Additionally, we used Spearman's Rho to identify the relationship between plant cover (shrub cover and herb cover respectively) and live stem density (number of live trees per hectare) at the plot level.

3. Results

3.1. Post-Treatment plant community trajectory

It is important to note that species composition differed across all the plots prior to treatment (Fig. 1). Our cluster analysis (not shown) showed that the plant communities were clustered by treatment rather than time since treatment, indicating that the initial plant community was a significant predictor of the post-treatment plant community. Treatments that included burning had the greatest divergence from the pre-treatment community during the 2003 sampling period. However, fifteen years post-treatment all treatments began to move towards zero in ordination space, indicating a transition toward a similar community assemblage dominated by *Ceanothus cordulatus* and *Arctostaphylos patula*. An overlay of environmental variables on the cross-year NMS indicated that the movement towards zero was driven by increases in litter and coarse woody debris and a reduction in the availability of bare ground (Fig. 2).

3.2. Relationships between ground cover and plant diversity and cover

Treatments had significant immediate effects on ground cover variables such as litter depth and bare ground (Table 1). The differences in these variables reflected the nature and intensity of each treatment. All burn treatments experienced significant increases in bare ground and decreases in litter cover immediately after treatment (2003), which

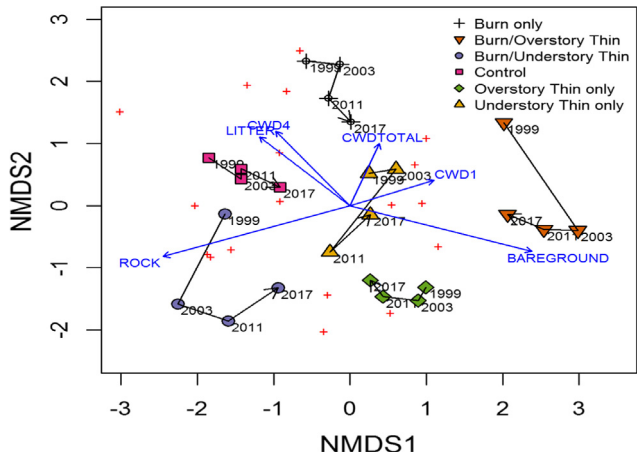

Fig. 2. NMS showing significant ($r^2 \geq 0.2$) environmental variables and the magnitude and direction of their gradient. CWD1 refers to coarse woody debris in decay classes 1–3 (relatively intact) and CWD4 refers to coarse woody debris in decay classes 4–5 (highly decayed).

exposed bare ground. However, ten and fifteen years after burning (2011/2012 and 2016/2017 respectively), litter depths and bare ground cover have largely returned to pre-treatment levels (Table 1). There were no significant differences between treatments for coarse woody debris 10- and 15-years post-treatment.

We found significant post-treatment correlations between environmental variables and plant cover and richness, which corresponded to the associations found in Wayman and North (2007). Increases in herb cover were associated with bare ground (Rho = 0.33, $p < 0.05$) while decreasing herb cover was associated with increasing litter depths (Rho = −0.23, $p < 0.05$). Similarly, species richness increased with bare ground (Rho = 0.31, $p < 0.05$) and decreased with increasing litter depths (Rho = −0.25, $p < 0.05$). Additionally, we found that increases in shrub cover were associated with a reduction in live tree stem density (Rho = 0.74, $p < 0.05$, Fig. 3). Shrub cover increased as the number of live stems per hectare was reduced through thinning, burning, and drought-related mortality.

3.3. Treatment differences in plant cover through time

Fifteen years after treatment, plant cover had increased over pre-treatment levels in all thin and burn (Burn/Overstory Thin = 100%, Burn/Understory Thin = 33%) and thin-only (Overstory Thin only = 66%, Understory Thin only = 21%) treatments. The largest increases in total plant cover were observed in the thin and burn treatments, while burn-only and control plots experienced reductions in plant cover from pre-treatment levels (Burn only = −64%, Control = −58%). Treatments had no significant effect on species richness, but did reduce species evenness as shrub cover increased (Fig. 4).

Prior to treatment, there were no significant differences in shrub cover between treatments (Fig. 5). Significant differences in shrub cover between treatments did not appear until ten years after treatment, with shrub cover increasing in the thin and burn treatments (Burn/Overstory Thin = 98%, Burn/Understory Thin = 55%) and thin-only treatments (Overstory Thin only = 40%, Understory Thin only = 37%) and decreasing in the burn-only treatment (Burn only = −47%). Fifteen years after treatment, shrub cover was significantly greater in the thin and burn treatments when compared to thin-only treatments and treatments that incorporated thinning had more shrub cover than the burn-only and control plots. Increases in shrub cover in thin and burn, and thin-only plots were largely driven by increases in mountain whitethorn compared to pre-treatment levels. Mountain whitethorn accounted for 40% of the increase in shrub cover in the thin-only treatments and 60% of the increase in thin and burn treatments. Green leaf manzanita also experienced significant increases in cover in both thin and burn (Burn/Overstory Thin = 30%, Burn/Understory Thin = 14%) and thin-only treatments (Overstory Thin

Table 1
Changes in percent cover of environmental variables by treatment and year. Different letters denote significant differences ($p < 0.05$) between treatments for a given year (Dunn's post hoc analysis of the Kruskal-Wallis Test). * denotes significant differences in post-treatment values from pre-treatment values ($p < 0.025$, Dunn's post hoc analysis of the Kruskal-Wallis Test).

		Burn only	Burn/understory thin	Burn/overstory thin	Control	Understory thin only	Overstory thin only
Bare ground							
1999	Mean	4.48^{a*}	2.91^{a*}	13.78^{b*}	3.00^{a*}	2.26^{a*}	2.24^{a*}
	SD	(13.82)	(11.99)	(26.92)	(12.70)	(14.07)	(11.14)
2003	Mean	17.00^{bd}	38.19^{a}	64.36^{c}	7.82^{d}	14.66^{bd}	11.61^{d}
	SD	(25.00)	(30.50)	(27.74)	(16.54)	(25.84)	(22.72)
2011	Mean	7.64^{a}	5.31^{ac}	17.26^{b}	4.33^{c*}	5.63^{ac}	4.98^{a}
	SD	(14.40)	(11.93)	(21.57)	(9.97)	(11.21)	(11.17)
2017	Mean	7.28^{a*}	7.09^{ab}	9.29^{b*}	4.31^{abc}	3.23^{c}	3.51^{abc}
	SD	(18.28)	(17.23)	(18.27)	(10.11)	(10.14)	(7.99)
Litter							
1999	Mean	4.28^{ab*}	4.72^{a*}	4.95^{ab*}	3.53^{b*}	3.98^{ab*}	5.02^{a*}
	SD	(3.98)	(4.91)	(5.29)	(3.94)	(3.85)	(4.90)
2003	Mean	1.67^{a}	1.80^{a}	0.71^{b}	3.22^{c*}	2.89^{c*}	3.61^{c*}
	SD	(1.80)	(1.66)	(1.14)	(3.16)	(2.82)	(3.18)
2011	Mean	2.77^{b*}	1.92^{ac}	1.66^{c}	4.02^{d}	3.46^{d*}	2.14^{a}
	SD	(1.75)	(1.02)	(1.13)	(2.85)	(2.07)	(1.41)
2017	Mean	3.40^{ad*}	3.07^{ab*}	2.37^{b*}	3.53^{ad*}	4.83^{c}	3.80^{d*}
	SD	(2.35)	(2.92)	(1.79)	(2.86)	(3.39)	(2.93)
Coarse woody debris							
1999	Mean	5.45^{b}	8.68^{a*}	7.70^{ab*}	9.85^{ab*}	10.63^{ab*}	6.27^{ab*}
	SD	(11.79)	(16.48)	(16.92)	(17.98)	(19.34)	(12.42)
2003	Mean	4.94^{b}	3.29^{a}	8.50^{c*}	8.61^{ab*}	13.16^{cd}	10.93^{d}
	SD	(9.41)	(6.69)	(14.24)	(18.32)	(20.93)	(16.07)
2011	Mean	4.41^{a}	2.21^{a}	3.57^{a}	5.75^{a}	5.42^{a}	4.18^{a*}
	SD	(9.52)	(5.60)	(10.06)	(11.47)	(12.91)	(8.61)
2017	Mean	2.96^{a}	3.89^{ab*}	2.36^{a*}	5.34^{ab*}	5.63^{b*}	4.73^{b*}
	SD	(5.88)	(7.76)	(3.79)	(9.39)	(10.59)	(8.61)

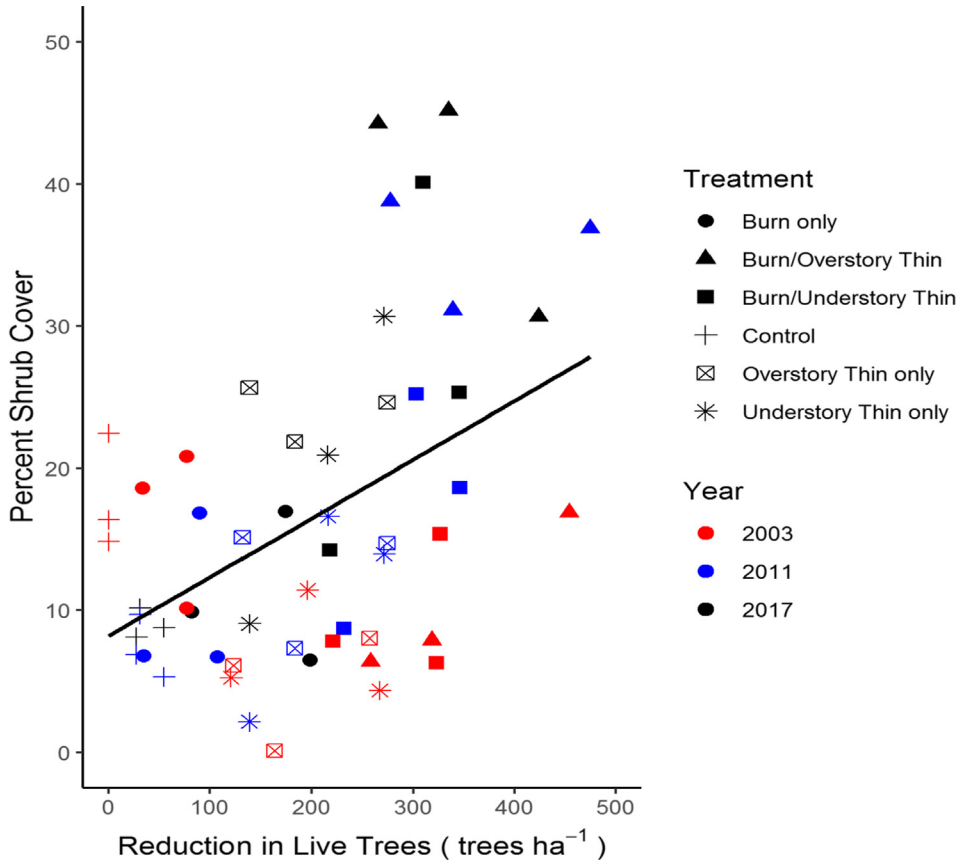

Fig. 3. The relationship (Spearman's Rho) between the average shrub cover for 2003, 2011, and 2017 and the reduction in live tree density from 1999 for each of the three post-treatment sampling years.

only = 42%, Understory Thin only = 33%).

Burn treatments experienced a significant increase in herb cover immediately after treatment when compared to thin-only treatments. Thin and burn plots had the largest increases in herb cover; more than a 3-fold increase compared to pre-treatment levels (Fig. 5). However, ten years after treatment, thin and burn and burn-only treatments experienced significant decreases in herb cover (Burn/Overstory Thin = −50%, Burn/Understory Thin = −40%, Burn/No Thin = −70%) when compared to thin-only treatments where herb cover continued to increase (Overstory Thin only = 14%, Understory Thin only = 22%). Fifteen years after treatment there was no significant difference in herb cover across the treatments and reductions in herb cover were observed across all treatment units.

4. Discussion

The reintroduction of surface fire as a disturbance process promotes biodiversity in mixed-conifer forests of the Sierra Nevada after nearly a century of fire exclusion. While Wayman and North (2007) found that fire and fire-surrogate treatments increased diversity immediately after treatment, our study showed that these effects are short lived in the absence of recurring disturbance. In our study, fire played a critical role in restoring species evenness and herbaceous cover to the understory community immediately after treatment. Mechanical thinning is often considered a partial fire-surrogate treatment because it reduces tree density and canopy cover, mimicking some of the structural effects of a fire treatment. However, we found thinning alone failed to reintroduce the functional processes of fire, including the reduction of litter and surface fuels, and its benefits for the understory plant community. Treatments that incorporated fire experienced a reduction in litter depth and coarse woody debris, increasing the amount of bare ground available for herb germination, while thin-only treatments reduced available bare ground. Increases in herb cover were also associated with an immediate reduction in shrub cover in all treatments, although the reduction was higher in thin and burn treatments (Burn/Overstory Thin = −78%, Burn/Understory Thin = −71%) than the reduction in thin-only treatments (Overstory Thin only = −68%, Understory Thin only = −45%) due to mechanical damage. While the effects of burning and thinning treatments on the understory diverged immediately after treatment, 15 years later, increased shrub cover and litter and woody fuel inputs reduced the bare ground substrate available for germination resulting in a decrease in herb cover. Our results suggest that the Sierra Nevada's high productivity and endemic fire-adapted shrubs with vigorous re-sprouting mechanisms, make frequent fire a necessity for restoring and maintaining a diverse understory plant community. Less productive dry forests, with lower fuel input rates and different shrub species may not experience as rapid a decline in herbaceous cover as we documented. As an example, in southwestern ponderosa pine forests, species richness in a thin and burn treatment did not surpass the control and thin-only treatments until 11 years after treatment (Laughlin et al., 2008).

4.1. Long term treatment effects on litter cover and plant cover

Our results show that the immediate effects of prescribed fire and mechanical thinning on litter cover and shrub cover are short lived, resulting in decreases in herb cover and a loss of evenness fifteen years after treatment. Litter accumulation in the burn treatments over the post-treatment period began to approximate values measured during the pretreatment period by 2017 (Table 1). Significant increases in shrub cover in thin and burn, and thin-only treatments also negatively affected herb cover because shrubs compete with herbs for light and

