

FOREST DENSIFICATION OVER 85 YEARS IN A SIERRA NEVADA MIXED-CONIFER  
FOREST DECREASES CONIFER REGENERATION AND  
LIMITS SURVIVAL

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## ABSTRACT

### Forest Densification Over 85 Years in a Sierra Nevada Mixed-Conifer Forest Decreases Conifer Regeneration and Limits Survival

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Forest densification in response to a century of fire suppression in Sierra Nevada mixed conifer forests has decreased conifer regeneration and survival. Increases in overstory biomass and decreases in canopy heterogeneity, along with decreases in shrub cover in the understory, has created unfavorable establishment site conditions for conifer species. Establishment site conditions are key in promoting germination and establishment of conifers seeds and in determining the survival of these seedlings into the overstory. These changes in establishment site suitability resulting from the removal of disturbance from these forests has decreased conifer regeneration and survival into other age classes. In Sierra Nevada mixed-conifer forests, the relationship between establishment site conditions and conifer regeneration is multifaceted, and changes to microsite conditions as a result of fire suppression further confounds our understanding of conifer regeneration requirements and survival probability. Additionally, the relationship between Sierra Nevada shrubs and conifer seedlings is complex and not clearly understood, as these studies have been over relatively short time frames, and no research has examined the relationship between shrub cover and conifer seedlings throughout time in the Sierra Nevada. Using a historic dataset beginning 85 years ago and a re-measurement of the same plots, I examined changes to conifer regeneration dynamics from historic to current forests in response to forest densification following a century of fire suppression. I also analyzed the importance of establishment conditions on seedling survival into the canopy and how these factors have changed throughout time. The relationships between seedlings and their establishment site conditions will influence regeneration and survival, which will ultimately determine the structure and composition of future forests.

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## 1. INTRODUCTION

Across the mixed-conifer forests of the Sierra Nevada, a century of active management, fire suppression, and altered disturbance regimes have led to shifts in ecosystem composition and structure. Historically, frequent (~8 – 25 years, Evans et al. 2011) low to moderate severity fire created a mosaic forested landscape of intact patches, canopy gaps of variable sizes, and both age and size class diversity (Weaver 1943; Dunning 1926; Cooper 1960; Agee 1998; Scholl and Taylor 2010; Knapp et al. 2013). This complex, multi-aged, and multi-sized forest maintained by frequent fire created a mosaic of patches for regeneration, an adjacent seed source, and a heterogeneous forest canopy. These stand- and landscape-level structural conditions translated to variable microenvironments for tree establishment and growth, promoting both shade tolerant and intolerant species and maintaining a diverse forest community (Stephens et al. 2015). Specifically, this heterogeneous structure provided high-light regeneration environments for the establishment of light demanding species. Lack of an active fire regime has altered forest composition and structure by closing canopy gaps (Lydersen et al. 2013) and facilitating the establishment of shade tolerant species, an increase in tree densities, and a decrease in age and size class diversity (Skinner 1995; Noss et al. 2006; Collins et al. 2011; Levine et al. 2016). Diameter distributions are now concentrated around smaller size classes, whereas some historic forests exhibited a more equal distribution of tree sizes – with more open understory conditions and a greater number of large diameter trees (Parsons and DeBennetti 1979; North et al. 2007; Fry et al. 2014). The absence of an active disturbance regime and loss of spatial complexity has led to canopy closure and impacted tree establishment, stand dynamics, and forest community composition.

Altered spatial heterogeneity and establishment conditions are consequences of varying disturbance return intervals, and short-term (<100 year) structural and compositional changes may drive regeneration failures and/or differential survival of seedlings (Harvey et al. 2016, Urza and Sibold 2017). Heterogeneity in the regeneration environment determines the suitability of establishment sites for competing conifer seedlings. In Sierra Nevada mixed-conifer forests, canopy closure has led to a shift in seedling abundance and density from light-demanding pines toward more shade tolerant conifers (Stephens and Finney 2002; Bigelow et al. 2011; Knapp et al. 2013; Stephens et al. 2015). Although pines persist in the canopy, they are largely absent from the regenerating community. Seedlings typically have a narrower range of tolerance to environmental conditions than mature individuals (Grubb 1977), and species-specific tolerances to light, moisture, and direct competition may further limit germination and survival (Gray et al. 2005; Bigelow et al. 2011). For instance, inter-species competition with shrub species is documented to both facilitate (Legras et al. 2010) and hinder (Plamboeck et al. 2008) conifer seedling establishment in the Sierra Nevada. Shrubs may act as facilitators and provide favorable microsite conditions for *Pinus* seedlings during dry summers by reducing solar radiation and soil temperature (Stark 1965; Legras et al. 2010) while increasing soil moisture during late spring and summer (Oakley et al. 2006). Shrubs may conversely, however, compete for soil moisture and are documented to restrict the survival of white fir and sugar pine seedlings (Plamboeck et al. 2008). Moreover, regeneration success can be further constrained by seed availability and dispersal limitations (Greene and Johnson 1995; Nathan et al. 2002; Higgins et al. 2003; Vander Wall 2008) and shifts in overstory community composition following varying intensity logging and fire suppression have decreased residual seed sources for historically more abundant *Pinus* species (Hasel et al. 1934; Bigelow et al. 2011). The canopy gaps and structural heterogeneity common under historic forest conditions (Weaver 1943; Knapp et al. 2013) provided heterogeneous environments for species with variable tolerances while also accommodating temporal and spatial variation in establishment driven by climate and disturbance variability.

Shifts in the regenerating community can have long-term consequences by changing the trajectory of stand dynamics and potentially driving type shifts (Collins and Roller 2013; Stevens and Latimer 2015; Bart et al. 2016). Although initial filters may be temporary and vary widely among years, survivors of the regeneration phase determine the composition, structure, and function of the forest ecosystem. In Sierra Nevada forests, the relationship between establishment site conditions and conifer regeneration is complex and highly variable, and changes in microsite conditions as a function of fire exclusion further confound our understanding of species' germination requirements and survival probability. Furthermore, the relationship between Sierra Nevada shrubs and conifer seedlings is complex and not clearly understood, as these studies have all been over relatively short time periods, and no research has examined the relationship between shrub cover and conifer seedlings throughout time in the Sierra Nevada.

Despite substantial changes in the composition and structure of Sierra Nevada mixed-conifer

forests from historic to current conditions, the influence of these changes on the conifer regeneration environment is not clearly understood, as few studies have had the ability to track these changes through time and associated forest densification. Identifying factors that are important to seedling survival during the first years following germination is critical for understanding regeneration dynamics (Simard et al. 2003) and essential to land management efforts aiming to favor particular species. In the Sierra Nevada, the historical “Methods of Cutting” plots, established in 1928-1929 (Dunning 1930; Hasel et al. 1934) and rediscovered in 2008 (Knapp et al. 2013), provide a unique opportunity for examining changes in the regeneration environment and its effects on seedling densities over time. I used this historic dataset in conjunction with plot re-measurement to: 1) quantify changes in the regeneration environment over time; 2) evaluate the effects of altered abiotic and biotic forest conditions on establishment and persistence of white fir, incense cedar, sugar pine, and ponderosa pine germinants and seedlings; and 3) track successful species and individuals through the process of stand development and forest densification. I hypothesized that historic conditions would be more favorable for *Pinus* species regeneration due to higher light conditions from the open canopy and lower density of smaller diameter trees. I also anticipated shifts in seedling densities toward shade-tolerant species over time since initiation of fire suppression efforts again due to the increased canopy cover.

## 2. METHODS

### 2.1. Study area

This study was conducted on the historic Methods of Cutting plots (Dunning 1930; Hasel et al. 1934) in the Stanislaus-Tuolumne Experimental Forest (STEF, 38°10.4'N, 120°0.0'W). The Experimental Forest is a mixed-conifer forest located on the Stanislaus National Forest in the western Sierra Nevada – approximately 35 miles northwest of Yosemite National Park (Fig. 1). Elevation within the forest varies from 1590 to 1950m, and slopes range between 16 and 20%. Soils are of the Wintoner (loam) and Inville (gravelly-loam) families (Table 1), which are well-drained soils derived from granite and tuff breccia, respectively (Soil Survey Staff, 2017). The region is characterized by a Mediterranean climate with a mean annual temperature of 10.4°C and mean annual precipitation of 807.2mm (WRCC RAWs Pinecrest 2 Station, 2011-2017).

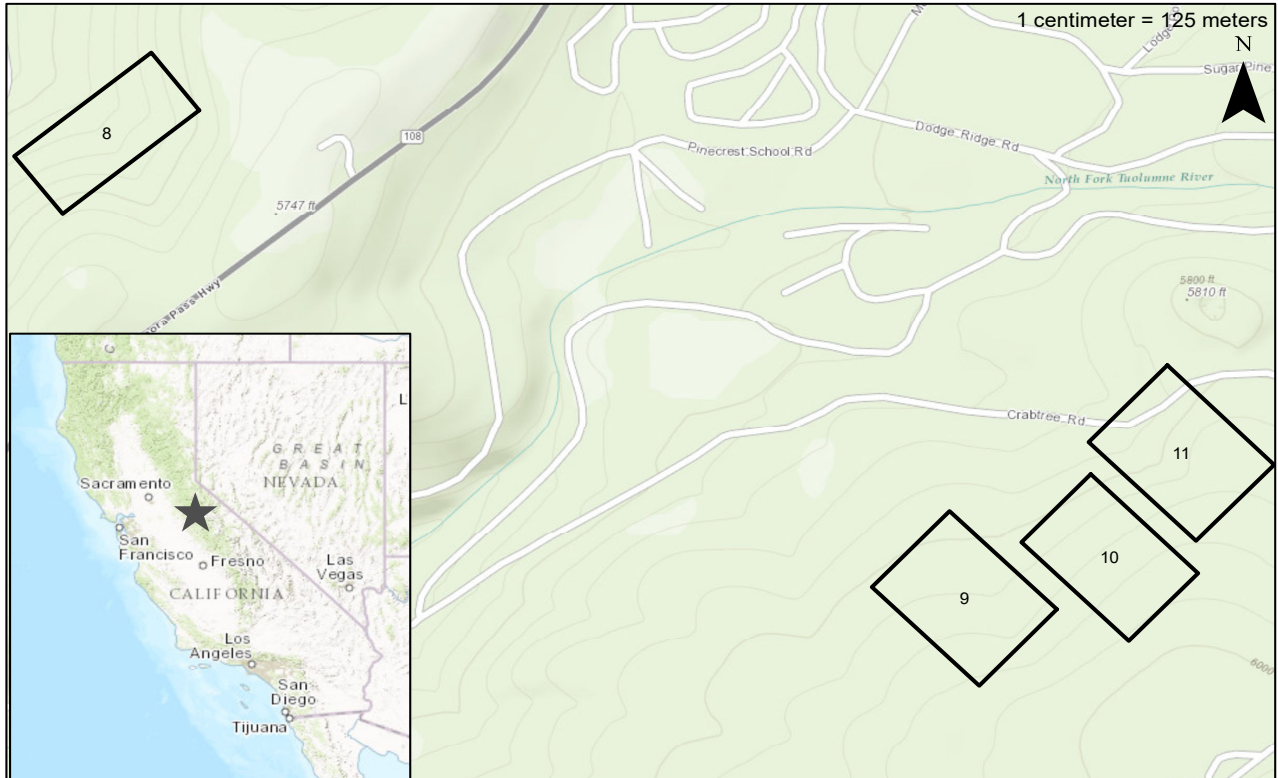


Figure 1. Location of the Stanislaus-Tuolumne Experimental Forest (shown by the star in the inset) and location of the four plots within the forest.

Table 1. Summary of the characteristics of the four historic plots established in 1928 and 1929 (Dunning 1930; Hasel et al. 1934; Knapp et al. 2013). Transect centroid represents the location of the center of each transect. Slope was averaged from the beginning, middle, and end of the transect and elevation was averaged across the transect points. Soil type was determined using the USDA Web Soil Survey. Silvicultural treatment represents the prescribed harvest carried out in 1929.

