Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest

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ABSTRACT

In many forests of the western US, increased potential for fires of uncharacteristic intensity and severity is frequently attributed to structural changes brought about by fire exclusion, past land management practices, and climate. Extent of forest change and effect on understory vegetation over time are not well understood, but such information is useful to forest management focused on restoring biodiversity and resilience to these ecosystems. We re-measured three large (4 ha) historical "Methods of Cutting" (MC) plots in mixed-conifer forest of the central Sierra Nevada installed in 1929 to evaluate the effects of different logging methods. Trees $\geqslant 10$ cm were surveyed across the entire plots and understory vegetation (tree seedlings, shrubs, and herbaceous species) was quantified within quadrats in the old-growth condition in 1929 prior to logging, later in 1929 after logging, and again in 2007 or 2008. We also compared forest structure in the MC plots with an adjacent unlogged "control" area and collected fire scar samples from nearby stumps to evaluate the historical fire regime. The contemporary tree density in the MC plots (739 trees ha^{-1}) was 2.4 times greater than the 1929 pre-logging density (314 trees ha^{-1}). Trees in the small and intermediate size classes (10–75 cm dbh) were significantly over-represented, and trees in the larger size classes (>90 cm dbh) generally significantly under-represented, compared with historical conditions. The proportion of pine dropped from 37% of tree basal area in 1929 to 21% in 2007/08. Density of small to intermediate sized trees was similar in the contemporary logged and unlogged control plots, suggesting that over the long term, ingrowth may have been influenced more by lack of fire than historical logging. Change to non-tree vegetation was most pronounced for shrub cover, which averaged 28.6% in 1929 but only 2.5% in 2008. CART analysis indicated that the highest shrub cover in 1929 was in areas having four or fewer trees growing within 15 m to the south of the quadrat, suggesting that reduced light was the most likely explanation for the decline over time. Herbaceous species richness in 2008 was significantly lower than in 1931, two years after logging, but did not differ significantly from 1929, prior to logging. Understory vegetation should benefit from thinning or prescribed fire treatments that lead to a greater abundance of higher light environments within stands.

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1. Introduction

Many forests of the western US with a history of frequent fire have experienced an increase in tree density and shifts in species composition in the absence of fire (Cooper, 1960; Parsons and DeBennedetti, 1979; Scholl and Taylor, 2010; Collins et al., 2011). Early logging, which removed many of the largest and most shade-intolerant trees, has also altered the structure of stands (Naficy et al., 2010). Other legacies of historical land use include grazing by domestic livestock that may have contributed to forest densification by removing understory vegetation and fuels, thereby affecting the fire regime (Leiberg, 1902; McKelvey and Johnston, 1992; Moore et al., 2004; Norman and Taylor 2005).

Long-term data from re-measurement of historical plots have proven to be useful for quantifying changes to the tree size distribution and shifts in species composition (Dolph et al., 1995; Moore et al., 2004; Scholl and Taylor, 2010; Hagmann et al., 2013). However, most early studies in seasonally dry western US forests were focused solely on trees. Some information about understory vegetation change can be gleaned from old photographs, which in the Western US generally show a decline with forest densification (Fulé et al., 1997; Gruell, 2001). Using aerial photographs, Nagel and Taylor (2005) reported a 62% drop in cover of shrubs between 1939 and 2000 within a study area in the Lake Tahoe Basin, and attributed the change to conifer encroachment. Other evidence for how altering the forest canopy has influenced understory development over the long term is indirect. When forest density

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is reduced with thinning or prescribed fire to levels closer to those found in historical forests, shrub and herbaceous species often increase in abundance (Wayman and North, 2007; Moore et al., 2006; Dodson et al., 2008).

Stand structural changes have led to a decline in the vigor of individual trees (Kolb et al., 1998), increased the probability of bark beetle outbreaks (Fettig et al., 2007), and contributed to a higher probability of uncharacteristic fire in many seasonally dry western US forests (Agee and Skinner, 2005). Historical logging removed many of the largest trees and often targeted the most fire-resistant pines. Small trees that have established, especially those of the more fire-sensitive species, can act as ladder fuels, leading to torching and crown fire behavior. Stand density may influence the rate of surface fuel accumulation (Maguire, 1994), and infilling of gaps produced a more continuous fuelbed (Agee and Skinner, 2005).