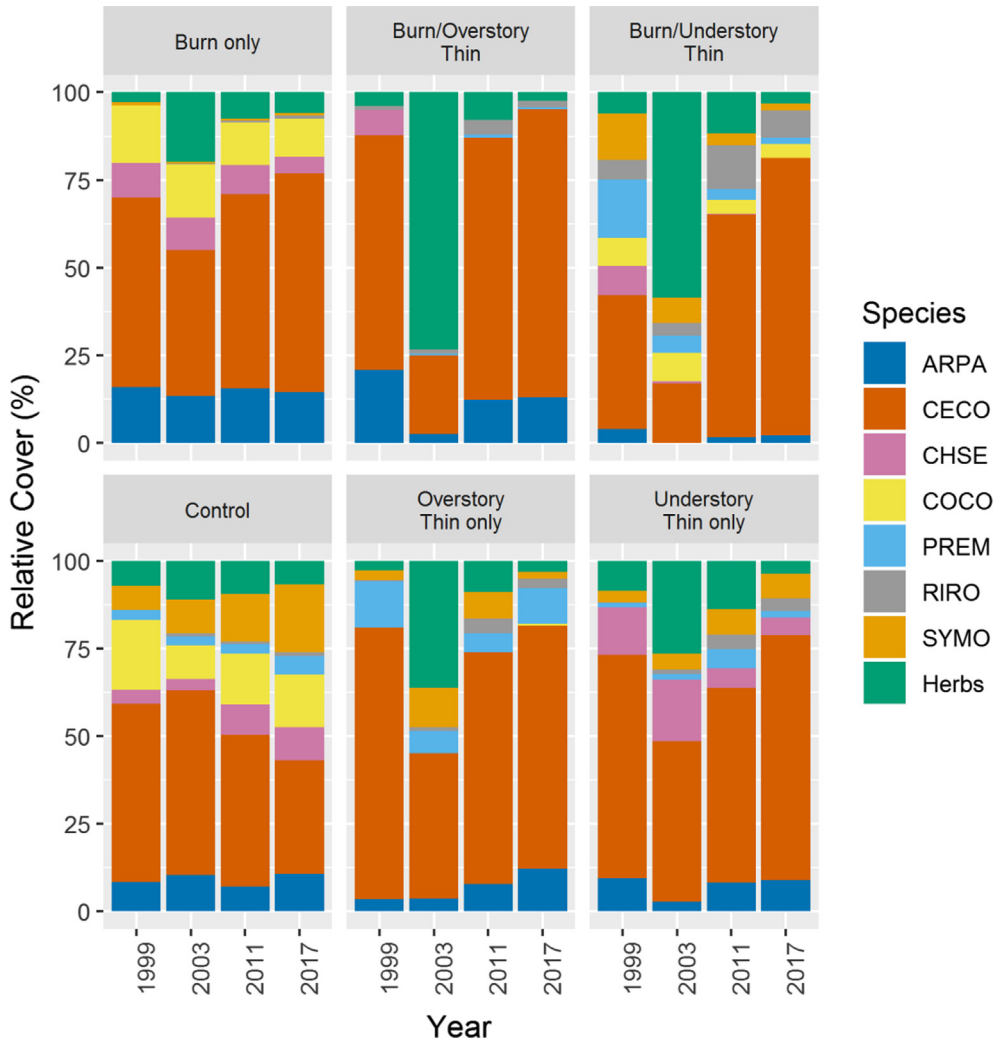

Fig. 4. Percent cover of the 19 most common shrub and herb species by treatment for all four sampling intervals. The four-letter codes correspond to the following species: ARPA = *Arctostaphylos patula*, CECO = *Ceanothus cordulatus*, CHSE = *Chrysolepis sempervirens*, COCO = *Corylus cornuta*, Herbs = *Calyptridium umbellatum, Eriogonum nudum, Gayophytum eriospermum, Kelloggia galioides, Linanthus ciliatus, Lupinus fulcratus, Monardella odoratissima, Poaceae family, Pteridium aquilinum, Pyrola picta, Senecio aronicoides*, and *Silene lemmonii*, PREM = *Prunus emarginata*, RIRO = *Ribes roezlii*, and SYMO = *Symphoricarpus mollis*.

soil moisture. Increased light availability from mechanical tree removal and subsequent mortality likely caused increasing light availability over the post-treatment period. Reductions in live tree biomass and increases in litter depth may also be due to high levels of tree mortality caused by the 4-year extreme drought experienced by the state of California from 2012 to 2015 (Young et al., 2017). Further, prior research that evaluated the effects of snowpack changes on understory plants at Teakettle found that decreasing snowpack led to increased shrub biomass. However, the difference was not significantly higher than the control over the four-year study (Hurteau and North, 2008). These two factors, increased light from drought-induced mortality and reduced snowpack during the drought, may have contributed to the increase in shrub cover. In addition to increased light availability, many of the shrub species found at Teakettle (*Ceanothus cordulatus, Arctostaphylos patula*, and *Ribes* sp.) have life history traits, such as resprouting and refractory seeds, that allow them to persist and proliferate after fire. As a result, the observed increases in plant cover were driven by the successional dynamics of these fire-enhanced shrub species. While total plant cover increased over the post-treatment period, the proliferation of shrubs caused an overall decline in evenness due to reductions in herb cover and a shifting of the understory towards a more homogenous plant community dominated by shrubs.

While other studies have found increases in non-native species in post-treatment understory communities (Griffis et al., 2001, Wienk et al., 2004), we found no non-native plant establishment. This is likely due to the remote setting of the Teakettle Experimental forest, which is relatively isolated and closed to public vehicles which can serve as a vector for invasive species transport (Wayman and North, 2007). However, the potential for invasive species establishment should be considered when applying these treatments to more accessible sites.

4.2. Implications for management

The homogenization of forest structure at the stand and landscape scales with fire exclusion in Sierran mixed-conifer forest results in a transition to a shrub-dominated state when high-severity wildfire occurs (Coppoletta et al., 2016). A homogenous, shrub-dominated understory can have a variety of ecological consequences in mixed-conifer forests. Re-sprouting species, such as *Ceanothus* and *Arctostaphylos*, have a significant competitive advantage over herbaceous species and conifer seedlings for light, moisture and space (Clark et al., 2013). The rapid post-fire development of the shrub canopy and their ability to extract soil water more efficiently than conifers reduces soil moisture, and the combined effects of light and water competition limit both herbaceous plant and conifer seedling germination and establishment (Bohlman et al., 2016; Gray et al., 2005; Royce and Barbour, 2001;

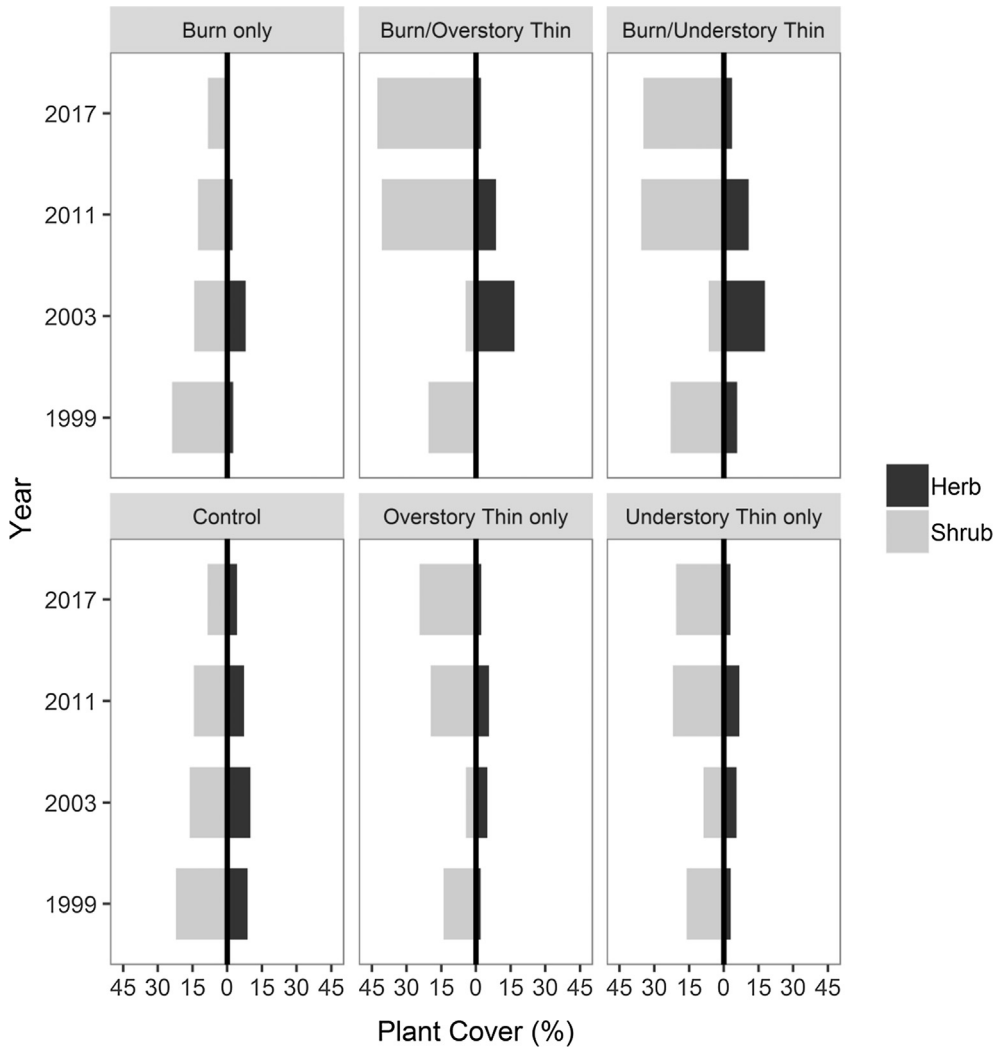

Fig. 5. Percent cover of herbs and shrubs by treatment for all four sampling intervals. Treatment differences were determined using Dunn's post hoc analysis for the Kruskal-Wallis test. Cross-year differences were determined using Friedman's test.

Shainsky and Radosevich, 1986). Our results demonstrate that following the reintroduction of surface fire in these systems, shrub species cover increases over time to the detriment of herbaceous species cover. It is unclear if subsequent burning at the historical mean fire return interval of 17-years will be sufficient to maintain herbaceous cover in the understory or if a shorter return interval will be required initially. However, in the absence of subsequent fire, the understory will likely remain dominated by shrubs and herbaceous and conifer species that are adapted to shade and deeper accumulations of litter. Given the historic fire frequency of Sierran mixed-conifer forests and changes that have occurred with fire exclusion, restoring forest structural heterogeneity across scales (from the site to the landscape) will help reduce the likelihood of transitioning from one homogenous state to another. Further, the effect of repeated burning on enhancing and maintaining understory diversity (Webster and Halpern, 2010), demonstrates the importance of restoring surface fire to these forests for maintaining the heterogeneity that supports understory plant diversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.058.

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