Plot	Transect Centroid	Average Slope (%)	Elevation (meters)	Soil Type	Silvicultural Treatment
8	38.184383, -120.016902	38	1676	Wintoner family; loam	16.4% retention No species preference
9	38.177439, -120.001223	21	1780	Wintoner-Inville family; Gravelly loam	18.2% retention <i>P. ponderosa</i> heaviest cut <i>P. lambertiana</i> lightest cut
10	38.178223, -119.998967	24	1789	Wintoner-Inville family; Gravelly loam	58.6% retention <i>P. ponderosa</i> heaviest cut <i>A. concolor</i> lightest cut
11	38.179883, -119.997896	39	1759	Wintoner-Inville family; Gravelly loam	10.2% retention <i>P. ponderosa</i> heaviest cut <i>A. concolor</i> lightest cut

The overstory is consistent with most Sierra Nevada mixed-conifer forests, with white fir (*Abies concolor*, Gord. & Glend.), incense cedar (*Calocedrus decurrens*, Torr.), sugar pine (*Pinus lambertiana*, Doug.), and some ponderosa pine (*Pinus ponderosa*, P & C Lawson). Historically, the shrub community was composed primarily of *Chamaebatia foliolosa*, *Arctostaphylos*, *Ceanothus cordulatus*, and *Ceanothus parvifolius* (Dunning 1930; Hasel et al. 1934). These shrubs are now mostly absent from the area, replaced by more shade tolerant species, such as *Chrysolepis sempervirens* (Knapp et al. 2013). Both the historic and current herbaceous communities consisted of similar species, including *Viola lobata*, *Iris hartwegii*, and *Hieracium albiflorum* (Dunning 1930; Hasel et al. 1934; Knapp et al. 2013).

Fire in STEF was likely driven by both natural and anthropogenic ignitions (Knapp et al. 2013). The historic median fire return interval for the forest was 6 years, with the last recorded fire occurring in 1889 (Knapp et al. 2013). The only timber harvest within the plots was implemented in 1928 and 1929 for the Methods of Cutting study (Dunning 1930; Hasel et al. 1934).

## 2.2. Historical data

Foresters with the US Forest Service established four 'Methods of Cutting' plots between 1928 and 1929 (MC8, MC9, MC10, & MC11) to track changes in forest composition and structure under varying intensity silvicultural treatments of differential canopy retention and species favored in harvest (Table 1). Once established, each plot was stem mapped, and data were collected on overstory, understory, and structural (e.g. coarse wood, bare ground) conditions. Trees >9.1cm diameter at breast height (1.37m, dbh) were tagged and sampled for species, dbh, height, and health. Tree seedlings and saplings (<1.37m height) were sampled within milacre (2m x 2m) quadrats along a transect traversing the entire plot. Individuals occurring within quadrats were tallied by species and height. Additionally, percent cover of shrubs, litter, rock, and woody debris were estimated in each quadrat. Herbaceous vegetation density was surveyed on every tenth quadrat by counting the number of stems per species.

After the plots were surveyed, each was treated according to a different silvicultural prescription. MC8 was treated in 1928, retaining no more than 20% of the board volume and favoring no species but removing any over-mature or defective timber (Dunning 1930). MC9, 10, and 11 were harvested in 1929. On MC9, the objective was to improve spacing for all species and age classes, so 18.2% board feet were retained with ponderosa pine cut the heaviest and sugar pine the lightest. MC10 had the lightest cut, retaining 58.6% of the board feet. This plot was marked according to an economic selection system chosen to give the highest short-term profit, cutting the largest and best trees, with ponderosa and sugar pine cut the heaviest. White fir and incense cedar were of lesser value and not targeted for cutting in MC10. The objective on MC11 was to provide the highest return to the landowner; this harvest was the heaviest of the four. All merchantable trees were harvested, retaining only 10.2% board feet. On MC11,

both ponderosa pine and sugar pine were heavily cut, while white fir was retained onsite due to its low economic return (Hasel et al. 1934). Plots were re-measured after harvest and again in 1930-1932, 1934-38, 1942, and 1947. See Knapp et al. (2013) for additional details on long-term sampling, harvest details, and plot resampling and mapping.

### **2.3. Plot re-measurement**

During the summer of 2016, I resampled the milacre quadrats along each transect following the original sampling methodologies to compare 2016 forests to the historic dataset ( $n_{\text{transects}}=4$ ,  $n_{\text{plots}}=4$ ,  $n_{\text{quadrats}}=440$ ). All trees >10cm dbh were sampled for species and dbh. Trees <10cm dbh were tallied by species and size class to identify the regenerating community: <10cm tall (germinant), >10cm but <137cm (seedling), and >137cm but <10cm dbh (sapling). Percent cover of shrub species, litter, bare soil, rock, woody debris, tree bole, and roots was also estimated within each quadrat for comparison to the original dataset.

In addition to the resampling efforts, data were collected on local site characteristics. Slope for each plot was averaged across measurements taken at the first, middle, and last quadrat. Litter depth to bare mineral soil was measured at the center of each quadrat. In July, percent soil moisture was recorded once outside every other quadrat using a time domain reflectometry probe (TDR, HS2 HydroSense II, 15cm probe, Campbell Scientific, Logan, UT, USA). Soil moisture data was collected for among-quadrat comparisons. All live trees over 10cm dbh within the quadrat boundaries were cored at 20cm to determine the establishment date and identify any trees established during the years sampled following treatment (from 1929-1947). Cores were prepared and analyzed using methods outlined by Shroder, Jr. (1980) and Stokes and Smiley (1996). Cores were measured using Measure J2X (Voor Tech Consulting 2008). If a core did not hit the pith, Coorecorder 9.0 (Cybis Elektronik, 2017) was used to estimate the number of years missed. Seedling growth data from MC8 was used to estimate the number of years required for the seedling to reach 20cm in height.

### **2.4. Biotic competition**

Overstory biomass was calculated from historic and current structure data and used as a surrogate for understory light availability and tree competition. Overstory trees were mapped in 2008 (MC9, MC10, MC11) and 2016 (MC8) using a laser rangefinder with a compass module on a tripod, and the dbh and species of trees over 10 cm were recorded (Knapp et al. 2013; Lydersen et al. 2013). Using the map of tree locations, I used ArcGIS (version 10.3) to identify all trees within a 15-meter radius of each quadrat center. Tree diameters were used to calculate species-specific biomass (kg) using genera-specific allometric equations (Jenkins et al. 2003) and scaled to a Mg/hectare basis. Because portions of the spatial data representing current forests were collected eight years apart, a random subsample of thirty 15-meter radius competition plots were sampled in the field in 2016 to identify significant changes in biomass between 2008 to 2016. Finally, I used ArcGIS to extract the number of trees within a 45.7-meter radius of milacre center, which was identified as the maximum distance sugar pine seeds are likely to disperse from the seed tree (Fowells 1944; Fowells 1950). I then pooled data by species to determine the number of potential seed trees around each quadrat.

### **2.5. Data analysis**

Biomass, trees per hectare, and shrub coverage data were analyzed using Wilcoxon Rank Sum tests that were paired between the time steps (pre-harvest, post-harvest, and 2016) to identify changes throughout time.

Prior to modeling, I ran a correlation analysis on all potential predictor variables to eliminate highly correlated variables ( $r>0.65$ ). Percent litter cover was not considered for inclusion due to a high correlation with shrub cover in 1929 (1929:  $r = -0.79$ ). I then ran a series of zero inflated negative binomial time series models by species and juvenile stage (germinant versus seedling) to examine the effect of change in condition over time (e.g. 1929 to 2016) on densities of each species. Germinants (<10cm height) and seedlings (>10cm and <137cm) were separated for analysis due to the higher temporal variability of first year germinants (Zald et al. 2008) and to identify potential differences in site requirements between the two juvenile stages. Models were run individually for each species (white fir, incense cedar, and pines) with germinant or seedling densities as response variables. Sugar pine and ponderosa pine were combined as pines for analysis due to low densities of ponderosa pine at all time steps. All potential predictors, with the exception of time, were centered to avoid overfitting by subtracting the variable group mean from each value, and full models included the following predictors: time, percent shade intolerant shrub cover, percent shade tolerant shrub cover, and the amount of overstory biomass (Mg/ha) in a 15m radius circular plot around the quadrat. Biomass was both centered and scaled, which

divides each centered value by the variable group standard deviation. Percent shrub cover was separated into shade tolerant and intolerant species as determined by the species reports on the Fire Effects Information System ([feis-crs.org/feis/](https://feis-crs.org/feis/), 2017). Post-harvest effects on the quadrat surface in the form of skid trails and burned patches from pile burns were included in models as indicator variables. Plot and quadrat were not included as random effects in the models due to the inability to add random effects to zero inflated negative binomial models. Instead, Chi-Squared tests were used to compare within year differences by species for quadrats, which represented potential spatial autocorrelation, and for plots, which represented historic silvicultural treatment effects.

The pre-harvest (1929) to post-harvest (1934, five years after harvest) model evaluated the influence of altered abiotic and biotic conditions following harvest on seedling densities to examine the effect of management on seedling densities of shade-tolerant versus shade-intolerant conifers. Data from 1934 was used to represent post-harvest conditions to eliminate seedlings that established prior to harvest from the analysis. The pre-harvest to 2016 model paired pre-harvest and current structure to compare current conditions and seedling densities to a historical reference. The pre-harvest forest was still likely influenced by fire suppression, as the last recorded fire in the area was in 1889 (Knapp et al. 2013). Lastly, the post-harvest to 2016 model tested the effects of long-term fire suppression and absence of management (over 85 years) on seedling densities to assess the effect of change in forest structure over time on species' densities. While these stands would have management influences, densities in the treated areas in 2007/08 were similar to those in untreated stands in the same forest, indicating that past logging was not a major factor and was more heavily influenced by fire suppression and potentially climate change (Knapp et al. 2013).

A zero inflated negative binomial model was used to examine germinant survival into the seedling stage throughout the historic dataset. This model included the number of seedlings from 1931, 1932, and 1935-1938. By including establishment conditions, these models tested whether establishment conditions influence germinant survival into the seedling class. A zero inflated negative binomial model was also used to test the potential influence of the number of seed trees within 45.7 meters of a quadrat on recruitment. Models included the number of germinants (<10cm tall) in each quadrat in 1931 separated by species as a function of the number of trees (>10cm dbh) of the same species within a 45.7-meter radius around the center of the quadrat. The data from 1931 was used to determine the influence of seed tree densities immediately after harvest on germination of conifer seeds.

The effect of shrub coverage, overstory biomass, and post-harvest management impacts on the quadrat surface (burned patches and skid trails) on the likelihood of a seedling in the historic dataset surviving to a tree >10cm dbh in 2016 and of a seedling surviving to a sapling (>137 tall, but <10cm dbh) in 1947 was examined through the use of a logistic regression model. Due to low numbers of trees in the quadrats in 2016, all species were combined in one model.

All analyses were run in R 1.0.136 (R Core Team, 2017). Zero-inflated negative binomial models were run using the *pscl* package (Zeileis, 2008).

### 3. RESULTS

#### 3.1 Overstory and understory changes

Pre-harvest forests were relatively open, with gaps in the overstory and a mix of size classes (Figs. 2, 3 & 4). The average biomass was 236 Mg/ha (+/- 8 Mg/ha) (Table 2, Fig. 5). The pre-harvest overstory (trees  $\geq 10$ cm dbh) was dominated by shade tolerant species (57% white fir & 23% incense cedar) with a small sugar pine (17%) and ponderosa pine (<3%) component. Post-harvest, the canopy was more open with fewer large diameter trees due to the treatments (Figs. 2, 3 & 4). The biomass was reduced to an average of 144 Mg/ha (+/- 11 Mg/ha), which represented a significant decrease from pre-harvest biomass (249 Mg/ha) ( $p < 0.001$ ) (Figs. 5). Following logging, the overstory was composed primarily of white fir (58% of trees  $\geq 10$ cm dbh) followed by incense cedar (24%) and sugar pine (17%) and with very little ponderosa pine (<2%). In 2016, 85 years after logging, the overstory was denser than both the pre- and post-harvest conditions, with increases in all diameter classes, especially smaller size classes (10cm –22cm) (Figs. 2, 3 & 4). The average biomass increased to 478 Mg/ha (+/- 9 Mg/ha), a doubling from pre-harvest ( $p < 0.001$ ) and greater than three-fold increase from post-harvest ( $p < 0.001$ ) conditions (Fig. 5). Across all plots, white fir continued to dominate the overstory into 2016, but alterations included an increase in incense cedar (38%) and continued decreases in sugar (7%) and ponderosa pine (4%).



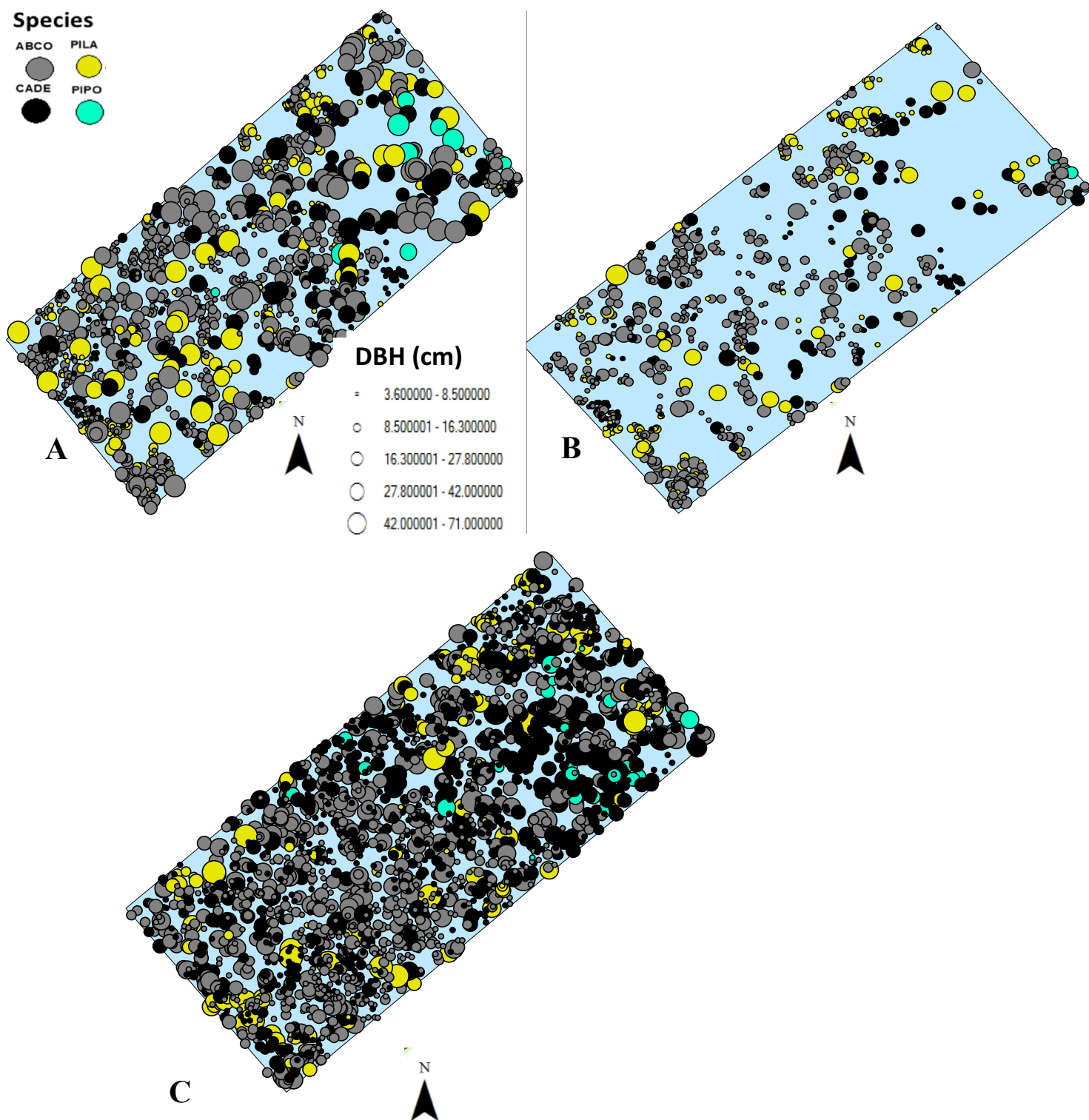


Figure 2. Stem maps created from the number of trees per hectare for Plot 8 Pre-Harvest 1929 (A), Post-Harvest 1931 (B), and 2016 (C). Species codes used in the map key are: *Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), and *Pinus ponderosa* (PIPO).

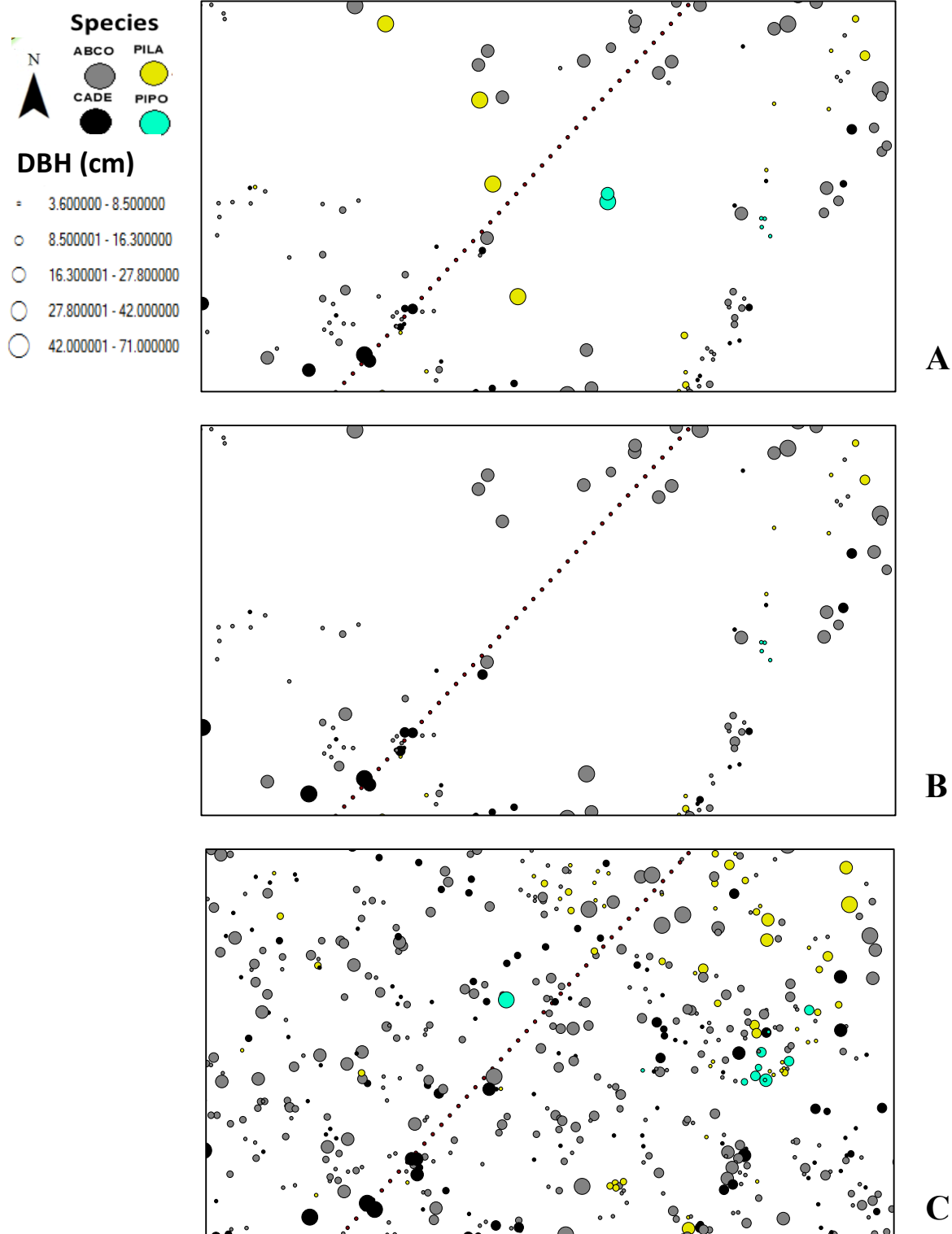


Figure 3. Close up of stem maps for Plot 10 to illustrate changes in canopy cover over the same quadrats from Pre-Harvest 1929 (A), Post-Harvest 1931 (B), and 2016 (C). Species codes used in the map key are: *Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), and *Pinus ponderosa* (PIPO). Small gray dots represent quadrats.

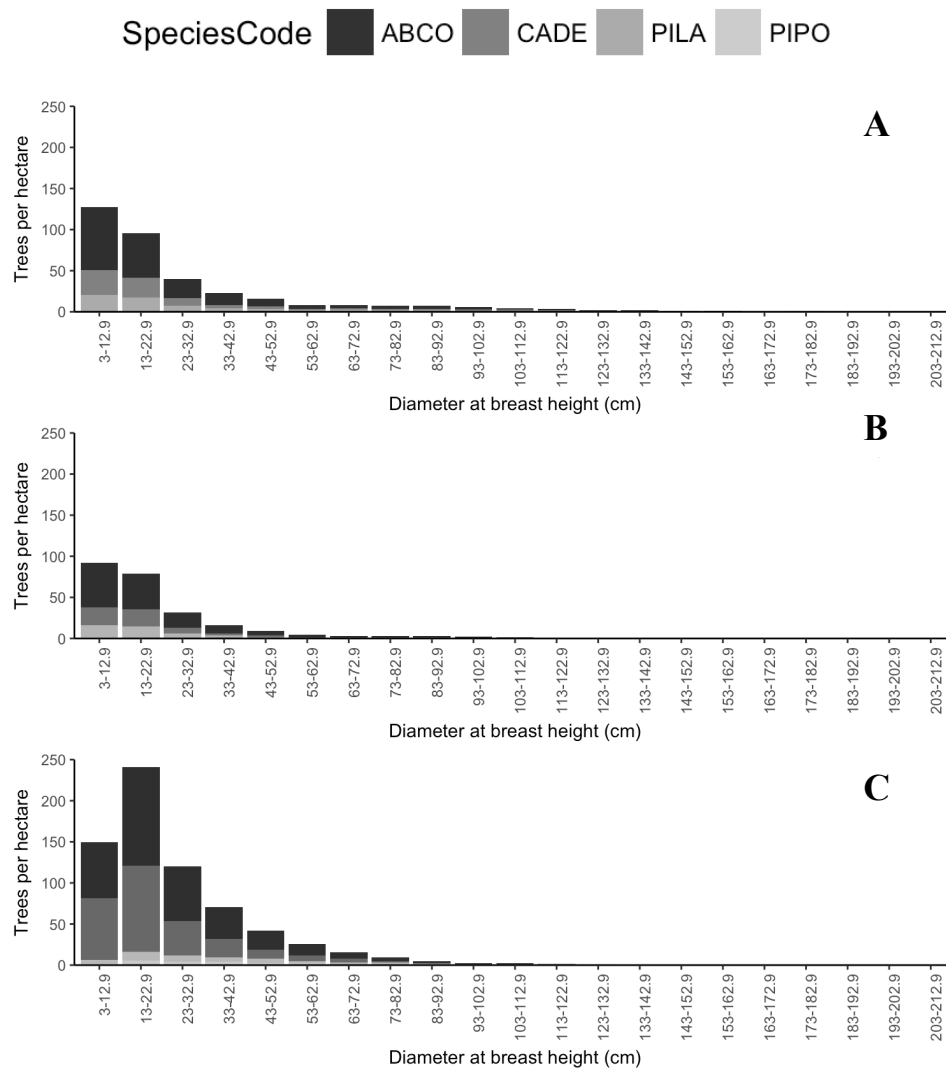


Figure 4. Diameter distributions per hectare for all trees >3cm across all four plots pre-harvest 1929 (A), post-harvest 1931 (B), and 85 years later in 2016 (C). Species codes are *Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), and *Pinus ponderosa* (PIPO).

Table 2. Averages ( $\pm$  standard errors) of each predictor variable across all four plots for pre-harvest (1929), post-harvest (1931), and 2016 forest conditions. Shrub and litter cover was estimated in each quadrat and biomass represents overstory biomass within a 15-meter radius circular plot from the center of each quadrat. Litter depth was measured at the center of each quadrat and soil moisture was taken in July outside of every other quadrat.

Year	Avg Shade Tolerant Shrub Cover (%)	Avg Shade Intolerant Shrub Cover (%)	Average Biomass (Mg/ha)	Average Litter Cover (%)	Average Litter Depth (cm)	Average Soil Moisture (%)
Pre-harvest 1929	3 $\pm$ 0.6	22 $\pm$ 1.7	236 $\pm$ 8	56 $\pm$ 2.0	-	-
Post-harvest 1931	2 $\pm$ 0.4	17 $\pm$ 1.4	144 $\pm$ 11	33 $\pm$ 1.8	-	-
2016	1 $\pm$ 0.2	1 $\pm$ 0.1	279 $\pm$ 9	53 $\pm$ 1.3	4.53 $\pm$ 0.2	3.74 $\pm$ 0.2

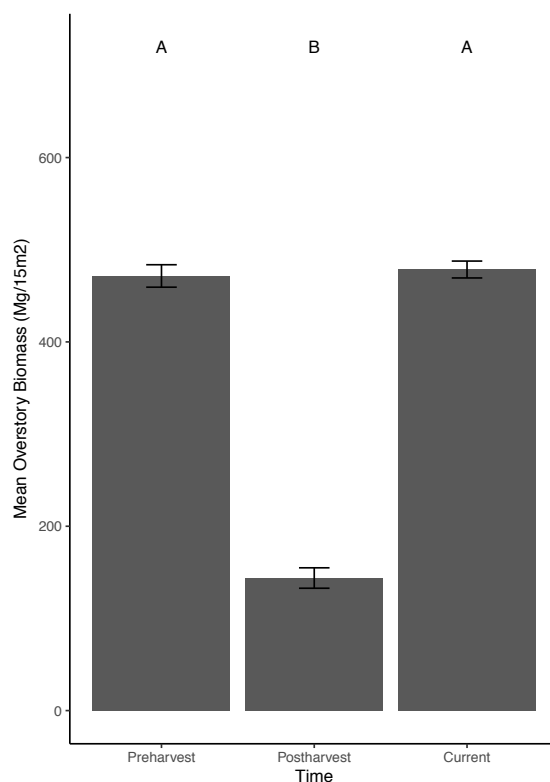


Figure 5. Mean Biomass (Mg) per hectare prior to harvest (1929), after harvest (1931), and in 2016. Biomass was averaged from separate 15-meter radius circles around the quadrat centers across all four plots. Significance determined using paired Wilcoxon Rank Sum tests.

The pre-harvest shrub community consisted of more shade intolerant species than shade tolerant species (21.62% cover per quadrat on average;  $p < 0.001$ ) (Table 2, Fig. 6). After harvest, cover for both shade tolerant ( $p = 0.006$ ) and intolerant shrub species ( $p = 0.03$ ) decreased from pre-harvest conditions, but there was still more shade intolerant shrub cover (17.32% cover per quadrat on average;  $p < 0.001$ ) (Table 2, Figs. 6, 7, & 8). In 2016, the average cover of shade tolerant and intolerant shrubs was not significantly different from each other (0.79%; 0.63%, respectively;  $p = 0.50$ ; Table 2 & Fig. 6). However, the average cover of shade tolerant and intolerant species decreased from both pre-harvest ( $p < 0.001$  and  $p < 0.001$ , respectively) and post-harvest ( $p < 0.001$ ;  $p < 0.001$ , respectively) forests (Figs. 7 & 8).

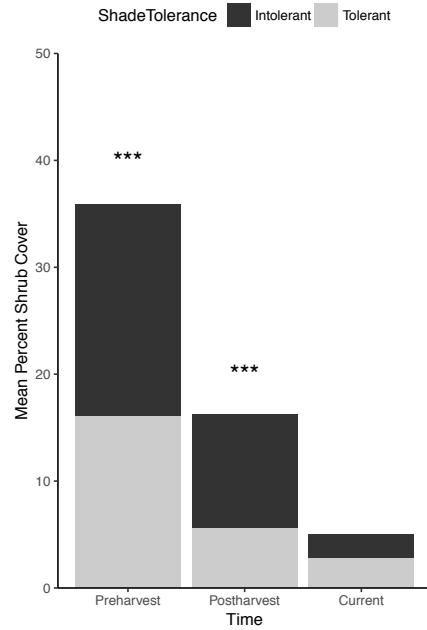


Figure 6. Mean percent shrub cover across all four plots prior to (1929) and after harvest (1931) and in 2016. Shrub cover is separated into shade tolerant and intolerant shrub species. Significance was determined using a paired Wilcoxon Rank Sum test between the total cover of shade tolerant and intolerant shrub species in each year and represents a p-value of  $<0.001$ .

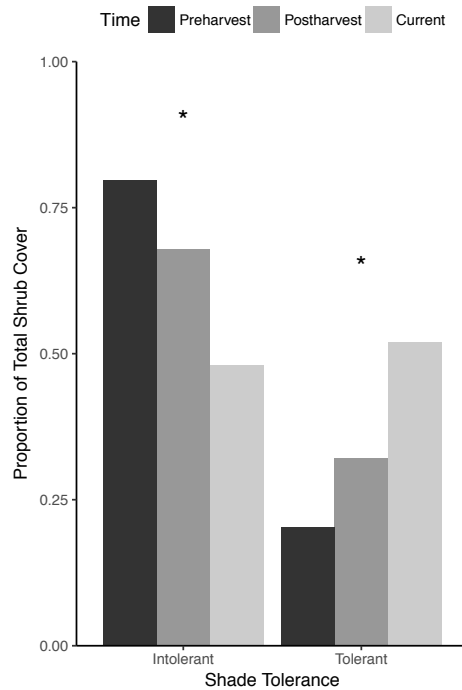


Figure 7. The proportion of shade intolerant and tolerant shrub species before harvest (1929), after harvest (1931), and in 2016. Proportion represents the amount of the total shrub cover across all plots for each time that is composed of shade tolerant or shade intolerant shrub species. Significance indicates that each between year pair for shade tolerant and intolerant species was significantly different from the other years ( $0.01 < p < 0.05$ ).

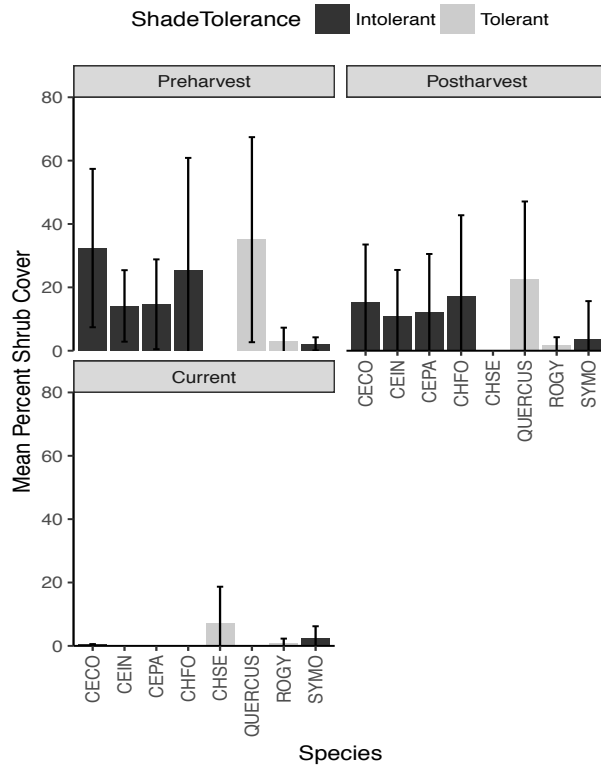


Figure 8. Mean percent cover of eight dominant shrub species separated by shade tolerant and intolerant. Mean is across all four plots prior to harvest (1929), after treatment (1931), and in current forests (2016). Shrub species include *Ceanothus cordulatus* (CECO), *Ceanothus integerrimus* (CEIN), *Ceanothus parvifolius* (CEPA), *Chamaebatia foliolosa* (CHFO), *Chrysolepis sempervirens* (CHSE), *Quercus kelloggii* (QUERCUS), *Rosa gymnocarpa* (ROGY), and *Symphoricarpos mollis* (SYMO).

Table 3. Average germinant and seedling densities per hectare of each species across all four plots for pre-harvest (1929), post-harvest (1934), and 2016 forest conditions. Species codes are ABCO (*Abies concolor*, white fir), CADE (*Calocedrus decurrens*, incense cedar), and PINE (*Pinus lambertiana*, sugar pine, and *Pinus ponderosa*, ponderosa pine, combined).

Year	Germinants (<10cm tall)			Seedlings (>10cm, but <137cm)		
	ABCO	CADE	PINE	ABCO	CADE	PINE
Pre-harvest 1929	1590	420	120	950	580	200
Post-harvest 1934	6	270	30	320	210	70
2016	30	220	20	520	440	70

Pre-harvest, germinant densities were highest for white fir and lowest for pines ( $p < 0.001$ ) (Table 3). Germinant densities of all species decreased significantly after harvest when compared to pre-harvest densities ( $p < 0.03$ ) (Table 3, Fig. 9). In 2016, average germinant densities were lower than both pre- and post-harvest averages for incense cedar and pines, while average white fir densities were higher than post-harvest conditions but lower than pre-harvest densities (Table 3, Fig. 9).

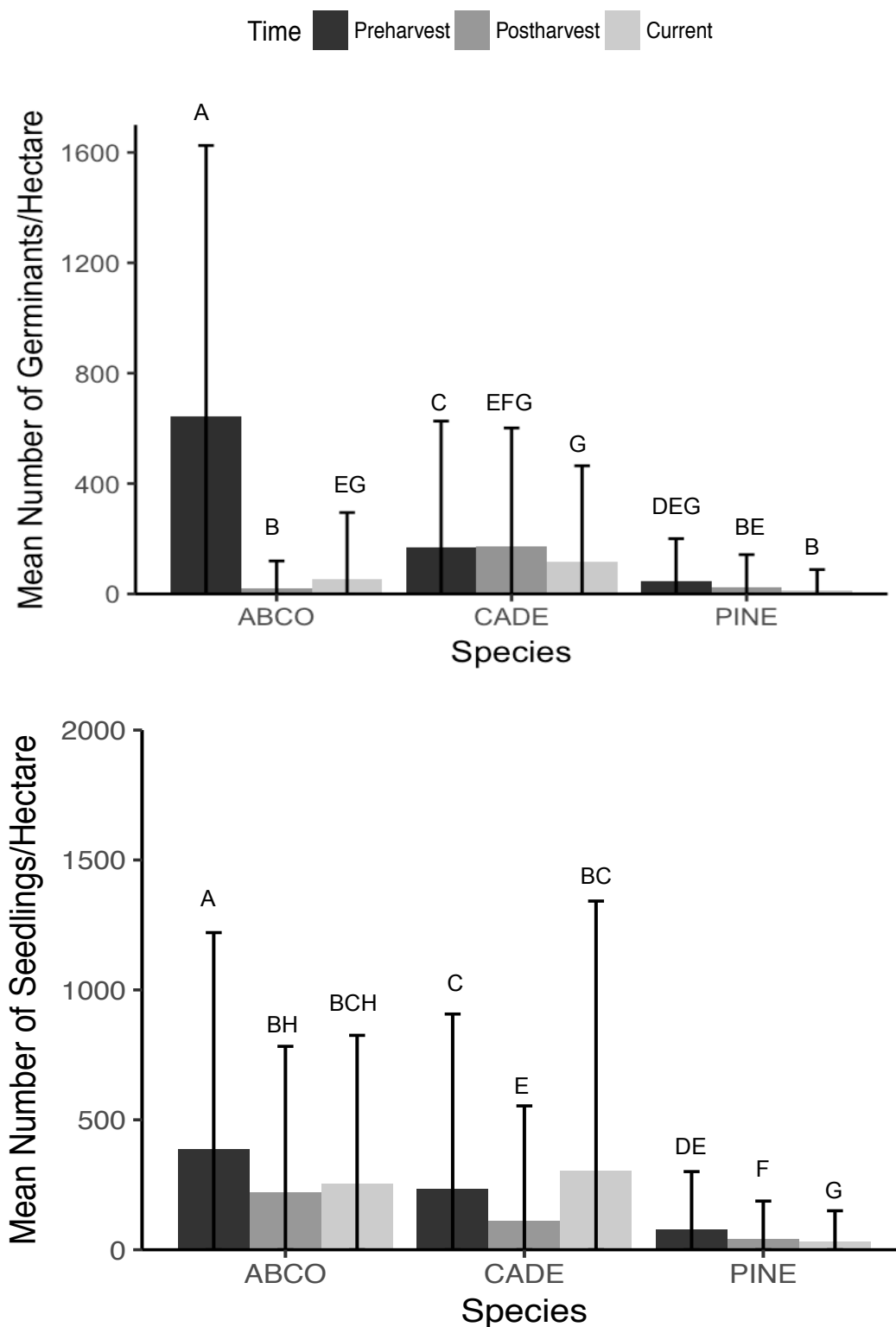


Figure 9. The mean number of germinants (Top; <10cm height) and the mean number of seedlings (Bottom; 10cm-134cm) per hectare of each species before (1929) and after harvest (1931) and in 2016. Letters indicate significant differences as determined using a paired Wilcoxon Rank Sum.

Seedling densities exhibited similar patterns as germinant densities. Pre-harvest, white fir had the highest seedling density, while pine density was the lowest (Table 3). After harvest, seedling densities of all species dropped, but white fir remained the densest and pines the least (Table 3, Fig. 9). In 2016, average seedling densities were higher than post-harvest, but lower than pre-harvest for all species except pines, which had the same average seedling density post-harvest and 85 years later (Table 3, Fig. 9).

### **3.2 Pre-harvest to post-harvest**

The change in biomass from pre-harvest to post-harvest significantly influenced white fir germinants ( $p=0.009$ ; Table 4). Overstory biomass was associated with an increase in white fir germinant densities both before and after harvest, but this relationship was stronger prior to harvest. The change in biomass from pre-harvest to post-harvest also significantly influenced germinant densities of incense cedar ( $p=0.05$ ; Table 4). Incense cedar germinant densities were positively associated with biomass before harvest, but there was no relationship with overstory biomass after harvest. In addition, incense cedar germinants were negatively associated with burned patches after harvest ( $p=0.02$ ; Table 4). The change in biomass from pre-harvest to post-harvest also significantly altered pine germinant densities ( $p=0.04$ ; Table 4). Pine germinant densities were positively associated with overstory biomass before harvest, but were negatively associated after harvest.



Table 4. Results for germinant (<10cm tall) interaction models before (1929) and after (1934) harvest and in 2016. Results are from individual zero inflated negative binomial models for each species across all plots. Bolded p-values indicate significance.

Time	Species	Predictor Variables	$\beta$	SE	z	P
Pre-harvest 1929 vs Post-harvest 1934	<i>Abies concolor</i>	Time 1934	-	-	-	-
		Shade tolerant shrub cover	-0.03	0.06	-0.47	0.64
		Shade intolerant shrub cover	-0.06	0.08	-0.82	0.41
		Biomass	0.08	0.12	0.67	0.50
		Skid trail	-	-	-	-
		Burn	-	-	-	-
		Skid trail and burn	-	-	-	-
		Time 1934 * Shade tolerant shrub cover	-0.25	0.68	-0.36	0.72
		Time 1934 * Shade intolerant shrub cover	0.38	0.47	0.80	0.42
		Time 1934 * Biomass	1.33	0.38	3.45	<b>&lt;0.001</b>
	<i>Calocedrus decurrens</i>	Time 1934	0.11	0.36	0.31	0.75
		Shade tolerant shrub cover	0.27	0.36	0.75	0.45
		Shade intolerant shrub cover	-0.20	0.16	-1.30	0.19
		Biomass	-0.27	0.21	-1.31	0.19
		Skid Trail	0.24	0.34	0.71	0.48
		Burn	-1.34	0.60	-2.24	<b>0.02</b>
		Skid trail and burn	0.66	0.67	0.98	0.33
		Time 1934 * Shade tolerant shrub cover	-0.37	0.40	-0.91	0.36
		Time 1934 * Shade intolerant shrub cover	0.44	0.28	1.53	0.13
		Time 1934 * Biomass	0.79	0.40	2.00	<b>0.05</b>
	<i>Pinus species</i>	Time 1934	-	-	-	-
		Shade tolerant shrub cover	0.74	0.44	1.70	0.09
		Shade intolerant shrub cover	0.03	0.16	0.17	0.87
		Biomass	0.02	0.21	0.08	0.93
		Skid Trail	-0.29	1.12	-0.26	0.80
		Burn	-1.38	1.36	-1.02	0.31
		Skid trail and burn	-0.69	1.55	-0.44	0.66
		Time 1934 * Shade tolerant shrub cover	-1.27	0.84	-1.51	0.13
		Time 1934 * Shade intolerant shrub cover	-0.78	0.53	-1.46	0.14
		Time 1934 * Biomass	1.04	0.50	2.07	<b>0.04</b>
Pre-harvest 1929 vs Current 2016	<i>Abies concolor</i>	Time 2016	-	-	-	-
		Shade tolerant shrub cover	-0.01	0.06	-0.17	0.87
		Shade intolerant shrub cover	-0.03	0.07	-0.39	0.70
		Biomass	0.46	0.23	2.00	<b>0.05</b>
		Time 2016 * Shade tolerant shrub cover	-0.73	13.20	-0.06	0.96
		Time 2016 * Shade intolerant shrub cover	4.92	3.52	1.40	0.16
		Time 2016 * Biomass	-1.58	0.51	-3.08	<b>0.002</b>
	<i>Calocedrus decurrens</i>	Time 2016	0.14	0.61	0.24	0.81
		Shade tolerant shrub cover	0.38	0.36	1.05	0.29
		Shade intolerant shrub cover	-0.21	0.14	-1.46	0.15
		Biomass	-0.52	0.40	-1.31	0.19
		Time 2016 * Shade tolerant shrub cover	-0.49	0.45	-1.08	0.28
		Time 2016 * Shade intolerant shrub cover	0.04	1.26	0.03	0.98
		Time 2016 * Biomass	-0.49	0.55	-0.89	0.37
	<i>Pinus species</i>	Time 2016	-2.78	1.91	-1.46	0.15
		Shade tolerant shrub cover	-0.59	0.33	-1.76	0.08
		Shade intolerant shrub cover	-0.05	0.30	-0.17	0.87
		Biomass	0.38	0.86	0.44	0.66
		Time 2016 * Shade tolerant shrub cover	-0.28	1.34	-0.21	0.83

		Time 2016 * Shade intolerant shrub cover	-2.63	4.41	-0.60	0.55
		Time 2016 * Biomass	0.18	1.11	0.17	0.87
Post-harvest 1934 vs Current 2016	<i>Abies concolor</i>	Time 2016	-	-	-	-
		Shade tolerant shrub cover	-	-	-	-
		Shade intolerant shrub cover	0.06	0.33	0.17	0.86
		Biomass	-0.94	2.96	-0.32	0.75
		Skid Trail	0.40	0.70	0.57	0.57
		Burn	0.79	1.79	0.44	0.66
		Skid trail and burn	-0.68	1.35	-0.50	0.62
		Time 2016 * Shade tolerant shrub cover	-	-	-	-
		Time 2016 * Shade intolerant shrub cover	4.56	3.23	1.41	0.16
		Time 2016 * Biomass	-0.02	3.00	-0.01	0.99
	<i>Calocedrus decurrens</i>	Time 2016	-3.14	1.89	-1.67	0.10
		Shade tolerant shrub cover	-0.06	0.10	-0.53	0.59
		Shade intolerant shrub cover	0.16	0.17	0.96	0.34
		Biomass	3.75	2.45	1.53	0.13
		Skid Trail	0.19	0.32	0.59	0.56
		Burn	-0.77	0.46	-1.69	0.09
		Skid trail and burn	0.16	0.59	0.27	0.79
		Time 2016 * Shade tolerant shrub cover	0.11	0.20	0.54	0.59
		Time 2016 * Shade intolerant shrub cover	-0.71	0.93	-0.77	0.44
		Time 2016 * Biomass	-5.04	2.48	-2.04	<b>0.04</b>
	<i>Pinus species</i>	Time 2016	9.66	3.43	2.81	<b>0.005</b>
		Shade tolerant shrub cover	0.11	0.47	0.24	0.81
		Shade intolerant shrub cover	-1.00	0.38	-2.63	<b>0.009</b>
		Biomass	-10.21	4.47	-2.28	<b>0.02</b>
		Skid Trail	-0.16	1.30	-0.13	0.90
		Burn	-0.93	1.72	-0.54	0.59
		Skid trail and burn	-0.64	1.92	-0.34	<b>0.74</b>
		Time 2016 * Shade tolerant shrub cover	2.91	1.08	2.71	<b>0.007</b>
		Time 2016 * Shade intolerant shrub cover	7.79	4.15	1.88	0.06
		Time 2016 * Biomass	9.28	4.49	2.07	<b>0.04</b>

There were no significant interactions between white fir seedling densities and changing establishment conditions between pre-harvest and post-harvest ( $p > 0.05$ ; Table 5). Regardless of time, white fir seedling densities were negatively associated with burned patches resulting from the post-harvest pile burns ( $p < 0.001$ ; Table 5). Incense cedar seedling densities were negatively associated with burned patches and on skid trails after harvest ( $p = 0.003$ ;  $p = 0.001$ , respectively). The change in shade intolerant shrub cover from pre-harvest to post-harvest significantly altered incense cedar seedling densities (0.004; Table 5). In both pre-harvest and post-harvest forests, shade intolerant shrub cover was associated with an increase in incense cedar seedlings. There were no significant interactions between pine seedlings and establishment conditions from pre-harvest to post-harvest ( $p > 0.05$ ; Table 5).

Table 5. Results for seedling (>10cm tall, but less than 137cm) interaction models before (1929) and after (1934) harvest and in 2016. Results are from individual zero inflated negative binomial models for each species across all plots. Bolded p-values indicate significance.

Time	Species	Predictor Variables	$\beta$	SE	z	P
Pre-harvest 1929 vs Post-harvest 1934	<i>Abies concolor</i>	Time 1934	-0.84	0.20	-4.16	<b>&lt;0.001</b>
		Shade tolerant shrub cover	0.12	0.06	2.09	<b>0.04</b>
		Shade intolerant shrub cover	0.11	0.15	0.77	0.44
		Biomass	-0.34	0.28	-1.20	0.23
		Skid trail	-0.62	0.39	-1.58	0.12
		Burn	-2.86	0.80	-3.59	<b>&lt;0.001</b>
		Skid trail and burn	-2.17	1.16	-1.87	0.06
		Time 1934 * Shade tolerant shrub cover	0.001	0.15	0.01	0.99
		Time 1934 * Shade intolerant shrub cover	0.20	0.21	0.96	0.34
		Time 1934 * Biomass	0.09	0.34	0.28	0.78
	<i>Calocedrus decurrens</i>	Time 1934	-1.09	0.28	-3.87	<b>&lt;0.001</b>
		Shade tolerant shrub cover	-0.06	0.09	-0.61	0.54
		Shade intolerant shrub cover	0.05	0.17	0.29	0.77
		Biomass	-0.91	0.22	-4.20	<b>&lt;0.001</b>
		Skid Trail	-1/50	0.41	-3.61	<b>0.003</b>
		Burn	-2.27	0.70	-3.23	<b>0.001</b>
		Skid trail and burn	-1.98	1.19	-1.66	0.10
		Time 1934 * Shade tolerant shrub cover	-0.05	0.26	-0.19	0.85
		Time 1934 * Shade intolerant shrub cover	0.71	0.25	2.90	<b>0.004</b>
		Time 1934 * Biomass	0.38	0.35	1.10	0.27
	<i>Pinus species</i>	Time 1934	0.28	0.69	0.41	0.69
		Shade tolerant shrub cover	0.19	0.08	2.50	<b>0.01</b>
		Shade intolerant shrub cover	0.20	0.20	0.99	0.32
		Biomass	0.39	0.37	1.04	0.30
		Skid Trail	-1.27	1.00	-1.26	0.21
		Burn	-0.13	0.98	-0.13	0.90
		Skid trail and burn	-1.82	1.02	-1.78	0.07
		Time 1934 * Shade tolerant shrub cover	0.18	0.20	0.91	0.36
		Time 1934 * Shade intolerant shrub cover	0.44	0.37	1.19	0.23
		Time 1934 * Biomass	1.32	0.74	1.79	0.07
Pre-harvest 1929 vs Current 2016	<i>Abies concolor</i>	Time 2016	0.22	0.47	0.47	0.64
		Shade tolerant shrub cover	0.11	0.05	2.19	<b>0.03</b>
		Shade intolerant shrub cover	0.09	0.11	0.84	0.40
		Biomass	-0.68	0.34	-2.01	<b>0.04</b>
		Time 2016 * Shade tolerant shrub cover	-0.15	0.21	-0.73	0.47
		Time 2016 * Shade intolerant shrub cover	-0.23	0.92	-0.25	0.80
		Time 2016 * Biomass	0.33	0.37	0.88	0.14
	<i>Calocedrus decurrens</i>	Time 2016	0.94	0.63	1.51	0.13
		Shade tolerant shrub cover	0.04	0.09	0.40	0.69
		Shade intolerant shrub cover	0.55	0.14	-1.26	<b>&lt;0.001</b>
		Biomass	-0.41	0.33	-1.26	0.21
		Time 2016 * Shade tolerant shrub cover	-1.42	0.72	-1.96	<b>0.05</b>
		Time 2016 * Shade intolerant shrub cover	-1.34	1.36	-1.00	0.32
		Time 2016* Biomass	-0.17	0.37	-0.45	0.65
	<i>Pinus species</i>	Time 2016	-0.65	0.59	-1.11	0.27
		Shade tolerant shrub cover	0.15	0.05	2.90	<b>0.004</b>
		Shade intolerant shrub cover	0.17	0.19	0.89	0.37
		Biomass	0.52	0.69	0.76	0.45
		Time 2016 * Shade tolerant shrub cover	0.10	0.79	0.12	0.90
		Time 2016 * Shade intolerant shrub cover	0.16	1.04	0.15	0.88

Post-harvest 1934 vs Current 2016	<i>Abies concolor</i>	Time 2016 * Biomass	-1.90	0.84	-2.27	<b>0.02</b>
		Time 2016	1.84	0.98	1.88	0.06
		Shade tolerant shrub cover	0.07	0.08	0.86	0.39
		Shade intolerant shrub cover	0.22	0.10	2.18	<b>0.03</b>
		Biomass	-1.92	1.38	-1.40	0.16
		Skid Trail	-0.27	0.28	-0.95	0.34
		Burn	0.37	0.42	0.89	0.38
		Skid trail and burn	0.29	0.67	0.44	0.66
		Time 2016 * Shade tolerant shrub cover	-0.06	0.14	-0.45	0.65
		Time 2016 * Shade intolerant shrub cover	-0.64	0.75	-0.85	0.40
	<i>Calocedrus decurrens</i>	Time 2016 * Biomass	1.43	1.38	1.04	0.30
		Time 2016	3.96	1.50	2.65	<b>0.008</b>
		Shade tolerant shrub cover	-0.06	0.14	-0.46	0.65
		Shade intolerant shrub cover	0.54	0.13	4.25	<b>&lt;0.001</b>
		Biomass	-3.88	1.99	-1.95	<b>0.05</b>
		Skid Trail	0.73	0.33	2.21	<b>0.03</b>
		Burn	-0.24	0.36	-0.67	0.50
		Skid trail and burn	0.37	0.63	0.60	0.55
		Time 2016 * Shade tolerant shrub cover	-0.82	0.46	-1.78	0.08
		Time 2016 * Shade intolerant shrub cover	-1.59	1.05	-1.51	0.13
	<i>Pinus species</i>	Time 2016 * Biomass	3.35	1.99	1.68	0.09
		Time 2016	-8.77	3.30	-2.66	<b>0.008</b>
		Shade tolerant shrub cover	0.22	0.10	2.20	<b>0.03</b>
		Shade intolerant shrub cover	0.47	0.22	2.16	<b>0.03</b>
		Biomass	12.84	4.35	2.95	<b>0.003</b>
		Skid Trail	-1.05	1.05	-1.00	0.32
		Burn	-0.57	1.04	-0.55	0.58
		Skid trail and burn	-2.04	1.07	-1.90	0.06
		Time 2016 * Shade tolerant shrub cover	-0.30	0.24	-1.22	0.22
		Time 2016 * Shade intolerant shrub cover	-0.19	0.89	-0.22	0.83
		Time 2016 * Biomass	-13.43	4.37	-3.08	<b>0.002</b>

### 3.3 Pre-harvest to 2016

The change in biomass from pre-harvest to 2016 significantly altered germinant densities of white fir ( $p=0.003$ ; Table 4). White fir germinant densities were positively associated with overstory biomass before harvest, but were negatively associated with biomass in 2016. There were no significant interactions between incense cedar or pine germinants and establishment conditions from pre-harvest to 2016 ( $p>0.05$ ; Table 4).

No interactions between white fir seedlings and establishment conditions from pre-harvest to 2016 were significant ( $p>0.05$ ; Table 5). The change in shade tolerant shrub cover from pre-harvest to 2016 significantly influenced incense cedar seedlings ( $p=0.05$ ; Table 5). Incense cedar seedling densities were not associated with shade tolerant shrub cover before harvest, but seedling densities were negatively associated with shade tolerant shrubs in 2016. The change in biomass from pre-harvest to 2016 significantly altered pine seedlings ( $p=0.02$ ; Table 5). Pre-harvest, there was no association between overstory biomass and pine seedlings, but in 2016 pine seedlings were negatively associated with biomass.

### 3.4 Post-harvest to 2016

No interactions between white fir germinants and changes in establishment conditions from post-harvest to 2016 were significant ( $p>0.05$ ; Table 4). Changes in biomass from post-harvest to 2016 significantly altered incense cedar germinants ( $p<0.001$ ; Table 4). Incense cedar germinant densities were not associated with overstory biomass in post-harvest forests, but were negatively associated with increasing biomass in 2016. The change in biomass and shade tolerant shrub cover from post-harvest to 2016 significantly influenced pine germinants ( $p<0.04$ ; Table 4). Pine germinant densities were negatively associated with overstory biomass in both post-harvest and 2016 forests, but the negative relationship was much stronger in 2016. After harvest, pine germinant densities were negatively associated with shade tolerant shrub cover, but in 2016 densities were not influenced by shade tolerant shrubs.

The relationships between white fir or incense cedar seedlings and their establishment conditions were not significantly changed between post-harvest and 2016 ( $p>0.05$ ; Table 5). Regardless of time, cedar seedlings densities were positively associated with skid trails ( $p=0.03$ ; Table 5). The change in overstory biomass from post-harvest to 2016 significantly influenced pine seedlings ( $p=0.002$ ; Table 5). Post-harvest, pine seedlings were slightly positively associated with overstory biomass, but in 2016 there was a strong negative association with increasing biomass.

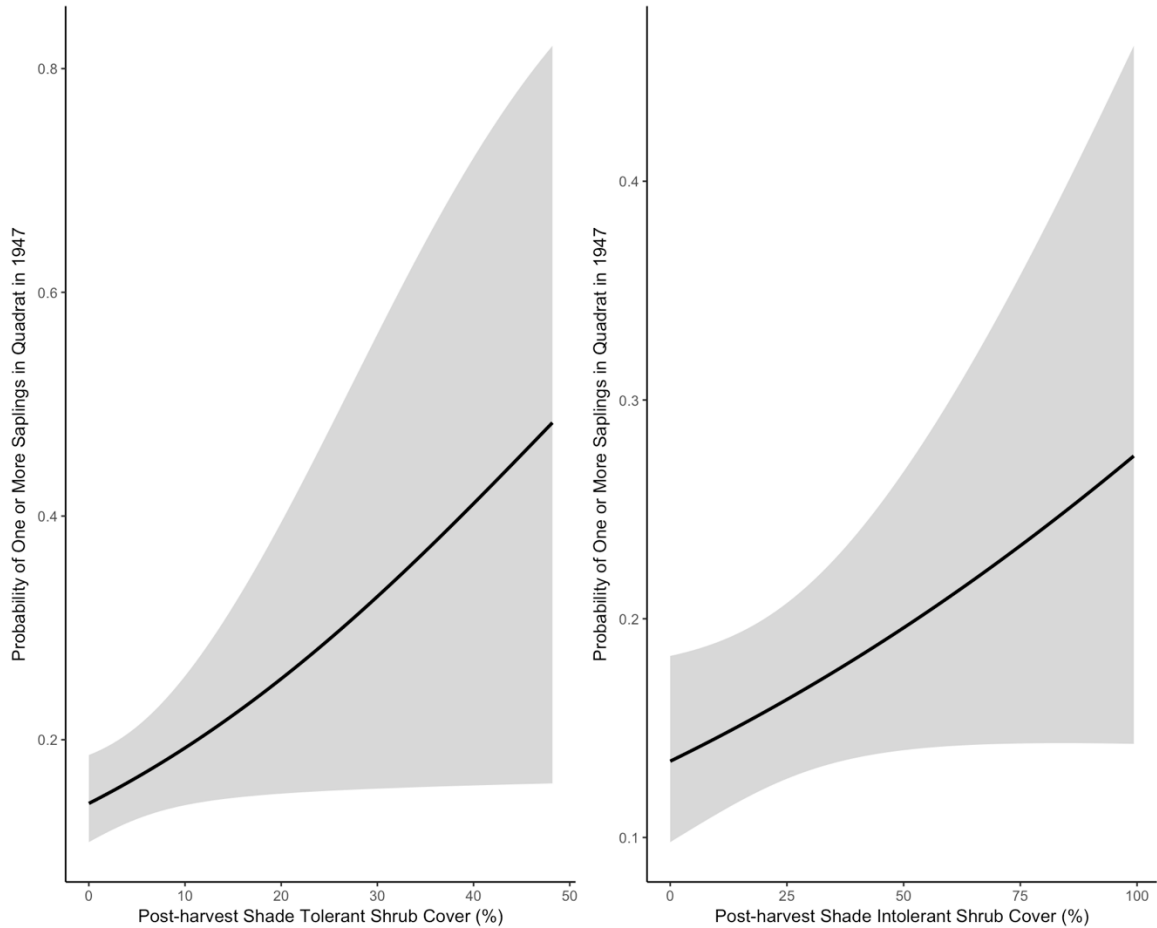
### 3.5 Seed tree and sapling models

White fir, incense cedar, and pine seedling densities were positively associated with germinant densities for each respective species in the previous year after accounting for post-harvest biomass and shrub cover ( $p<0.001$ ; Table 6). The number of trees of the same species above 10cm dbh in a 45.7m radius of a quadrat were positively correlated with the number of white fir germinants pre-harvest ( $p=0.02$ ) but negatively correlated with germinants in 2016 ( $p=0.04$ ). The density of seed trees was not a significant driver ( $p>0.05$ ) of germinant densities for incense cedar or pines at any time step.

*Table 6. Results for models with seedling (no cotyledons) densities from 1931, 1932, and 1935-1938. Previous year germinants indicates the number of germinants (with cotyledons) of each species from the year prior to the number of seedling. Results are from individual zero inflated negative binomial models for each species across all plots. Bolded p-values indicate significance.*

Species	Predictor Variables	$\beta$	SE	z	P
<i>Abies concolor</i>	Previous year germinants	0.27	0.11	2.49	<b>&lt;0.001</b>
	Shade tolerant shrub cover	-0.0006	0.006	-0.09	0.93
	Shade intolerant shrub cover	0.006	0.0017	3.38	<b>&lt;0.001</b>
	Biomass	-0.002	0.0003	-6.24	<b>&lt;0.001</b>
<i>Calocedrus decurrens</i>	Previous year germinants	0.28	0.006	5.83	<b>&lt;0.001</b>
	Shade tolerant shrub cover	-0.03	0.01	-3.53	<b>&lt;0.001</b>
	Shade intolerant shrub cover	0.01	0.003	4.70	<b>&lt;0.001</b>
	Biomass	0.007	0.0009	8.30	<b>&lt;0.001</b>
<i>Pinus species</i>	Previous year germinants	0.60	0.15	3.94	<b>&lt;0.001</b>
	Shade tolerant shrub cover	-0.005	0.01	-0.41	0.68
	Shade intolerant shrub cover	-0.005	0.005	-1.02	0.31
	Biomass	-0.002	0.0004	-4.21	<b>&lt;0.001</b>

The probability of a seedling of any species after harvest surviving into the sapling class in 1947 was influenced by shade tolerant and intolerant shrub coverage, and treatment effects on the quadrat surface. The probability of a sapling occurring increased by 51% with increasing shade tolerant shrub cover and by 50% with shade intolerant shrub cover ( $p=0.04$  and  $0.02$ , respectively; Fig. 10). Lastly, burned patches resulting from post-harvest pile burns was correlated with a decrease in the probability of a sapling occurring in 1947 by 10% ( $p=0.03$ ).