Some of the characteristics of stands that have changed over time are also linked to habitat quality for many non-tree forest species. For example, presence of large trees and dense forest conditions are often favored as nesting or resting habitat for the spotted owl and the Pacific fisher (Bond et al., 2004; Zielinski et al., 2004). Conversely, stands with too high a density of small trees may hinder the the ability of forest-dwelling raptors to fly or capture prey (Reynolds et al., 1992; Irwin et al., 2004). Fire historically thinned out these small trees, and variability in fire effects created gaps and forest edge environments within stands (Weaver, 1943). Understory vegetation is another important component of wildlife habitat in many forest ecosystems (Hagar, 2007) and the presence of a robust understory in seasonally dry western US forests is frequently positively associated with light and/or soil moisture (North et al., 2005). Shrubs and herbaceous species provide cover for birds (Raphael et al., 1987; Humple and Burnett, 2010) and small mammals that endangered raptors depend on for prey (Reynolds et al., 1992) and are an important browse for ungulates (Kie, 1986). The understory also can facilitate germination and initial survival of conifer seedlings by creating microsites less likely to desiccate during long, dry summers (Legras et al., 2010). While shrubs can also compete with and reduce conifer height growth in the short term (Conard and Radosevich, 1982; Erickson and Harrington, 2006), some species such as Ceanothus sp. may improve conditions for tree growth by fixing nitrogen (Busse et al., 1996).

Greater recognition of how changes have influenced ecosystem processes, increased the probability of uncharacteristic fire, and altered the habitat for associated forest species has led to a greater emphasis on management designed to restore structural features, enhance biodiversity and improve ecological resilience. Planning corrective action requires information on the magnitude to which forests and key processes have been altered as well as an understanding of mechanisms and interactions among species.

In this paper we describe changes that have occurred to both overstory and understory vegetation over a period of 78+ years in three large (4 ha) "Methods of Cutting" plots located in a productive mixed-conifer forest in California's Sierra Nevada. Vegetation was first quantified in these plots in 1929, prior to logging. Plots were then logged using three different methods, and vegetation quantified again after logging, and finally in 2007/08. Long-term data of both overstory and understory vegetation are rare; this dataset represents a unique opportunity to quantify how forests have changed over time and develop possible mechanistic links between overstory structure and understory vegetation development. We also examine how representative the historical data might be of conditions prior to extensive change associated with Euroamerican settlement, and what these changes may mean for managers interested in restoring more resilient and biodiverse conditions to second-growth forests.

2. Materials and methods

2.1. Historical background

In 1929, three permanent plots were established in unlogged old-growth stands on the Stanislaus National Forest to "determine the growth rate and net growth, and to determine the rate of restocking after a light, a moderate and a heavy selection cutting" (Hasel et al., 1934). These "Methods of Cutting" plots were part of a network in different timber types and sites varying in productivity throughout national forests of California (Dunning, 1926), and are similar to plots established by US Forest Service Research in other regions of the United States as early as 1909 (Moore et al., 2004). The three Methods of Cutting plots (hereafter designated as MC9, MC10 and MC11) range from 3.9 to 4.4 ha, and are located immediately adjacent to each other on a gentle NW-facing slope in mixed-conifer forest at elevations ranging from 1740 to 1805 m within the Stanislaus-Tuolumne Experimental Forest (STEF) in the central Sierra Nevada (Fig. 1). The site is highly productive, with deep and well-drained loam to gravelly loam soils of the Wintoner-Inville families complex, derived from granite or weathered from tuff breccia. Climate is Mediterranean, with the majority of the annual precipitation (1030 mm year^{-1} between the years 1922–2012 [Station PNC 1922-1999, PCR 1999-2012]) occurring during fall, winter, and spring, and more than half falling as snow.

Plots were originally surveyed in the spring of 1929, with metal posts installed at the corners and every two chains (40.2 m) along
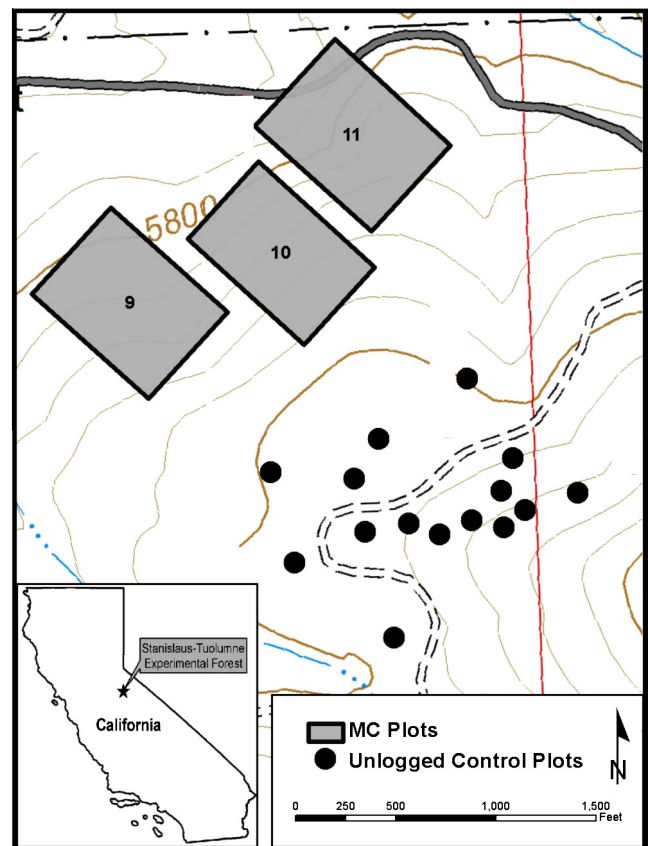

Fig. 1. Map of study area showing the location of Methods of Cutting plots 9, 10, and 11, established on the Stanislaus National Forest (within what later became the Stanislaus-Tuolumne Experimental Forest) in 1929. Locations of the 0.081 ha plots established in an adjacent unlogged stand and used as "controls" are noted with circular symbols.

the plot edges. All trees within plots with a diameter at breast height (dbh) ⩾ 9.1 cm were mapped along with the perimeters of tree seedling and sapling (<9.1 cm dbh) patches, shrubs, downed logs, and rock (Hasel et al., 1934) (Fig. 2). Trees were individually numbered with a steel tag, dbh and height were measured, and species and health were noted. One transect composed of adjacent 2.01 m × 2.01 m (milacre) quadrats was established across the narrow end of each plot (Fig. 2). Tree seedlings and saplings were mapped within each quadrat, species determined and height measured. Shrub cover was estimated by species (or groups of species when growing together). Number of stems of herbaceous species was counted in every tenth quadrat.

After the initial mapping and data collection, the plots were logged with three different methods in the summer of 1929. MC9 was marked according to standard US Forest Service practice at the time ("USFS cut"), removing larger overstory trees of all species. The objective, according to Hasel et al. (1934) was "an improvement cutting in all species and size classes for salvage, sanitation, release of pines, spacing for seed trees and improved net growth and composition in the reserve stand". MC10 was marked according to a "light economic selection" system, with the objective being the highest return to the operator for the first cut. Only the largest and best pines (*Pinus lambertiana*, *P. ponderosa*, and *P. jeffreyi*) were removed (Hasel et al., 1934). White fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*), having lower value, were not targeted for cutting. MC11 was marked by the head faller for the Pickering Lumber Company, with the objective of removing all merchantable trees ("heavy cut") before abandoning the land – a common practice on private timber lands at the time.

The study area was fenced after logging to exclude livestock, but fencing was not tall enough to exclude deer. Tree data were again collected in the fall of 1929 after logging, and repeated in 1934 and 1939 (although 1939 data for plot MC11 have not been found). The milacre quadrats were initially re-measured yearly and then periodically until 1947. Data were used in various publications including tree volume tables and site classification (Dunning, 1942), and stand development post-logging (Fowells and Schubert, 1951).

2.2. Discovery and re-measurement

When plots were rediscovered in 2006, most posts delineating the plot boundaries and corners of the milacre quadrats were still in place and many trees still contained numbered tags. Fencing around the plots was no longer intact and it is not known when fencing ceased to be effective. However, during the time of our re-measurement, no evidence of livestock was observed.

Plot maps from 1929 were digitized and registered to location using data from plot corners determined with a global positioning system (GPS) with external antenna and later differentially corrected to obtain sub-meter accuracy. Hand-written data for numbered trees were found in the National Archives in San Bruno, CA. We mapped the X and Y coordinates of trees ⩾10 cm dbh in all plots in 2007 (MC11) and 2008 (MC9 and MC10) using a laser rangefinder containing a compass module mounted on a tripod. If the tree dbh was >61 cm, two locations on either side of the tree perpendicular to the laser were shot and averaged to establish tree location. We labeled all trees ⩾10 cm dbh with an individually numbered tag at breast height (1.37 m) (unless the original 1929 tag could be located), and diameter was measured. Data for ponderosa and Jeffrey pine were combined in the 2007/08 census, because Jeffrey pine is uncommon (5% of "yellow pines" in 2007/08),

and was either not present in 1929, or the two species were not differentiated.

A road was built in the 1970s that bisected the north-eastern corner of MC11 and the area to the north of the road was thinned in 2006, removing approximately 0.7 ha from the plot. Therefore, all comparisons among years used only the portion of the plot remaining unaffected at the time of the 2007/08 mapping. Similarly, we only considered trees ⩾10 cm dbh in all analyses because that was the size threshold in the 2007/08 remapping.

We resampled understory vegetation within the milacre quadrats during the summer of 2008, repeating the methods used in 1929 and 1931. Cover of shrubs was visually estimated by species on all quadrats and number of stems of herbaceous vegetation was counted by species on every tenth quadrat.
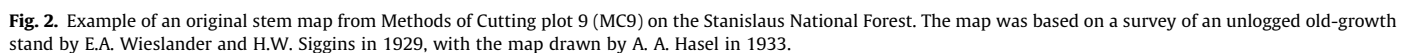
2.3. Control plots

Because an unlogged "control" was not set aside at the time the three MC plots were installed, we established fifteen 0.081 ha circular plots in an adjacent unlogged area within the Experimental Forest in June 2012, using a combination of systematic and random methods (Fig. 1). The unlogged area was located on the same aspect but at an average elevation 30–100 m higher than the MC plots. Points within 35 m of a road were rejected, as were points where any stumps were found in the vicinity. Diameter was measured and species noted for all trees with the center rooted within the plot.

2.4. