



# Shrub removal in reforested post-fire areas increases native plant species richness



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## ABSTRACT

Large, high severity fires are becoming more prevalent in Sierra Nevada mixed-conifer forests, largely due to heavy fuel loading and forest densification caused by past and current management practices. In post-fire areas distant from seed trees, conifers are often planted to re-establish a forest and to prevent a potential type-conversion to shrub fields. Typical reforestation efforts promote conifer survival and growth by reducing competing shrub cover, yet the effects of these practices on plant species richness and composition are not well understood. We compared the effects of treatment and time since fire on (1) native and exotic plant species richness, (2) plant community composition, and (3) stand structure. Plots were installed throughout three different aged but proximate fires located in the canyon of the South Fork of the American River in California, 10, 22, and 41 years after fire. All three fires included large patches of stand-replacing fire that had been reforested with conifers as well as unplanted areas. Native plant species richness was significantly higher in planted areas where shrub cover was lower and planted trees successfully established. Native species richness decreased as time since fire increased, but the relationship between shrub control and richness persisted. Exotic species richness was higher on treated sites in the more recent fires, while the opposite was true in the oldest fire. As time since fire increased, understory species composition shifted from a community dominated by annuals and perennials to one dominated by shrubs and shade-tolerant trees. Shrub cover and July soil moisture were the top two factors influencing understory richness levels. Natural regeneration was low in the youngest fire and high in the oldest fire but highly heterogeneous in all three fires. Our study suggests that while retaining some shrub cover for post-fire habitat may be desirable, some level of shrub reduction does favor native plant richness and overall herbaceous cover.

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## 1. Introduction

Sierra Nevada mixed-conifer forests are experiencing an unprecedented increase in the number and size of stand-replacing fires (Miller et al., 2009; Miller and Safford, 2012; Mallek et al., 2013). While fire has always played an integral role in maintaining the structure and resilience of these forests, the increase in fuels and stand density over the past century due to logging and fire suppression (van Wagtenonk and Fites-Kaufman, 2006; Fites-Kaufman et al., 2007; Lydersen et al., 2013; Safford and Stevens, in press) has led to an increase in fire severity – a measure of biomass loss to fire – as well as high-severity patch

size, thus increasing the distance to adequate seed sources necessary for forest re-establishment (Bonnet et al., 2005; Donato et al., 2009). In the Sierra Nevada, high intensity fire also initiates the germination and establishment of highly competitive shrub species – especially from the genera *Ceanothus* and *Arctostaphylos* – that quickly become dominant in high burn severity sites and can remain dominant for several decades to a century or more (Cronmiller, 1959; Kauffman and Martin, 1991; Nagel and Taylor, 2005; Lauvaux et al., 2016). As mixed-conifer forests continue to experience large, stand-replacing fires, land managers must determine which silvicultural practices are most effective for promoting forest re-establishment while retaining some shrub habitat and a diverse herbaceous understory.

A major focus of silvicultural methods has long been the maximization of wood production by manipulating developing forest

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tree stocking. To reach desired stocking rates more quickly in post-fire environments, land managers often employ silvicultural techniques that enhance establishment, survival, and growth of desirable tree species (Graham and Jain, 2004). While post-fire reforestation can include a number of management practices (e.g., salvage logging, tree propagation and planting, etc.), tree seedling survival and growth often require early control of competing vegetation (Zhang et al., 2006, 2008; McDonald and Fiddler, 2010). Since the focus of forest management is typically the health and survival of (usually conifer) trees, relatively few studies have focused on how understory species richness and composition are altered by post-fire management practices (DiTomaso et al., 1997; McGinnis et al., 2010; Kayes et al., 2011; Leverkus et al., 2014). In Sierra Nevada mixed-conifer forests, most plant species are found in the understory and herbaceous understory plants are important sources of wildlife, livestock, and human foodstuffs (Weeden, 1996; Potter, 1998, 2005) while also providing other ecosystem services such as ground cover, nutrient cycling, and essential wildlife habitat (Beedy, 1981; Hagar, 2007; Kuhn et al., 2011).

Competition for water and light is one of the main factors determining the future stand dynamics of a burned landscape (Halpern, 1989; Vilá and Sardans, 1999; Royo and Carson, 2006; DeSiervo et al., 2015). Initially, availability is high following stand-replacing fire (Noble and Slatyer, 1977; Grime, 1977), but as vegetation becomes denser, competition increases. Many shrub species consume high levels of soil water (Royce and Barbour, 2001), often outcompeting herbs and small trees in the initial years after disturbance. Where seed sources are available and sites remain disturbance free, growing trees can eventually overtop competing shrubs to create a low light and low soil moisture environment which reduces the abundance of shrubs and other species in the understory (Schoonmaker and McKee, 1988). Common management practices such as post-fire logging, herbicide application and grubbing (hand removal of competing plants) can greatly modify these competitive dynamics and have a significant long-term influence on the developing forest and its understory community (McDonald and Everest, 1996; Nagel and Taylor, 2005; Batatineh et al., 2006; Abella and Springer, 2015). While shrubs may be

strong competitors with regenerating trees, they were certainly not absent in pre-Euroamerican settlement forests (average shrub cover in such forests has been estimated at 15–30% [Knapp et al., 2013; Safford and Stevens, in press]) and shrubs provide important ecological services such as habitat provision for small mammals and birds (Converse et al., 2006; Humple and Burnett, 2010) and some species are major nitrogen fixers (Delwiche et al., 1965; Oakley et al., 2006).

We conducted a field study to determine how post-fire reforestation affects understory plant species richness and composition in areas that were severely burned and reforested at three different times in the past. We hypothesized that vegetation control in reforestation areas would increase both native and exotic species richness through its positive effect on light and water availability. Since post-fire reforestation in California encompasses a suite of components that are almost always carried out in concert our study aimed to measure the outcome of the treatment regime rather than each element separately. To do this we compared the effects of treatment and time since fire by looking at three categories of plant responses: (1) richness of native and exotic plant species, (2) understory plant community composition, and (3) characteristics of overstory stand structure. The three fires selected for this study occurred within 25 km of each other, burned predominantly in mixed-conifer forest and were 10, 22 and 41 years old at the time of study, providing insights into three different temporal stages of post-fire development.

## 2. Methods

### 2.1. Study area

Our study was conducted in the Eldorado National Forest (ENF), which is located in the central Sierra Nevada (Fig. 1) of California. Elevation of the study area ranged from 1365 m to 2075 m. The climate is Mediterranean with cold, wet winters and warm, dry summers. Annual precipitation in the area ranges from 100 cm to 180 cm, with most of it falling between October and April as rain or snow, depending on the elevation (National Climatic Data

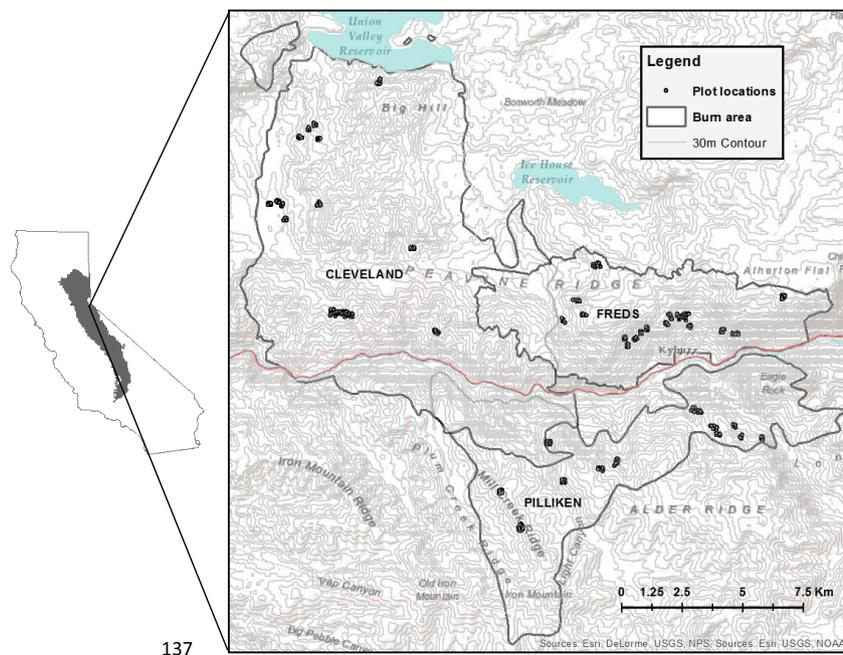


Fig. 1. Location of study sites in the Eldorado National Forest, CA, with the three studied fires identified.

Center, <http://www.ncdc.noaa.gov/>). Soils in the area are relatively deep and well-drained, and are formed from granitic, volcanic, gabbroic and low-grade metamorphic substrates (Wagner et al., 1981; Soil Survey Staff, 2015). The dominant forest type is mixed-conifer, composed of ponderosa pine (*Pinus ponderosa*), black oak (*Quercus kelloggii*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), canyon live oak (*Quercus chrysolepis*), and incense cedar (*Calocedrus decurrens*), with some Jeffrey pine (*Pinus jeffreyi*) at higher elevations. Montane hardwood forests dominate lower elevations (mostly *Q. kelloggii* and *Q. chrysolepis*), and red fir (*Abies magnifica*) forests are present at the higher elevations.

### 2.1.1. Fires and post-burn management

**2.1.1.1. Fire.** Our study encompasses three wildfires; the Freds Fire (October 2004; 3196 ha), the Cleveland Fire (September 1992; 9342 ha) and the Pilliken Fire (August 1973; 4174 ha). All three fires burned in the South Fork of the American River canyon and resulted in large patches of severely-burned forest. This study focuses only on those areas that burned at high severity (>75% basal area mortality of canopy trees) on Forest Service land. High severity burning occurred on 58% of the Freds Fire, 64% of the Cleveland Fire and >50% of the Pilliken Fire. Vegetation burn severity was assessed in the Freds and Cleveland Fires from Landsat-based imagery (Miller and Thode, 2007), but the Pilliken Fire predated Landsat, so in this case we identified high-severity burn areas using a 1974 false-color composite Landsat Multispectral Scanner System (MSS) image mapped to near infrared, red and green bands (wavelengths 0.7–0.8, 0.6–0.7 and 0.5–0.6  $\mu\text{m}$ ) as well as pre- and post-fire aerial photos. Although basal area mortality could not be specifically assessed using MSS imagery, the bands can clearly identify areas where there is no green foliage, a condition similar to the high-severity areas in the Freds and Cleveland Fire areas. We used these three adjacent fires as a chronosequence to approximate potential vegetation changes through time.

Although substituting space for time has been frequently used in ecology field studies (Pickett, 1989; Fukami and Wardle, 2005), chronosequences have several limitations that we attempted to minimize through careful plot selection (Johnson and Miyanishi, 2008). All three fires occurred in the same general area (all plots were within 25 km of one another; Fig. 1), have approximately the same mix of parent materials, share the same species, and experienced

similar management histories. According to Walker et al. (2010) it is most appropriate to use a chronosequence when studying relatively short-term temporal changes (1–100 years) where the successional trajectories are predictable, where there are few dominant species, and where succession proceeds through relatively few discrete seral stages. While our mixed-conifer study system meets these basic guidelines, we caution that any study substituting space for time provides an imperfect analysis of temporal trends in understory richness and composition.

**2.1.1.2. Treatments.** Our goal was not to assess the effectiveness or the direct impacts of individual management techniques, but rather to assess the current conditions of forest stands resulting from the standard combination of reforestation practices used by the Forest Service in the Sierra Nevada (see Appendix A for management specifics). We focused on comparing sites that were successfully reforested (i.e., currently have planted trees established on the landscape) or not (stands that are currently shrubfields or are otherwise unreforested). We grouped these plots into two general categories (“Treated” and “Not Treated”) based on whether or not reforestation activities included planted tree establishment in combination with “effective” control of competing vegetation (mostly shrubs; Fig. 2). Vegetation control was assumed to have been effective if planted trees established successfully. On the Eldorado National Forest, vegetation/shrub control has usually been accomplished with hand-applied herbicide (Glyphosate, Hexazinone, and/or Triclopyr; FACTS database; D. Errington, US Forest Service, pers. comm.), along with some component of hand (“grubbing”) or mechanical removal. In addition to planting and shrub removal, 96% of the treated plots in the two older fires also experienced some level of pre-commercial thinning, a common practice for planted stands exceeding 20 years of age.

A few stands in our study were untreated except for post-burn salvage logging (i.e., the removal of dead trees). McGinnis et al. (2010), who included the Cleveland Fire in their study assessing post-fire fuels, observed no difference in shrub, grass, or forb cover between logged and unlogged sites. Using a subset of plots, we also examined whether there was a significant difference in understory shrub and herbaceous cover and diversity between untreated sites that were either logged or unlogged. In the Freds Fire, 25 logged plots were compared with 41 unlogged plots using a

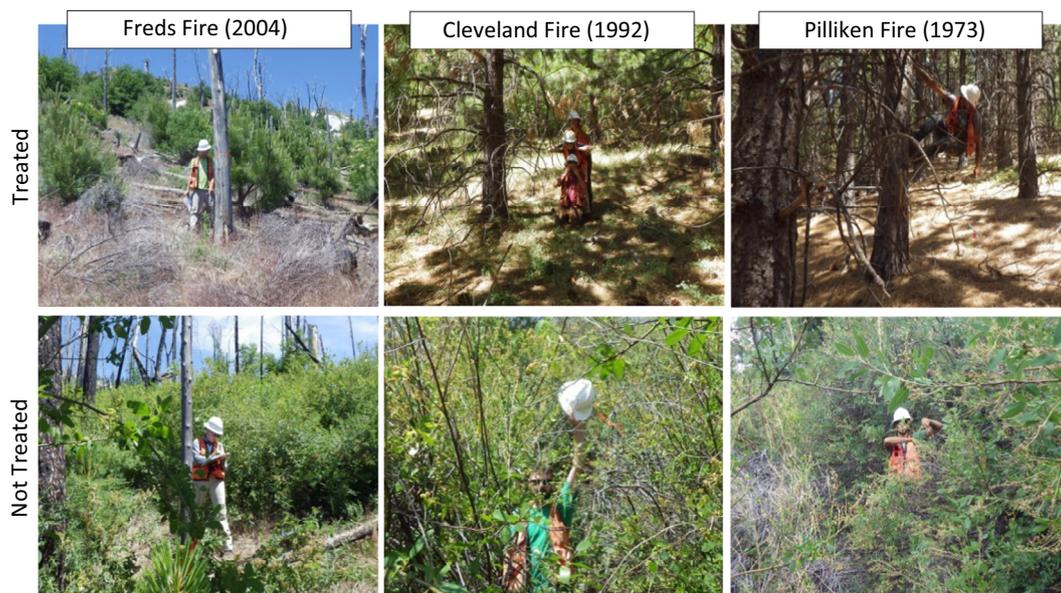


Fig. 2. Plot photos from different treatment and fire combinations.

non-parametric, unpaired Mann-Whitney test (Mann and Whitney, 1947). There was no difference in shrub cover ( $p = 0.73$ ), herb cover ( $p = 0.08$ ), or diversity ( $p = 0.10$ ). We did the same analysis for the Cleveland Fire with 11 logged plots and 25 unlogged plots. Shrub cover was different ( $p = 0.01$ ) but in both cases was  $>70\%$  on average and the difference can be attributed to differences in site conditions. There was no difference in herb cover ( $p = 0.08$ ) or diversity ( $p = 0.86$ ). Additionally, some of the plots in the Cleveland Fire were planted but had no chemical control of shrubs. These plots received some targeted non-chemical grubbing associated with planting but had no additional shrub control treatments, making these treatments ultimately ineffective.

## 2.2. Data collection

In 2014 we established a total of 341 60-m<sup>2</sup> circular plots in areas that had burned at high severity in the Freds, Cleveland and Pilliken fires. High severity patches were located using relativized delta Normalized Burn Ratio (RdNBR) maps (Miller and Thode, 2007) for the Freds and Cleveland Fires, and infrared pre- and post-fire aerial photos for the Pilliken Fire. We determined plot locations in ArcGIS by placing a 50 × 50 m UTM grid over high severity areas. Plot centers were occasionally shifted in order to maintain a minimum distance of at least 20 m from treatment boundaries and/or riparian areas, while maintaining a minimum distance of 30 m between plots. We targeted sites that had two distinct management strategies (Treated or Not Treated) located adjacently (distance  $< 500$  m) so that paired plots were in close geographic proximity, but in some cases (mostly in the Pilliken Fire) we paired plots across wider distances.

Treated and Not Treated plots in each fire were paired based on similarities in aspect, elevation and slope. A total of 194 plots were included in the paired analysis: 82, 58 and 54 for the Freds, Cleveland, and Pilliken fires, respectively. 128/194 paired plots were located within 500 m of each other. 54/194 plots were within 2 km of one another and 10/194 plots were separated by approximately 4 km. These more distant plot pairings were all in the Pilliken Fire, which offered limited sampling locations, as much of the landscape is privately owned and, due to its age, many areas had experienced other forms of management. In addition to the paired plots, we sampled 147 plots that were not paired in order to increase our sample size for the non-paired analyses across the chronosequence (see Appendix A). Of the unpaired plots, 96 were treated (16 in the Freds, 51 in the Cleveland, and 29 in the Pilliken) and 51 were not treated (25 in the Freds, 7 in the Cleveland, and 19 in the Pilliken). These additional plots were distributed throughout each burn area in order to maximize the topographic and environmental variation captured.

At each plot, we measured slopes and aspect in the field. Plot history was recorded based on field observations as well as information obtained from the U.S. Forest Service's FACTS (Forest Activity Tracking System) database and from personal communications with Forest Service employees involved in the management. We collected data on ground cover which included percent cover of bare ground, rock, basal vegetation, litter, and coarse woody debris. Litter depth on each plot was taken in three random locations and then averaged. We ocularly estimated overall vegetation covers of all vegetation strata (trees, shrubs, herbs) and categorized them by overstory and understory as well as by live and dead.

We collected data on densities and growth of regenerating tree species at each plot. All seedlings ( $< 1.37$  m tall) and saplings ( $> 1.37$  m tall and  $\leq 10$  cm diameter at breast height) were counted and identified to species. We also recorded the height and previous year's growth for each seedling and sapling. Measurements of diameter at breast height (DBH) and height for each tree with a DBH  $\geq 10$  cm were also taken. We noted whether each tree was

planted or established naturally by identifying whether multiple trees appeared to be the same age, coinciding with the age of the fire or a few years after based on their size and/or number of whorls, and arrayed with consistent spacing.

We used a spherical densiometer to assess canopy closure (a measure inversely related to light availability) at each plot. Densiometer readings were taken at 'elbow' height facing each cardinal direction and then averaged. Another set of readings was taken at 30 cm above the ground, again facing each cardinal direction and then averaged. This latter set of readings was taken to capture the canopy closure at the level where most herbaceous species occur. We took soil moisture measurements at five locations in each plot using a time domain reflectometry (TDR) unit with 12 cm probes. One measurement was taken at plot center and then four more measurements were taken, one in each cardinal direction 2 m from plot center. These data were collected at a strategic time (over the month of July 2014) to target the period when site differences in soil moisture depletion are most apparent in the landscape (Ziemer, 1964; authors' pers. obs.).

We collected data on plant species composition and areal cover in the field. The timing of plot visits was determined based on elevation and potential direct incident radiation in order to account for differing site phenologies. We estimated vegetation cover and modal heights for all lifeforms including trees, shrubs, and herbaceous species (forbs and graminoids), as well as for each species present in the plot. Trees were classified as either hardwood or conifer and percent cover was estimated for each species. Woody vegetation was further broken down based on the following height classes: trees  $\geq 2$  m, trees  $< 2$  m, shrubs  $\geq 2$  m, shrubs  $\geq 0.5$  m and  $< 2$  m, and shrubs  $< 0.5$  m. Cover estimates were made to the nearest percent for values  $< 10\%$  and to the nearest multiple of 5 for values  $> 10\%$ . Any plant that was present in the plot but had  $< 1\%$  cover was recorded as "trace" cover, which was converted to 0.5% cover for the purposes of analysis. All plants were identified to species when possible using the Jepson Manual, 2nd edition (Baldwin et al., 2012) and specimens at the J.M. Tucker and Beecher Crampton Herbaria, located at UC Davis.

## 2.3. Data analysis

From the species composition data we calculated total understory species richness for each plot. We did the same for native and exotic species richness. We used Q-Q plots and the Shapiro-Wilks test to verify normality in the data. When assumptions of normality were not met, we used nonparametric tests when appropriate. As stated above, we compared shrub and herbaceous cover and diversity between logged untreated and not logged untreated plots and found no significant differences ( $p > 0.5$ ). We combined these few logged/untreated plots with the unlogged/untreated plots in the remainder of our analyses.

A Poisson-distributed generalized linear mixed-effects model (GLMM) was used to test for the effect of 'planting + shrub control' on understory richness (using the *lme4* package in R 3.1.2). In comparison with a random intercept-only model and fixed effect + random intercept model (i.e., no random slope), the following model was the best fit, accounting for 51% of the normalized model likelihoods (i.e., AIC model weights):

$$\text{Richness} \sim \text{Trtmnt} + (\text{Trtmnt}|\text{TSI}) \quad (1)$$

where Richness = species richness; Trtmnt = 'planting + shrub control' treatment; and TSI = time since fire (10, 22, and 41 years). Treatment was included as a fixed effect and as a random slope for each time since fire. Fire was included as a random intercept. All treated plots included in the GLMM analysis were also pre-commercially thinned except for in the case of the Freds Fire. Standard errors around fixed and random effects were estimated using

the *R arm* package (Gelman and Hill, 2006). Confidence intervals around fitted parameters were estimated using *lme4* R package. To compare how treatment varied within a given fire, we ran 1000 parametric bootstrap simulations to obtain conditional probabilities surrounding the predicted medians (using function *bootMer* in package *lme4*, R 3.1.2). We then used paired *t*-tests and, when necessary, the Wilcoxon signed rank nonparametric test using the *exactRankTests* R package to compare differences in species richness along with other variables between specific paired plots.

We summarized both natural and artificial tree regeneration by calculating seedling and sapling densities per hectare for each fire-by-treatment combination. We first did this for separate genera and also for separate species. Slope corrections were made according to Abella et al. (2004). We did the same for natural and planted trees (>10 cm DBH) in each fire and treatment combination. We ran a series of regressions using understory plant species richness as the dependent variable and tree (>10 cm DBH) density as the independent variable. Analyses were performed in R 3.1.2 (R Core Team, 2014) unless otherwise noted.

In order to identify the key environmental gradients associated with understory species richness in each fire, we performed three conditional inference tree analyses. This was done using function *ctree* in the *party* package (R 3.1.2), which is a non-parametric conditional inference tree that uses binary recursive partitioning to estimate a regression relationship and uses permutation-based significance tests for variable selection. We included all available environmental variables in this analysis. Soil moisture data were available for 306/341 plots and canopy closure measurements were made for 332/341 plots, so analyses utilizing these variables had a slightly smaller sample size. We then used the previously selected GLMM model to assess the effect of treatment and time since fire on the biological variable selected as the strongest predictor of richness according to the conditional inference tree. As above, standard errors around fixed and random effects were estimated using the *R arm* package (Gelman and Hill, 2006) and confidence intervals around fitted parameters were estimated using *lme4* R package. We again ran 1000 parametric bootstrap simulations to obtain conditional probabilities surrounding the predicted medians of the biological variable (using function *bootMer* in package *lme4*, R 3.1.2).

We conducted an indicator species analysis (ISA; see Dufrêne and Legendre (1997) for a description of this method) in PC-ORD 6.0 (McCune and Medford, 2011) to test whether individual species showed significant associations with particular treatment and fire combinations. We looked at all understory species, and then native and exotic species separately. Species are typically considered good indicators if they have an indicator value  $\geq 25$  and a *p*-value < 0.05 (Dufrêne and Legendre, 1997).

### 3. Results

From the 341 plots, a total of 243 understory plant species were identified, 63 of which were present in at least 5% of plots ( $\geq 17$  plots, see Appendix B). The 2004 fire was the most speciose (182 plants sampled in 123 plots), followed by the 1992 fire (144 plants sampled in 116 plots), and then the 1973 fire (98 plants sampled in 102 plots), indicating a decline in overall richness as time since fire increases. This pattern was mirrored by the plot-level richness values, which decreased by >50% in both treated and untreated plots between the youngest and oldest fire (Table 1). There were a total of 21 exotic species identified but of those only 7 were abundant (>5% of all plots) with the three most abundant being *Bromus tectorum* (cheatgrass), *Lactuca serriola* (prickly lettuce) and *Tragopogon dubius* (salsify). Native plant species richness in the

**Table 1**

Means of environmental variables, vegetation cover, and understory richness in post-fire Sierra Nevada mixed-conifer stands for two different management regimes within three different fires (standard error in parentheses). T = Treated, NT = Not Treated. Significant differences ( $p < 0.05$ ) within fires are indicated in bold.

	Freds Fire (2004)		Cleveland Fire (1992)		Pilliken Fire (1973)	
	T	NT	T	NT	T	NT
Sample size (n)	41	41	29	29	27	27
Canopy closure (%)	<b>5.8</b> (1.1)	<b>20.3</b> (3.4)	54.7 (5.3)	58.2 (6.7)	<b>86.5</b> (1.7)	<b>58.9</b> (5.5)
Canopy closure at 30 cm (%)	<b>11.5</b> (1.9)	<b>37.8</b> (4.5)	59.7 (4.8)	64.7 (6.0)	<b>87.4</b> (1.6)	<b>73.4</b> (4.9)
Conifer cover (%)	<b>4</b> (1.1)	<b>0.5</b> (0.2)	<b>44.8</b> (4.6)	<b>1.9</b> (0.9)	<b>70.5</b> (4.1)	<b>4.2</b> (2.3)
Hardwood cover (%)	2.8 (0.8)	4.6 (1.2)	0.5 (0.2)	3.5 (2.1)	<b>0.1</b> (0.0)	<b>9.6</b> (4.5)
Shrub cover (%)	<b>7.3</b> (1.7)	<b>67.2</b> (4.4)	<b>19.9</b> (4.9)	<b>87.2</b> (4.1)	<b>39.8</b> (5.9)	<b>83.7</b> (4.6)
Herb cover (%)	<b>69</b> (4.8)	<b>27.5</b> (4.1)	<b>44.6</b> (5.5)	<b>3.1</b> (1.1)	2.5 (0.9)	6.7 (2.0)
Bare ground (%)	8.3 (2.4)	2.5 (0.5)	4.4 (1.7)	6.4 (1.4)	<b>0.3</b> (0.1)	<b>7</b> (1.7)
Litter depth (cm)	1.8 (0.1)	1.8 (0.2)	3 (0.2)	2.5 (0.3)	<b>5.5</b> (0.3)	<b>3.9</b> (1.0)
July soil moisture (% VWC <sup>a</sup> )	4.5 (0.3)	4.4 (0.2)	5.5 (0.4)	3.8 (0.4)	<b>1.3</b> (0.1)	<b>0.3</b> (0.1)
Evenness	0.44	0.49	0.53	0.56	<b>0.73</b>	<b>0.51</b>
Understory species richness/60 m <sup>2</sup>	<b>17.1</b> (0.7)	<b>15.0</b> (0.6)	<b>14.2</b> (0.8)	<b>6.2</b> (0.7)	7 (0.6)	5.3 (0.7)
Native species richness/60 m <sup>2</sup>	<b>14.2</b> (0.6)	<b>12.8</b> (0.6)	<b>10.9</b> (0.5)	<b>5.5</b> (0.6)	<b>6.9</b> (0.6)	<b>4.9</b> (0.6)
Exotic species richness/60 m <sup>2</sup>	<b>3.0</b> (0.2)	<b>2.2</b> (0.2)	<b>3.3</b> (0.4)	<b>0.4</b> (0.2)	<b>0.1</b> (0.1)	<b>0.5</b> (0.1)
Exotic cover (%)	<b>47.9</b> (5.8)	<b>15.9</b> (2.8)	<b>11.8</b> (3.5)	<b>0.2</b> (0.1)	<b>0.0</b> (0.0)	<b>0.7</b> (0.3)
Exotic graminoid cover (%)	<b>46.7</b> (5.8)	<b>15.1</b> (2.7)	<b>10.2</b> (3.4)	<b>0.0</b> (0.0)	<b>0.0</b> (0.0)	<b>0.7</b> (0.3)
Density of trees ( $\geq 10$ cm DBH; TPH) <sup>b</sup>	0 (0)	0 (0)	346.7 (41.1)	30.9 (12.8)	516.5 (41)	41.6 (18.1)
Mean tree seedling and sapling density ( $\leq 10$ cm DBH; TPH) <sup>b</sup>	467.7 (61.5)	141.7 (49.7)	322.3 (79.5)	49.1 (15)	196.4 (79.5)	2420.8 (1104.1)

<sup>a</sup> VWC = volumetric water content.

<sup>b</sup> DBH = diameter at breast height (1.37 m); natural and artificial regeneration are included here. TPH = trees per hectare.

understory was significantly higher in the treated plots for all three fires (Freds: *p*-value < 0.05; Cleveland: *p*-value < 0.001; Pilliken: *p*-value < 0.02). Exotic plant species richness was significantly higher in the treated plots for the two younger fires (Freds: *p*-value < 0.02; Cleveland: *p*-value < 0.001) but was higher in the untreated plots in the oldest fire (Pilliken: *p*-value < 0.05; Table 1).

Multiple species showed significant associations with each treatment and fire combination when all understory species were included, however only a small portion had a maximum indicator value ( $IV_{\max}$ )  $\geq 25$  (Appendix C). The strongest indicator species was *C. decurrens*, which indicated treated areas in the Pilliken Fire ( $IV_{\max} = 50.4$ ;  $p = 0.0002$ ). It was also the most abundant species in the understory of these plots. *L. serriola* was the second best indicator species and indicated treated areas in the Freds Fire ( $IV_{\max} = 33.3$ ;  $p = 0.0002$ ). The third best indicator species was *Clarkia rhomboidea* in untreated areas of the Freds Fire ( $IV_{\max} = 32.5$ ;  $p = 0.0002$ ). Areas that were not treated in the Cleveland and the Pilliken fires did not have strong indicator species, and  $IV_{\max}$  for all species was <20. These areas, along with the treated Pilliken areas, were dominated by shrub and tree species in the understory.

Average overall densities of natural (unplanted) regeneration were highest in the Pilliken Fire with 2350 seedlings and saplings

per hectare in the untreated plots and 1173/ha in the treated plots. Treated Cleveland plots had the third highest density with 647/ha followed by untreated Freds plots (218/ha) and treated Freds plots (210/ha). The lowest natural regeneration densities were found in the untreated Cleveland plots with only 67 seedlings and saplings per hectare. The high amount of regeneration found in the untreated Pilliken plots was driven almost exclusively by *Q. kelloggii* (black oak; 2118/ha) while regeneration in the treated Pilliken plots had a more even species distribution (Appendix D; Fig. 3). It is important to note that, although mean seedling and sapling densities were relatively high in some cases, median densities for all species (with the exception of ponderosa pine in treated Cleveland plots), were zero, indicating a high level of heterogeneity. When artificial regeneration was included, average densities on treated Freds plots jumped from 210/ha to 579/ha with a median of 559/ha. Densities in treated Cleveland plots also increased due to some of the planted trees still being present in the sapling size class.

Overall tree (>10 cm DBH) densities were highest in the treated plots of the Pilliken Fire with 552 trees per hectare (TPH; median of 540 TPH) followed by treated Cleveland plots with 365 TPH (median of 356 TPH). In both cases these high densities were driven by *P. ponderosa* that were planted post-fire (Appendix E). When only planted trees were included, densities in both the Cleveland and Pilliken were very similar (353 TPH and 414 TPH respectively). Untreated areas in both of these fires had very few trees on average and median densities were zero. The Freds Fire had no trees present due to the young stands. We found a negative correlation between tree density and species richness in treated plots of the Cleveland and the Pilliken fires but the amount of variance explained was very low ( $r^2 = 0.04\%$ ;  $p < 0.05$ ). For the Freds Fire, seedling and sapling densities showed a positive correlation with species richness ( $r^2 = 0.12\%$ ;  $p < 0.05$ ).

Results from the pairwise comparisons showed that stand conditions varied considerably with treatment and time since fire (Table 1). In treated areas of the youngest fire, canopy closure was very low (5.8% mean closure) with a relatively high percentage

of bare ground (mean = 8.3%) and minimal amounts of litter (1.8 cm mean depth). Treated areas in the oldest fire exhibited a dense canopy closure (86.5% mean closure) with almost no bare ground (0.3% mean cover) and a relatively deep litter layer (5.5 cm mean depth). Untreated areas had significantly higher shrub cover and lower conifer cover than their counterparts, which was expected given that management in the treated areas was focused on promoting conifer establishment and growth while reducing competition from shrubs (and occasionally hardwood tree species).

The results of the conditional inference tree analyses indicated that overall shrub cover, soil moisture, and cover of tall shrubs (>2 m height) were the strongest environmental drivers of understory species richness. Lower plant species richness was associated with higher shrub cover and higher plant species richness was associated with higher soil moisture (Fig. 4). Soil moisture values were quite low but were similar to those reported in other studies (Stevens et al., 2014; North et al., 2005). Forty-one years after fire soil moisture was significantly lower in untreated plots dominated by shrubs than in treated plots dominated by trees ( $p = 0.0001$ ).

Results from the Poisson-distributed generalized linear mixed-effects model showed that the effect of treatment (planting + shrub control) on richness was positive but varied in strength with time since fire (see Appendix F.1 for model results). The effect was strongest at 22 years after fire and weakest at 41 years after fire (Fig. 5). There is also a clear effect of treatment and time since fire on shrub cover, and at 22 years after fire this effect was also the strongest (Fig. 6; see Appendix F.2 for model results).

#### 4. Discussion

Our results show higher native plant species richness for as long as 40 years post-fire in areas that experienced control of competing shrubs associated with post-fire reforestation. Exotic species richness was also higher in treated plots, yet this may be a temporary effect as exotics were mostly absent in the oldest fire. Species richness levels in general decreased with time since fire whether the stand was treated or not, a trend typical of most forest and shrubland ecosystems due to processes of competitive exclusion and shading (Huston, 1979; Connell and Slatyer, 1977). Along with decreasing richness, understory species composition shifted from a community dominated by annuals and herbaceous perennials to one dominated by shrubs and shade-tolerant trees. Our study points to high levels of shrub cover and the associated competition for resources as the major driver of reduced species richness in untreated plots. In treated plots of the oldest fire, a similar reduction in soil moisture and understory light availability can be attributed to the dense overstory of conifers and infilling of shade-tolerant woody species. Tree density alone is not a strong influence on richness and other factors, such as canopy cover, play a more important role. Other studies that assessed the mechanisms behind diversity levels and the cover and density of understory species in semiarid forest and shrub environments have found similar results with regard to soil moisture and canopy closure (e.g., Anderson et al., 1969; Riegel et al., 1995; North et al., 2005; Kuhn et al., 2011).

Competition for light and water appear to be the major drivers of richness levels in the understory of the fires we studied, with shrub cover and soil moisture the two environmental variables most influencing the number of species. In the Sierra Nevada's Mediterranean climate, soil moisture has a key influence on understory communities (North et al., 2005; Gray et al., 2005). North et al. (2005) found that soil moisture, light, and litter depth significantly influenced understory patterns in an old-growth Sierra Nevada mixed-conifer forest. Riegel et al. (1995) studying the

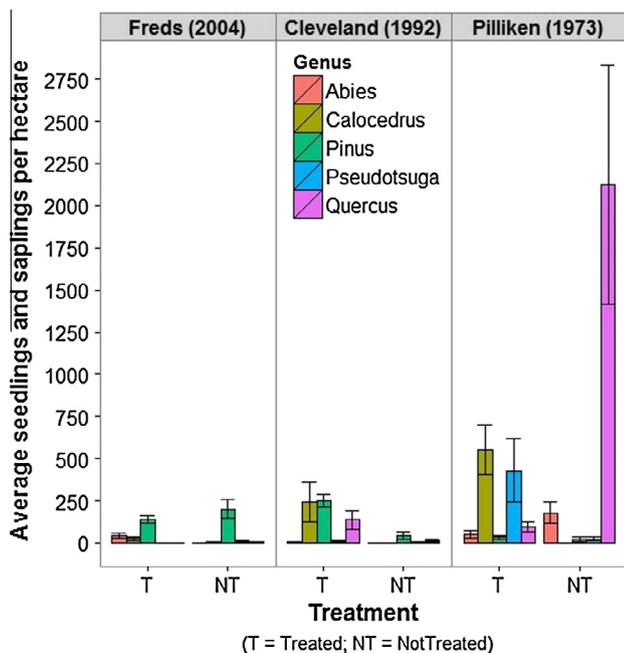


Fig. 3. Mean seedlings and saplings per hectare separated by genus, fire, and treatment. Planted trees are excluded from this figure. Error bars indicate  $\pm$  the standard error from the mean.

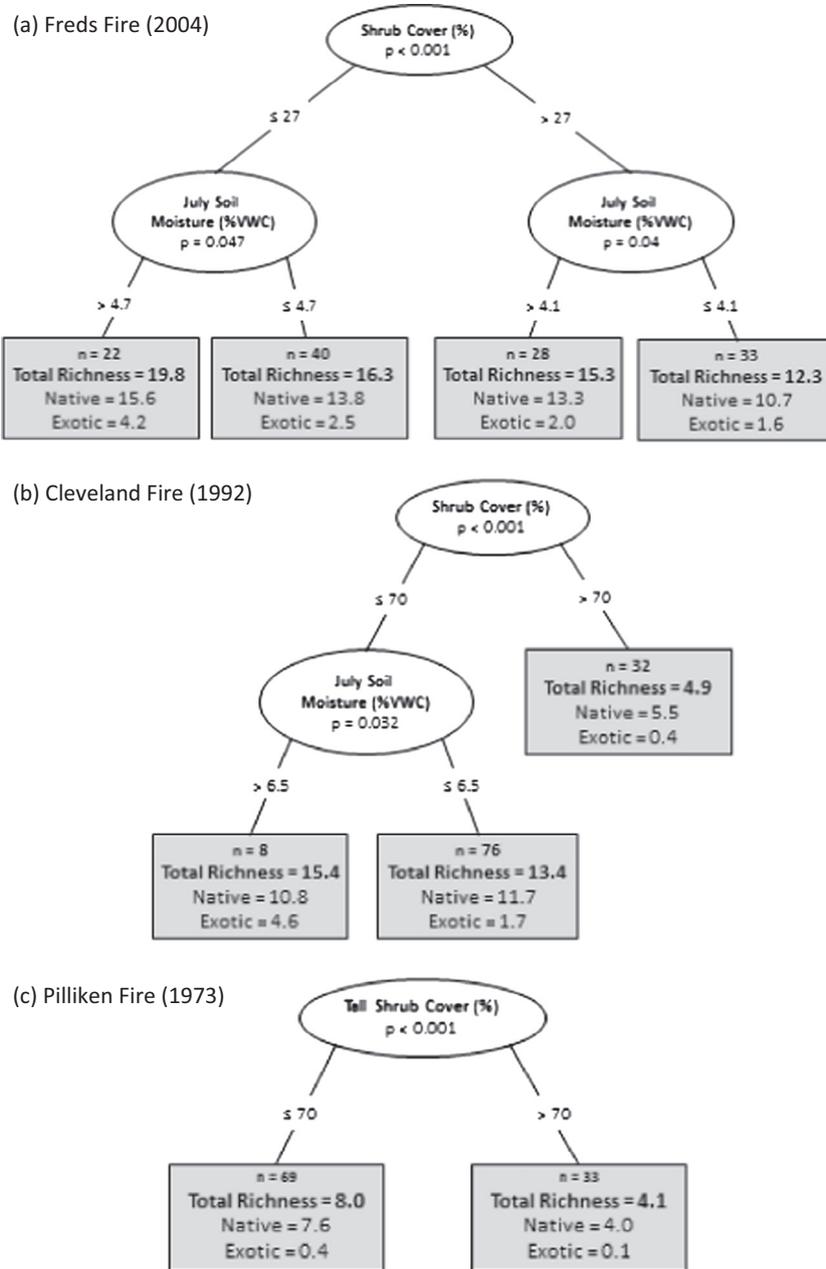


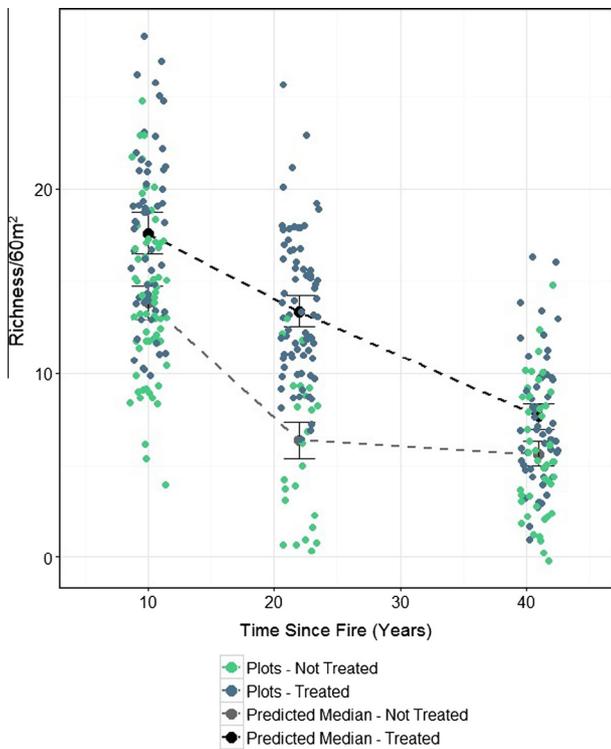
Fig. 4. Three conditional inference trees showing predicted understory species richness per 60 m<sup>2</sup> based on significant environmental variables for each fire.

effects of both canopy thinning and root reduction in ponderosa pine found that the combination of increased light due to the canopy reduction and increased soil resources (water and nutrients) due to root-reduction led to an increase in understory species cover, with the largest increase occurring with graminoids (124% increase 2 years after treatment). They also found that canopy reduction alone did not cause a significant increase in plant cover nor did it affect the composition of lifeforms, but they did find that species composition within lifeforms changed. Riegel et al. (1995) concluded that no single resource controls understory species dynamics and that they are likely controlled by a combination of light, soil moisture and nutrients.

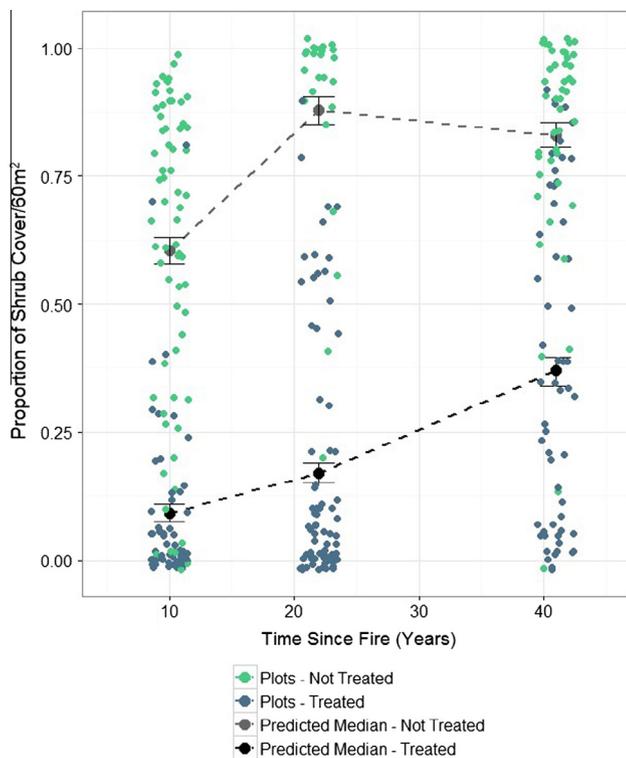
Shrubs extract moisture from the soil more completely than conifers, leading to more rapid soil moisture depletion (Shainsky and Radosevich, 1986; Royce and Barbour, 2001). Consistent with these studies, we found that soil moisture tended to be higher in treated plots (high conifer cover, low shrub cover) than in

untreated plots (low conifer cover, high shrub cover) although this result was only significant in the oldest fire. Shainsky and Radosevich (1986) found that soil moisture levels were lower in stands where shrubs were present than in pine monocultures and that the relative canopy growth rates of the pine seedlings decreased as the proportion of shrub seedlings increased.

At 10 years after fire, the Freds Fire can be considered early successional. In both treated and untreated areas, understory richness was the highest of all three fires, matched only by treated areas in the Cleveland Fire. At this point the Freds Fire area is still in the “stand initiation” stage of forest development (Oliver, 1981) and neither conifers nor shrubs have become dominant enough to greatly reduce understory richness (Greenberg et al., 2011). Natural tree regeneration in the areas we sampled in the Freds Fire was low (the median density was zero for natural seedlings and saplings on the landscape) and artificial regeneration made up the majority of young trees on the landscape. With a low density of



**Fig. 5.** Raw richness data plotted with predicted median richness with 95% prediction intervals\* against time since fire. Upper dashed line represents treated, lower dashed line represents untreated. (\*Plotted prediction intervals include uncertainty in the fixed effects only and do not include uncertainty associated with the random intercept and slope.)



**Fig. 6.** Raw data on proportion of shrub cover plotted with predicted median shrub cover proportions with 95% prediction intervals\* against time since fire. Upper dashed line represents untreated, lower dashed line represents treated. (\*Plotted prediction intervals include uncertainty in the fixed effects only and do not include uncertainty associated with the random intercept and slope.)

surviving seed sources and with intense competition with shrubs, natural conifer establishment in these areas is likely to remain sparse for some time (Royo and Carson, 2006; Turner et al., 1998), especially if fire recurs, or the recent climatic drying trend continues in future years. Collins and Roller (2013) found a similar lack of regeneration coupled with high shrub cover in unplanted stands in their study looking at fires ranging from 2 to 11 years old.

At 22 and 41 years after fire, the areas that were not reforested in the Cleveland and Pilliken fires had very few trees per hectare and median tree densities in our plots were zero. Planted areas on the other hand support high median stand densities, as well as higher numbers of native species. Areas that were not reforested in these older sites are often occupied by tall, dense stands of montane chaparral. Some of these stands are up to four meters tall and are dominated by a few shrub species (e.g., *Ceanothus integerrimus*, *Arctostaphylos viscida*, *Ceanothus cuneatus*) that strongly reduce both light and water availability in the understory (Shainsky and Radosevich, 1986; Plamboeck et al., 2008). If these sites do not re-burn, such low diversity stands of fire-initiated montane chaparral can persist for many years, until they are eventually shaded out by conifers that can tolerate decades of low light (usually shade-tolerant, fire-sensitive species like white fir). In an area such as the South Fork of the American River canyon, where human-ignited fires commonly occur, there is a reasonable likelihood that these shrub-dominated landscapes will re-burn before conifers are able to repopulate them. Re-burns of these chaparral stands tend to burn at high severity, further inhibiting conifer regeneration, leading to a potentially permanent type-conversion to shrubfields depending on fire frequency (Lauvaux et al., 2016; Coppoletta et al., 2016).

Our study suggests that a species-rich understory in areas burned by high-severity wildfire is associated with low levels of shrub cover. Given the variety of ecosystem services provided by shrubs (wildlife habitat, nitrogen fixing, soil retention, etc.), however, we are not suggesting eliminating them from post-fire habitats. Variability in shrub cover and canopy closure can be promoted by heterogeneous fire effects (Stevens et al., 2014), or by post-fire management activities which act to create variable light conditions associated with different topographic and soil moisture conditions.

McGinnis et al. (2010) carried out a fuels-focused study of four fires in the Sierra Nevada, including the Cleveland Fire from our study that also assessed effects of post-fire logging and herbicide use on the understory plant community. McGinnis et al. (2010) found that native species richness was only nominally higher in herbicide treated plots (in the Cleveland Fire: 35.5 species per plot treated vs. 28.5 species per plot untreated; their plots were much larger than ours). McGinnis et al. (2010) also found a strong response of exotic species and overall cover, similar to our study. In the Cleveland Fire, our studies both found that exotic grass cover increased by >20 times (in our case, 0–10.2%; in theirs, 0.3–7.1%) in herbicide treated vs. untreated plots. However, McGinnis et al. (2010) found that native grass species also responded strongly to treatment, and overall native species cover was >80% of the cover in their treated plots. Unlike our study, McGinnis et al.'s (2010) data do not show an obvious effect of time on exotic species cover, but this may be due to large geographic distances between their fires and associated physiographic and floristic variability.

A common management concern is the potential of invasive grasses to generate sufficient biomass to increase fire hazard. Similar to other studies, our research found an increase in the richness and biomass of exotic grasses in reforested areas treated by herbicide (e.g., McGinnis et al., 2010; McDonald and Everest, 1996), creating a potential fire hazard worth considering when using herbicides to control shrubs during reforestation. Indiscriminate broadcast spraying seems especially likely to create continuous and dense layers of grassy fuels that may increase fire hazard

and threaten the survival of tree plantations when they burn. Our results suggest that this may be more of a concern for young plantations than in mature stands. McGinnis et al. (2010) provide an overview of the tradeoffs involved in designing and implementing post-fire management, but unlike our study they don't include native species diversity in their assessment.

In addition to the high densities of established trees in planted areas of the two older fires, we sampled many individuals of shade-tolerant tree species that had seeded into the understory in the two to four decades since planting. This unchecked infilling of shade-tolerant species in the understory of many planted stands is driving these areas toward the same fuel accumulation/high fire severity conundrum that plagues most of the rest of the Sierra Nevada (Ansley and Battles, 1998; McKelvey et al., 1996; Safford and Stevens, in press). As with understory species diversity, live and dead fuel accumulations in planted forests might be better managed by promoting more open-canopied (preferably heterogeneous) stand conditions using spatially and temporally variable forest thinning, prescribed fire, or naturally ignited wildfires under moderate weather conditions (Youngblood, 2005; Kobziar et al., 2009). By creating open conditions early in stand development, it may be more feasible to use prescribed fire as a silvicultural tool influencing seral development.

## 5. Management implications

Reforestation success in this study has been largely attributed to the control of shrub species surrounding planted conifers. While we have shown the benefit this can have on understory species diversity, it is important to keep in mind the benefit of having shrubs in the system, especially immediately following fire. A few of the ecosystem benefits shrubs provide include nitrogen fixation, soil stabilization, and wildlife habitat (Delwiche et al., 1965; Busse et al., 1996; Hagar, 2007). The potential importance of shrubs during initial stages of pine establishment through their role as possible nurse plants has also been discussed in the literature. Gómez-Aparicio et al. (2004) conducted a meta-analysis looking at the use of shrubs as nurse plants in Mediterranean environments of southeast Spain. They found that nurse shrubs had a strong facilitative effect on seedlings when on hot, dry slopes. However, when looking just at pine seedlings, the magnitude of this effect was larger for survival than for growth and in general lower than all other species. These findings are from a different Mediterranean system, however, and a recent correlational study centered on the Sierra Nevada found little evidence of a nurse-shrub effect in post-fire conifer regeneration (Welch, 2015).

In our study, shrub control included some hand- and mechanical removal, but it primarily consisted of hand spraying of herbicide (FACTS database; D. Errington, pers. comm.; also see McGinnis et al., 2010). The use of herbicide in the control of competing vegetation in forest plantations has a long history and a well-documented record of success in promoting faster, more robust reforestation (McDonald and Fiddler, 1993, 2010; McDonald and Everest, 1996). Our study suggests that some level of herbicide use can also have measureable native plant diversity benefits. However, public opposition to the use of herbicides is strong in some circles (Little et al., 2006), partially due to the concern of herbicide use promoting exotic species. Although our data do show that herbicide use can cause an early increase in the richness and cover of exotic species, this effect was not apparent several decades after fire.

Disturbance in Sierra Nevada forests can provide structural diversity (Bonnicksen and Stone, 1982; Lydersen et al., 2013; Parks et al., 2014), increasing the heterogeneity of resource (light, water, nutrients) availability, ultimately influencing biodiversity

patterns. Small patches of early-seral habitat (including shrubs) caused by severe forest disturbances can be a key resource for a variety of species and are considered an important component of properly functioning mixed-conifer forest ecosystems (Swanson et al., 2011). With the increasing prevalence of large, severe fires however (Miller et al., 2009; Miller and Safford, 2012), the geography of early-seral forests is experiencing a major state change. The spatial scale and arrangement of early seral conditions in burned areas has shifted from a fine-scale arrangement of smaller patches, which characterized mixed conifer forests before Euroamerican settlement, to a coarse-scale arrangement dominated by large high severity patches (Mallek et al., 2013; Harris and Taylor, 2015; Safford and Stevens, in press). As a result, modern fires often decrease fine scale heterogeneity and potentially the biodiversity associated with local microclimate and habitat variability. This suggests that post-fire restoration may need to provide some of that heterogeneity by managing for different objectives at fine scales.

In extensive high-severity patches, natural re-colonization of sites is limited to species that are either capable of resprouting after fire, are obligate seeders dependent on fire, have an ample seed bank capable of surviving fire, or are highly successful wind-dispersers. This potentially eliminates species like ponderosa, Jeffrey and sugar pine (which were dominant trees in pre-Euroamerican settlement forests) that have limited seed dispersal and struggle to establish in sites that are already dominated by highly competitive species. Our study suggests that active reforestation that helps trees establish in these landscapes by utilizing a variety of management tools to either control or localize shrub cover can also help sustain overall biodiversity on the landscape. Since intensive reforestation may not always be feasible at the landscape level given the size of high-severity patches in many recent Sierra Nevada wildfires (>1000 ha patches are no longer uncommon), selecting smaller patches to reforest and maintain within a larger high-severity area become necessary triage (Schönenberger, 2001; Holl et al., 2011; Stanturf et al., 2014). This concept, sometimes termed “applied nucleation” or “founder stands”, may be beneficial when resources are limited and seed sources are distant. Allowing topography to help direct the location and type of different management practices and objectives can be useful in returning vegetation heterogeneity to the system while minimizing the likelihood of an unwanted re-burn. For instance, understory diversity might be the first priority in more mesic locations, shrubs in more xeric locales, and tree regeneration on moderate and steep slopes. More experimentation needs to be done to determine the viability of these sorts of restoration strategies in the Sierra Nevada (Boanares and Azevedo, 2014) and with any of these strategies, vulnerability to re-burns needs to be a serious consideration so that restoration efforts are not derailed.

## Acknowledgments

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## Appendix A

The number of treated and untreated plots for each fire by management activities. Numbers in parentheses indicate plots that were included in the paired analysis.

	Fred's Fire (2004)		Cleveland Fire (1992)		Pilliken Fire (1973)	
	Treated	Not treated	Treated	Not treated <sup>a</sup>	Treated	Not treated
Planted	57 (41)	0	80 (29)	11 (4)	56 (27)	0
Not planted	0	66 (41)	0	25 (25)	0	46 (27)
Herbicide treatment	57 (41)	0	80 (29)	0	56 (27)	0
No herbicide treatment	0	66 (41)	0	36 (29)	0	46 (27)
Salvage logged	57 (41)	25 (12)	61 (10)	11 (4)	56 (27)	46 (27)
Not salvage logged	0	41 (29)	19 (19)	25 (25)	0	0
Pre-commercial thin	0	0	75 (24)	0	56 (27)	0
No pre-commercial thin	57 (41)	66 (41)	5 (5)	36 (29)	0	46 (27)
Spacing of planted trees <sup>b</sup>	Groups of 2–3 seedlings, every ~5.2 m apart (±25%)		Groups of 2 seedlings, every 3–6 m (±25%)		1 seedling, every ~4 m (inferred from planting densities of 300 TPA)	
Average size of high severity patches (ha) <sup>c</sup>	675 (150–1200)		1870 (1650–2090)		1143 (200–2085)	

<sup>a</sup> “Not Treated” plots in the Cleveland Fire that were planted experienced some non-chemical grubbing associated with planting but were otherwise unmanaged.

<sup>b</sup> Numbers for the Fred's Fire and the Cleveland Fire have been taken from EIS reports while numbers for the Pilliken Fire were inferred from details recorded on forest management stand cards.

<sup>c</sup> Patch sizes were conservatively estimated using ArcGIS and only include patches where plots were installed.

## Appendix B

Species list.

Species name	Species code	Growth/lifeform	Origin
<i>Pteridium aquilinum</i>	PTEAQU	Perennial Forb	N
<i>Acmispon americanus</i>	ACMAME	Annual Forb	N
<i>Acmispon nevadensis</i>	ACMNEV	Perennial Forb	N
<i>Agoseris grandiflora</i>	AGOGRA	Perennial Forb	N
<i>Agoseris retrorsa</i>	AGORET	Perennial Forb	N
<i>Allophyllum gilioides</i>	ALLGIL	Annual Forb	N
<i>Apocynum androsaemifolium</i>	APOAND	Perennial Forb	N
<i>Cirsium vulgare</i>	CIRVUL	Perennial Forb	E
<i>Clarkia rhomboidea</i>	CLARHO	Annual Forb	N
<i>Claytonia parviflora</i>	CLAPAR	Annual Forb	N
<i>Cryptantha echinella</i>	CRYECH	Annual Forb	N
<i>Epilobium brachycarpum</i>	EPIBRA	Annual Forb	N
<i>Erigeron inornatus</i>	ERIINO	Perennial Forb	N
<i>Eriophyllum lanatum</i>	ERILAN	Perennial Forb	N
<i>Galium aparine</i>	GALAPA	Annual Forb	N
<i>Galium bolanderi</i>	GALBOL	Perennial Forb	N
<i>Galium sparsiflorum</i>	GALSPA	Perennial Forb	N
<i>Gayophytum diffusum</i>	GAYDIF	Annual Forb	N
<i>Gilia capitata</i>	GILCAP	Annual Forb	N
<i>Hosackia crassifolius</i>	HOSCRA	Perennial Forb	N
<i>Iris hartwegii</i>	IRIHAR	Perennial Forb	N
<i>Lactuca serriola</i>	LACSER	Annual Forb	E
<i>Leptosiphon ciliatus</i>	LEPCIL	Annual Forb	N
<i>Lupinus grayi</i>	LUPGRA	Perennial Forb	N
<i>Madia gracilis</i>	MADGRA	Annual Forb	N
<i>Mimulus torreyi</i>	MIMTOR	Annual Forb	N
<i>Phacelia imbricata</i>	PHAIMB	Perennial Forb	N
<i>Pseudognaphalium canescens</i>	PSECAN	Perennial Forb	N
<i>Stephanomeria lactucina</i>	STELAC	Perennial Forb	N
<i>Tragopogon dubius</i>	TRADUB	Perennial Forb	E

## Appendix B (continued)

Species name	Species code	Growth/lifeform	Origin
<i>Trifolium breweri</i>	TRIBRE	Perennial Forb	N
<i>Verbascum thapsus</i>	VERTHA	Perennial Forb	E
<i>Vicia americana</i>	VICAME	Perennial Forb	N
<i>Viola pinetorum</i>	VIOPIN	Perennial Forb	N
<i>Bromus carinatus</i>	BROCAR	Perennial Graminoid	N
<i>Bromus tectorum</i>	BROTEC	Annual Graminoid	E
<i>Carex multicaulis</i>	CARMUL	Perennial Graminoid	N
<i>Carex rossii</i>	CARROS	Perennial Graminoid	N
<i>Cynosurus echinatus</i>	CYNECH	Annual Graminoid	E
<i>Elymus elymoides</i>	ELYELY	Perennial Graminoid	N
<i>Elymus glaucus</i>	ELYGLA	Perennial Graminoid	N
<i>Elymus trachycaulus</i>	ELYTRA	Perennial Graminoid	N
<i>Festuca myuros</i>	FESMYU	Annual Graminoid	E
<i>Melica aristata</i>	MELARI	Perennial Graminoid	N
<i>Poa secunda</i>	POASEC	Perennial Graminoid	N
<i>Stipa occidentalis</i>	STIOCC	Perennial Graminoid	N
<i>Arctostaphylos patula</i>	ARCPAT	Shrub	N
<i>Ceanothus cordulatus</i>	CEACOR	Shrub	N
<i>Ceanothus integerrimus</i>	CEAINT	Shrub	N
<i>Ceanothus prostratus</i>	CEAPRO	Shrub	N
<i>Chamaebatia foliosa</i>	CHAFOL	Shrub	N
<i>Chrysolepis sempervirens</i>	CHRSEM	Shrub	N
<i>Frangula californica</i>	FRACAL	Shrub	N
<i>Prunus emarginata</i>	PRUEMA	Shrub	N
<i>Ribes roezlii</i>	RIBROE	Shrub	N
<i>Symphoricarpus mollis</i>	SYMMOL	Shrub	N
<i>Abies concolor</i>	ABCO	Conifer	N
<i>Calocedrus decurrens</i>	CADE	Conifer	N
<i>Pinus lambertiana</i>	PILA	Conifer	N
<i>Pinus ponderosa</i>	PIPO	Conifer	N
<i>Pseudotsuga mensiesii</i>	PSME	Conifer	N
<i>Quercus chrysolepis</i>	QUCH	Hardwood	N
<i>Quercus kelloggii</i>	QUKE	Hardwood	N

## Appendix C

The top 5 indicator species representing each fire and treatment combination. Indicator species analysis was conducted using PC-ORD 6.0 (McCune and Medford, 2011) and determined which species showed significant associations with each group. IV = Indicator Value.

Fire	Treatment	Species	Life form	IV <sub>max</sub>	p-value
Freds (2004)	Treated	<i>Lactuca serriola</i> <sup>a</sup>	Annual forb	33.3	0.0002
		<i>Gayophytum diffusum</i>	Annual forb	31.2	0.0002
		<i>Epilobium brachycarpum</i>	Annual forb	28.8	0.0002
		<i>Acmispon nevadensis</i>	Perennial forb	28.8	0.0002
		<i>Pinus ponderosa</i>	Tree	28.6	0.0002
	Not Treated	<i>Clarkia rhomboidea</i>	Annual forb	32.5	0.0002
		<i>Galium bolanderi</i>	Perennial forb	17.6	0.0006
		<i>Madia gracilis</i>	Annual forb	16.7	0.0004
		<i>Claytonia parviflora</i>	Annual forb	15.5	0.0008
		<i>Quercus chrysolepis</i>	Tree	13.1	0.009
Cleveland (1992)	Treated	<i>Viola pinetorum</i>	Perennial forb	26.2	0.0002
		<i>Agoseris grandiflora</i>	Perennial forb	25.9	0.0002
		<i>Tragopogon dubius</i> <sup>a</sup>	Annual forb	24.9	0.0002
		<i>Cynosurus echinatus</i> <sup>a</sup>	Annual grass	17.1	0.0016
		<i>Eriophyllum lanatum</i>	Perennial forb	15.6	0.0014
	Not Treated	<i>Polygala cornuta</i>	Perennial forb	18.3	0.0002

(continued on next page)

## Appendix C (continued)

Fire	Treatment	Species	Life form	IV <sub>max</sub>	p-value
Pilliken (1973)	Treated	<i>Ceanothus cuneatus</i>	Shrub	17.5	0.0002
		<i>Prunus emarginata</i>	Shrub	11.6	0.0218
		<i>Drymocallis glandulosa</i>	Perennial forb	10.6	0.0036
		<i>Angelica breweri</i>	Perennial forb	4.5	0.0344
	Not Treated	<i>Calocedrus decurrens</i>	Tree	50.4	0.0002
		<i>Quercus kelloggii</i>	Tree	17.3	0.0032
		<i>Symphoricarpus mollis</i>	Shrub	16.3	0.0024
		<i>Abies concolor</i>	Tree	13.2	0.0064
		<i>Pseudotsuga menziesii</i>	Tree	13.1	0.0004
		<i>Pteridium aquilinum</i>	Perennial forb	12.3	0.0008
		<i>Rubus glaucifolius</i>	Shrub	7.3	0.0102
		–	–	–	–
		–	–	–	–
		–	–	–	–

<sup>a</sup> Exotic species.

## Appendix D

Average densities of natural and artificial tree regeneration. Median densities are given in parentheses. T = Treated; NT = Not Treated.

Genus	Average seedlings and saplings per hectare (median)					
	Fred's Fire		Cleveland Fire		Pilliken Fire	
	T	NT	T	NT	T	NT
<i>Abies</i>	87.9 (0)	0 (0)	4.5 (0)	0 (0)	52.7(0)	180.3 (0)
<i>Calocedrus</i>	29.3 (0)	5.6 (0)	245.4 (0)	0 (0)	555.7 (0)	0 (0)
<i>Pinus</i>	461.7 (529.2)	201.4 (0)	260.9 (176.4)	46.6 (0)	35.9 (0)	19.6 (0)
<i>Pseudotsuga</i>	0 (0)	6.2 (0)	8.8 (0)	4.9 (0)	430.7 (0)	24.3 (0)
<i>Quercus</i>	0 (0)	5.4 (0)	139.2 (0)	15.0 (0)	97.7 (0)	2126.6 (0)
Total	578.9 (558.9)	218.5 (0)	658.6 (349.1)	66.5 (0)	1172.6 (183.8)	2350.8 (184.1)

## Appendix E

Average trees per hectare for both natural and artificial regeneration. Median trees per hectare are given in parentheses. T = Treated; NT = Not Treated; S = Naturally seeded; P = Planted.

Species	Average trees per hectare (median)											
	Fred's Fire				Cleveland Fire				Pilliken Fire			
	T		NT		T		NT		T		NT	
	S	P	S	P	S	P	S	P	S	P	S	P
<i>Abies concolor</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4.6 (0)	0 (0)	0 (0)	6.6 (0)	46.3 (0)	28.6 (0)	0 (0)
<i>Calocedrus decurrens</i>	0 (0)	0 (0)	0 (0)	0 (0)	4.4 (0)	0 (0)	0 (0)	0 (0)	85.7 (0)	6.7 (0)	12.2 (0)	0 (0)
<i>Pinus jeffreyi</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	6.8 (0)	6.6 (0)	0 (0)	0 (0)
<i>Pinus lambertiana</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	13.3 (0)	0 (0)	0 (0)	0 (0)	3.2 (0)	0 (0)	0 (0)
<i>Pinus ponderosa</i>	0 (0)	0 (0)	0 (0)	0 (0)	7.0 (0)	326.2 (352.1)	20.0 (0)	4.9 (0)	32.5 (0)	334.2 (357.0)	12.2 (0)	0 (0)
<i>Pseudotsuga menziesii</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	9.3 (0)	0 (0)	0 (0)	6.8 (0)	17.0 (0)	4.0 (0)	0 (0)

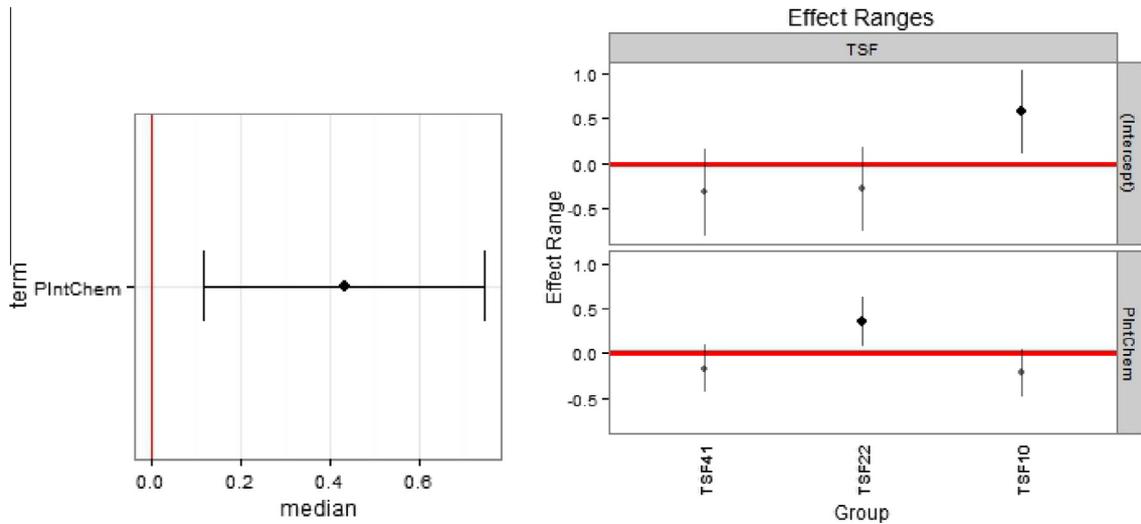
Appendix E (continued)

Species	Average trees per hectare (median)													
	Fred's Fire				Cleveland Fire				Pilliken Fire					
	T		NT		T		NT		T		NT			
	S	P	S	P	S	P	S	P	S	P	S	P		
Total	0	0	0	0	364.7	24.9	552.3	57.0	(0)	(0)	(356.2)	(0)	(540.3)	(0)

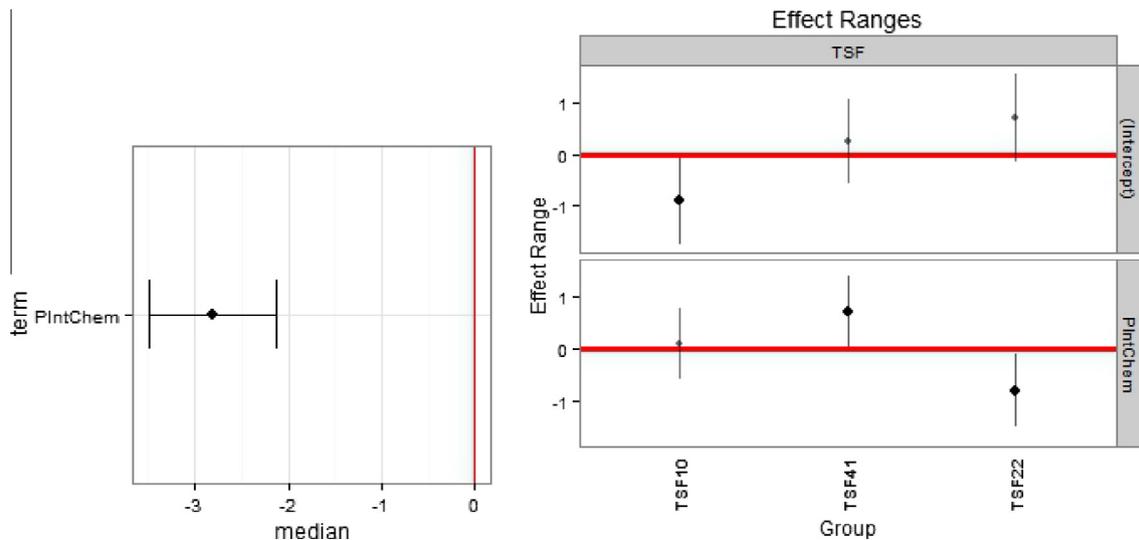
Appendix F

Plots showing the simulated fixed effect of treatment (PlntChem = planted + shrub control) and the simulated random effects of treatment, as a random slope, and time since fire (TSF), as a random intercept, on (1) richness and (2) shrub cover. Error bars indicate  $\pm$  the standard deviation from the mean. Results summary table providing the following: coefficient estimates  $\beta$ , standard errors SE ( $\beta$ ), and associated Wald's z-score ( $z = \beta/SE(\beta)$ ). \* $p \leq 0.05$ ; \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ .

(1) Richness  $\sim$  Trtmnt + (Trtmnt|TSI)



Predictor	Coef. $\beta$	SE( $\beta$ )	z	Pr(> z )
<i>Fixed effect</i>				
Intercept	2.0577	0.2401	8.568	<2e-16***
Trtmnt	0.4379	0.1557	2.812	0.00492**
<i>Random effect</i>				
Intercept – TSF = 10	0.5742247	0.03275040		
TSF = 10	-0.2017792	0.04495919		
Intercept – TSF = 22	-0.2451946	0.07713542		
TSF = 22	0.3503820	0.08224342		
Intercept – TSF = 41	-0.3239869	0.06028936		
TSF = 41	-0.1515323	0.07533521		

(2) Shrub Cover  $\sim$  Trtmnt + (Trtmnt|TSI)

Predictor	Coef. $\beta$	SE( $\beta$ )	z	Pr(> z )
<b>Fixed effect</b>				
Intercept	1.3412	0.3992	3.36	0.000781***
Trtmnt	-2.8165	0.3750	-7.51	5.93e-14***
<b>Random effect</b>				
Intercept – TSF = 10	-0.9214213	0.05597561		
TSF = 10	0.1050198	0.1149902		
Intercept – TSF = 22	0.6802898	0.13491513		
TSF = 22	-0.8019866	0.1502734		
Intercept – TSF = 41	0.2319510	0.08632884		
TSF = 41	0.7121472	0.1055251		

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