**Figure 10.** Probability plots for all significant variables ( $p < 0.05$ ) from logistic regression of the presence of a sapling ( $>137\text{cm}$  tall, but  $<10\text{cm}$  dbh) in a quadrat in 1947 of any species as a function of biomass and percent cover of shade tolerant and intolerant shrub species after harvest in 1931.

### 3.6 Overstory trees

Overall, 99.99% of the germinants and seedlings in the quadrats of the historic dataset did not survive to become mature trees in 2016. Of the  $<0.01\%$  of the seedlings that survived, 54% were incense cedars, while the other 46% was white fir (Table 7). There were fewer trees surviving the establishment years directly after harvest and during the time period of the historical dataset (1929-1947) than from the 1950s and after (Fig. 11), and the number of surviving trees in 2016 decreased with increases in post-harvest overstory biomass and increased with shade intolerant shrub cover ( $p < 0.04$ ). The likelihood of a seedling of any species surviving to become a tree in 2016 decreased by 50% with increasing post-harvest biomass and increased by 50% with shade intolerant shrub cover (Fig. 12).

Table 7. Total number of germinants (<10cm tall) and seedlings (>10cm, but <137cm tall) during each of the historic years, summed across all quadrats and plots and separated by species. Also shown is the number of live trees (>10cm dbh) within all quadrats and across all plots in 2016 that identified as establishing in each year.

Establishment Year	Species	# of Germinants	# of Seedlings	# Surviving in 2016
Post-harvest (1929)	ABCO	160	251	2
	CADE	54	150	0
	PINE	17	50	0
1930	ABCO	80	253	0
	CADE	27	137	0
	PINE	36	50	0
1931	ABCO	45	268	0
	CADE	145	139	2
	PINE	29	51	0
1932	ABCO	23	49	0
	CADE	76	30	2
	PINE	10	12	0
1934	ABCO	25	263	0
	CADE	195	153	1
	PINE	28	60	0
1935	ABCO	334	259	2
	CADE	2614	192	0
	PINE	24	67	0
1936	ABCO	243	245	1
	CADE	1710	262	0
	PINE	12	74	0
1937	ABCO	139	269	0
	CADE	1041	657	0
	PINE	17	74	0
1938	ABCO	115	269	1
	CADE	1485	709	2
	PINE	9	74	0
1947	ABCO	131	280	0
	CADE	376	767	0
	PINE	3	54	0

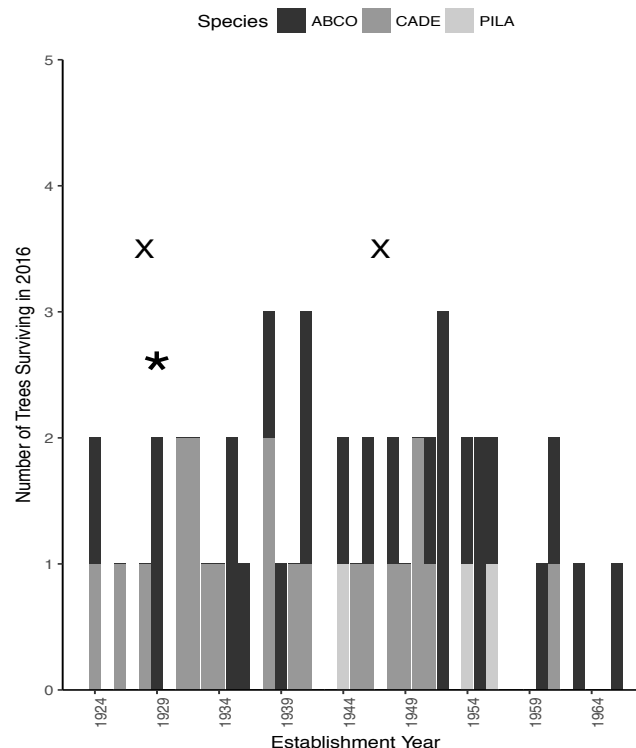
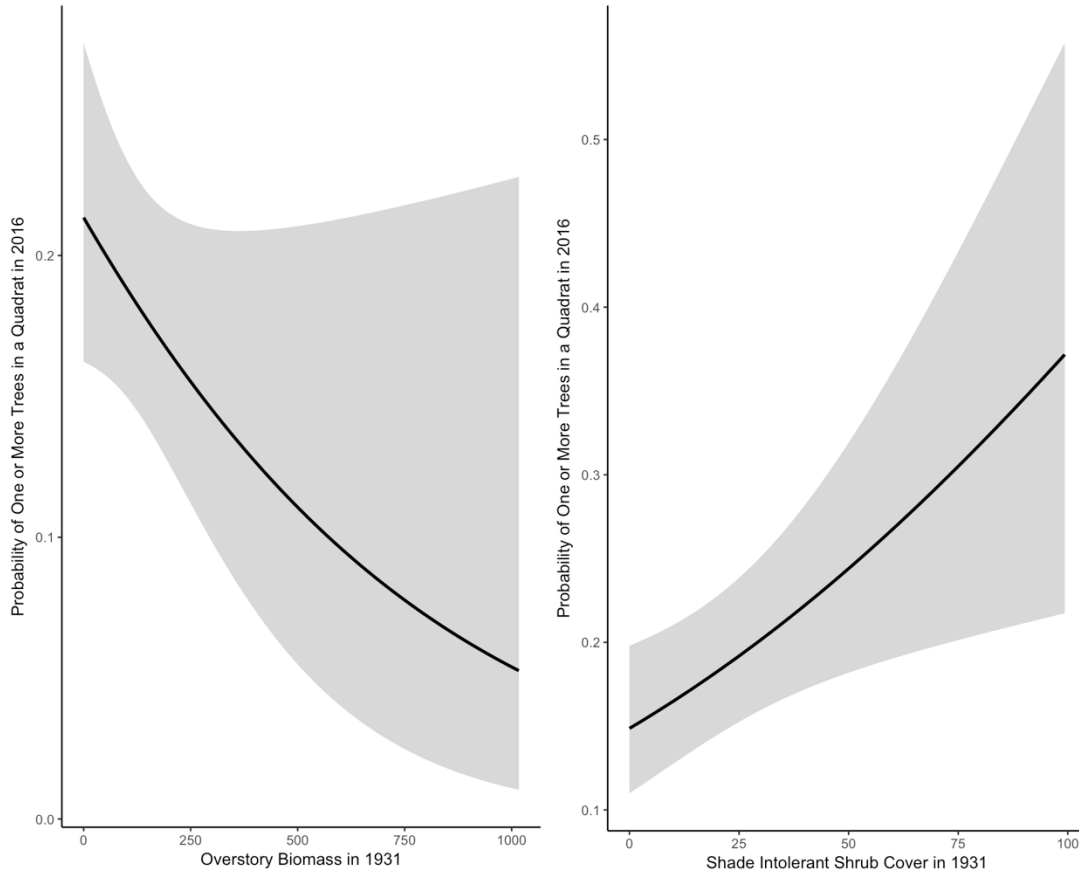


Figure 11. The number of trees >10cm dbh within the quadrat boundary (4m<sup>2</sup>) that were alive in 2016 and which year they established in. Establishment year was determined by coring live trees as close to the base as possible, counting the number of rings, and estimating the number of rings missed by the core using CooRecorder 9.0 and seedling growth data from MC8 in 1928. The X represents the earliest start (1928) and end (1947) of the historical dataset and the \* represents the year the plots were treated with different silvicultural prescriptions (1929).



*Figure 12. Probability plot for only significant variables ( $p=0.03$ ) from logistic regression of the presence of a live tree ( $>10\text{cm dbh}$ ) of any species in a quadrat in 2016 as a function of overstory percent cover of shade tolerant and intolerant shrub species after harvest in 1931.*

### 3.7 Treatment effects

Germinant densities were not different between quadrats across plots for any species before and after harvest ( $\chi^2=120$ ,  $p>.30$ ). Germinant densities were significantly different among quadrats for both incense cedar and pines 85 years after management ( $\chi^2=1493.1$ ,  $p<0.001$ ;  $\chi^2=5259.9$ ,  $p<0.001$ , respectively), but white fir germinant densities did not change among quadrats ( $\chi^2=177.72$ ,  $p=0.07$ ). Seedling densities were not significantly different across all quadrats at any time step for any species ( $\chi^2>100$ ,  $p>0.48$ ), with the exception of pine seedlings 85 years after management ( $\chi^2=5259.9$ ,  $p<0.001$ ).

Pre-harvest, germinant densities for white fir and incense cedar were significantly different between proposed treatment areas ( $\chi^2=36.87$ ,  $p<0.001$ ;  $\chi^2=36.87$ ,  $p=0.002$ , respectively), while pine germinants were not significantly different ( $\chi^2=10.79$ ,  $p=0.24$ ). Pre-harvest seedling densities for all species were significantly different between treatment areas prior to harvest (fir:  $\chi^2=126.5$ ,  $p<0.001$ ; cedar:  $\chi^2=124.05$ ,  $p<0.001$ ;  $\chi^2=45.40$ ,  $p<0.001$ ). After harvest, white fir and incense cedar germinant densities were not significantly different between treatments ( $\chi^2>1$ ,  $p>0.5$ ), while pine germinant densities varied between treatments ( $\chi^2=19.45$ ,  $p=0.002$ ). White fir and incense cedar seedling densities were significantly different following silvicultural treatments ( $\chi^2=23.94$ ,  $p=0.05$ ;  $\chi^2=37.57$ ,  $p=0.004$ ), but pine densities were not ( $\chi^2=4.48$ ,  $p=0.21$ ). Following 85 years of fire suppression and an absence of management, white fir and incense cedar densities were significantly different between historic treatments ( $\chi^2=6.98$ ,  $p=0.07$ ;  $\chi^2=36.68$ ,  $p=0.002$ , respectively), but pine densities did not differ ( $\chi^2=51.06$ ,  $p=1$ ). No seedlings densities for any species were significantly different between past silvicultural treatments after 85 years ( $\chi^2>24$ ,  $p>0.40$ ).



## 4. DISCUSSION

### 4.1 Overall forest changes

Intense historic management practices that removed large portions of the overstory (>50%) and over a century of fire suppression have altered the regeneration environment, leading to species-specific changes in seedling densities and a significant decrease in pine regeneration. Sierra Nevada forests are now generally denser than they were under historic conditions (Figs. 2, 3, 4, & 5) (North et al. 2007; Knapp et al. 2013; Levine et al. 2016). Densification restricts light availability in the understory and favors establishment of shade tolerant species. Using a long-term, historic dataset and plot re-measurement, I found a decrease in conifer regeneration and an absence of pines surviving into the overstory, indicating that shifts in forest structure and composition are influencing pine regeneration and survival in this forest (Table 3, Fig. 9). Altered disturbance regimes and changes in management practices across the mixed-conifer forests of western North America are resulting in similar shifts in structure and composition in the Sierra Nevada (Knapp et al. 2013; Stephens et al. 2015), the Rocky Mountains (Naficy et al. 2010; Foster et al. 2017), and other western forests (Pasch and Koprowski 2011).

While seed tree densities did not influence germinants in this forest, the amount of seeds and the actual germination and establishment of seeds is a major factor in determining how many seedlings will be present. Seedling densities of each species were heavily influenced by the number of germinants in the previous year, indicating that seed availability, establishment, and survival are important in determining germinant and therefore seedling densities for conifers in this forest. Areas where germinants were able to establish and persist are assumed to have both adequate seed source and favorable environmental conditions for the species (Zald et al. 2005). Seed production for white fir and incense cedar is 5-26 times greater than that of pine species (Zald et al. 2008), which, along with the shift in the composition of the overstory towards more shade tolerant species, is leading to differences in regeneration success.

In addition to seed availability and mast years, establishment site determines conifer regeneration success, which is driven by species-specific responses to establishment conditions. White fir prefers mesic sites (Franklin and Dyrness 1973; Rundel et al. 1977) and is sensitive to soil drying and heating, with seedlings under shaded, moist conditions exhibiting better survival rates (Gordon 1970; Barbour 1990; Laacke 1991; Zouhar 2001). Incense cedar germinates and survives best in half shaded areas (Stark 1965) and both incense cedar and sugar pine seedlings have higher densities on moist, cool sites (Barbour et al. 1990; Habeck 1992a; Gray et al. 2005; Meyer et al. 2007; Tollefson 2008). Ponderosa pine germination and seedling survival decreases under reduced moisture conditions (Oliver and Ryker 1990; Habeck 1992b). The importance of moisture availability for conifer seedlings in Sierra Nevada mixed-conifer forests means that these species will be sensitive to increased moisture stress that might result from increasing forest density. Pines experienced a 65% decrease in seedling densities compared to pre-harvest conditions, significantly lower than white fir and incense cedar. Pine germination and seedling survival is highest in full light and lowest in dense shade (Stark 1965). In contrast, white fir and incense cedar seedlings increase in density under closed canopies, such as those found in 2016 forests (Figs. 4 & 5) (Miller and Urban 1999; Stephens and Finney 2002; Bigelow et al. 2011).

In the understory, there were similar shifts towards more shade tolerant species. Many of the shrub species present in the historical forests were completely absent from current forests, likely because the increase in the number of smaller diameter trees closed the canopy and reduced the probability of success for many species within the regional species pool (Figs. 6 & 8). This shift was evident in the proportion of the overall shrub cover consisting of shade tolerant species, which experienced an increase in coverage between pre-harvest forests and 2016 (Fig. 7). These changes were to be expected, as an increase in the number of smaller diameter trees and a closing in of the canopy would create a shift towards shade tolerant species (North et al. 2007). After 85 years, overall shrub coverage decreased from pre-harvest conditions, suggesting that even shade tolerant species were not present as they were in historic forests. These changes in shrub cover were consistent with an earlier study from the same sites, which found a similar absence in historic shrub species and a 11-fold decline in coverage from 1929 to 2008 (Knapp et al. 2013).

### 4.2 Changes in regeneration dynamics through time

Changes throughout time in the amount of overstory biomass were important for regeneration of all species. A loss of the canopy heterogeneity of historic forests with numerous gaps of varying sizes (Figs. 2 & 3) created conditions under which the more shade tolerant species could persist. The light environment in these forests would be limited, and species such as white fir and incense cedar increase

in density under shaded to half shaded conditions (Stark 1965; Gordon 1970; Barbour 1990; Laacke 1991; Zouhar 2001). White fir and incense cedar also exhibited higher densities on moist sites so the open post-harvest could have created unfavorable dry conditions (Barbour et al. 1990; Gray et al. 2005; Meyer et al. 2007; Tollefson 2008). A decrease in canopy heterogeneity and an increase in overstory biomass would be especially detrimental for pine species, which are generally limited in shade tolerance. While sugar pine is moderately shade tolerant, it has low survival in dense shade (Stark 1965). The shift from the open canopy in post-harvest forests to the high canopy cover conditions in 2016 (Fig. 3) would have created a high number of very shaded sites, providing limited suitable establishment sites for pine regeneration.

In 2016, overstory biomass was detrimental even for regeneration of shade tolerant species. The large increase in density of smaller diameter trees from historic to current forests could have resulted in large amounts of competition for moisture (Ferrell et al. 1994; Ferrell 1996; North et al. 2007), such that even regeneration of shade tolerant trees is experiencing negative effects of canopy closure. Both white fir and incense cedar require moist environments and are sensitive to drought (Barbour et al. 1990; Gray et al. 2005; Tollefson 2008). The increased competition for scarce soil moisture during dry Sierran summers created by the increase in the density of smaller trees could have created conditions that were unfavorable for regeneration and establishment of shade tolerant conifers. These negative associations were expected for the more shade intolerant pine species. Studies under similar conditions found lower levels of pine regeneration in fire suppressed forests (Cooper 1960; Kilgore 1973; Helms and Tappeiner 1996; Gray et al. 2004) and over time when compared to historic datasets (Knapp et al. 2013).

Spatial and size class distributions were very different from historic to current forests. While historic forests were open with variable gap sizes and diameter classes, forests in 2016 had very few gaps and a large number of smaller diameter trees. This increase in biomass in the smaller diameter size classes created a heavily stocked forest with little room for establishing seedlings of any species to survive. These conditions were also likely to increase litter cover, and some studies have shown that pine seedlings can be more successful when establishing on bare mineral soil, which could further explain the stronger decrease in current forests (Cooper 1960; Stark 1965; Kilgore 1973; Knapp et al. 2013). This overstocking, along with the increased competition resulting from increased overstory biomass, will reduce conifer regeneration.

Changes to the shrub community can also have important impacts on the regeneration success of conifer species. The positive association between shade intolerant shrubs and pine seedlings was likely due to the lower light environment. These shrubs are more commonly found in areas where there is more light, which corresponds with areas preferred by pine seedlings. As the overstory conditions changed, this influenced the shrub community and had further impacts on conifer regeneration. Additionally, in these more open areas, shrubs could have provided safe sites to protect seedlings from drying out (Oakley et al. 2006) and from direct solar radiation (Stark 1965; Legras et al. 2010). Negative impacts on cedar regeneration from shade intolerant shrubs was likely a result of the increase in biotic competition from the increased stocking in 2016. Pre-harvest, shade intolerant shrubs, which were not necessarily confined only to open areas of the forest, would likely have had little competitive impact on incense cedar seedlings under the less dense forest conditions. In 2016, there was a significant increase in the frequency of smaller diameter trees (Fig. 4), and the forest was overstocked, thus increasing biotic competition and decreasing seedling densities. In these conditions, any increases in competition for soil moisture and growing space, especially in areas that are more open, would be detrimental to the more shade tolerant, moisture competition sensitive incense cedar (Barbour et al. 1990; Gray et al. 2005; Meyer et al. 2007; Tollefson 2008). In post-harvest forests, shade tolerant shrubs were negatively associated with pine germinants. Shrubs can compete with seedlings for water (Plamboeck et al. 2008), especially during dry summer months, and shrubs have been found to suppress regeneration in managed forests (Lanini and Radosevich 1986; Tappeiner and McDonald 1996; Gray et al. 2004). This competition could have been more pronounced in the open, post-harvest forest where it might have been drier and the preference of shaded areas by these shrubs would have created further competition for the moderately shade intolerant pines.

Management effects on the establishment surface, including skid trails and surfaces burned during pile burning, influenced white fir regeneration, but not pine. White fir seedlings can germinate successfully after a fire (Kauffman and Martin 1989; Habeck 1992a; Zouhar 2001). However, the burned areas in this study represent pile burnings, which can increase soil pH, decrease organic carbon and total soil nitrogen (Korb et al. 2004), and alter soil physical properties, such as water infiltration, porosity, and

water repellency (Hubbert et al. 2013). Pile burns would also decrease shrub cover, which, combined with a decrease in canopy cover after treatment, would increase solar radiation and desiccation. These changes could decrease densities, especially for species sensitive to low moisture and drought conditions, such as white fir (Gordon 1970; Barbour et al. 1990; Zouhar 2001). In contrast, incense cedar seedlings increased on skid trails. This response was to be expected, as this species generally does well in disturbed sites, such as road cuts (Horton 1949; Tollefson 2008). It is also possible that the post-harvest year followed a big seed production year for incense cedar, which had higher germinant densities than both pines and white fir after harvest (Fig. 9).

#### **4.3 Survival**

Overstory biomass and shrub cover were important for seedling survival throughout time (Figs. 10 & 12; Table 6). Soil moisture (Zald et al. 2005), litter depth, and solar radiation are important for conifer seedling survival (Waring and Angell 2011; Gray et al. 2005; North et al. 2005) and are highly related to overstory biomass. While decreasing solar radiation would increase the likelihood of a seedling surviving to a sapling, litter depth and soil moisture changes would hinder densities and survival. Additionally, increases in biomass would increase stocking and decrease establishment space for seedlings to move into saplings. Both shade tolerant and intolerant shrub cover increased seedling survival under an open canopy. The higher light environment would have created unfavorable soil moisture and solar radiation conditions for seedlings to establish and survive. Shrub cover could provide protection from these conditions (Legras et al. 2010; Zald et al. 2005) and increase the likelihood that a seedling survives to become a sapling.

Very few seedlings from the historic dataset survived to become a tree in 2016 (Fig. 11). The low survival of the high number of seedlings that established in the relatively open post-harvest conditions (Table 7) indicates that germinant and seedlings are largely ephemeral in this forest. This trend was reflected in the diameter distributions (Fig. 3) that exhibit a higher frequency of shade tolerant trees in the lower diameter classes when compared to historic forests and relatively few larger diameter trees. Survival of seedlings to this stage was influenced by shade intolerant shrub cover after harvest. In the low density post-harvest forests, light levels and temperatures would have been high, and desiccation is an important factor in the survival of all three species in the understory (Zald et al. 2005). The presence of shade intolerant shrubs in the post-harvest forest could have provided safe sites for seedlings (Zald et al. 2005; Tappeiner and Helms 1971) that allowed them to persist and continue into larger size classes. There are likely to be other factors that were important in determining survival that were outside the scope of this project, such as soil moisture (Zald et al. 2005), nutrient availability, and protection from herbivory (Fox 1977; Simard et al. 2003).

#### **4.4 Management implications**

A century of fire suppression and a removal of disturbance has increased forest density, as in many Sierra Nevada mixed conifer forests (Turner et al. 1997; Broncano et al. 2005; McIntire et al. 2005; Odion et al. 2010; Crotteau et al. 2013). These significant increases are limiting regeneration and survival of conifer seedlings in these forests, especially for pines, which will ultimately influence future forest composition. Mixed-conifer forests in the Sierra Nevada are primary habitat for more species of vertebrates than any other California forest community type (Mayer and Laudenslayer 1989; North et al. 2007), so alterations to forest structure and composition can have major impacts across the ecosystem. Pines, especially sugar pines, are an important component in mixed-conifer forests (Waring and Angell 2011) and were historically more abundant (Knapp et al. 2013). Sugar pines provide food and habitat for a variety of birds and mammals, including Douglas' squirrels, white-headed woodpeckers, and owls (Kinloch and Scheuner 1990; Habeck 1992a). As a result, promoting pine regeneration and survival into the overstory is often a key management focus for mixed-conifer forests. Forest management practices that reduce forest density, open the canopy, and create gaps will be essential for promoting pine regeneration (Bigelow et al. 2011; Lydersen et al. 2013; Knapp et al. 2013). Prescribed fire in addition to a silvicultural treatment that thins the canopy could further increase regeneration of pine species. Prescribed fire could remove areas of heavy litter as well as limit build up of slash and debris on the surface, which would increase favorable sites for germination, and numerous studies have shown pine germination to increase following prescribed fire (Kilgore 1973; McDonald 1976; Helms and Tappeiner 1996; Zald et al. 2008). The thinning of the canopy should also increase shrub cover, especially of shade intolerant species, to levels similar to those seen in historic forests. Many of the shade intolerant species respond well to fire (Quick and Quick 1961; Kauffman and Martin 1991; Knapp et al. 2013) and seeds from these species could still be present in the seed bank (Quick 1956; Knapp et al. 2012; Knapp et al.

2013), as small seedlings of *Ceanothus* were found in the field. Regardless of the treatments, overstory density must decrease if pine densities are to return to historic levels and if seedlings are to be allowed to persist into the newly thinned canopy. These changes would help return the forest to conditions produced under an active fire regime by reducing the density of smaller size classes (North et al. 2007), increasing the proportion of pines in the overstory (Knapp et al. 2013), and restoring canopy heterogeneity (Lydersen et al. 2013).

#### **4.5 Conclusion**

Changing forest structure and composition from the early twentieth century to 2016 has resulted in significant decreases to conifer regeneration in Sierra Nevada mixed-conifer forests. The increase in forest density and canopy closure resulting from a century of fire suppression and the removal of disturbance from these forests has created unfavorable establishment conditions for conifer regeneration. Establishment conditions are critical in determining conifer regeneration and survival and changes to these conditions throughout time influence the regeneration dynamics of the forests. The changes that are occurring to establishment conditions during fire suppression are creating unfavorable conditions in the form of increased biomass and decreased canopy gaps, which is preventing conifer seedlings from establishing and limiting seedling survival. Removal of disturbances and the resulting forest densification in Sierra Nevada forests and mixed conifer forests in western North America can have major impacts on conifer regeneration and survival of conifer species into the overstory, ultimately influencing the future structure and composition of these forests.

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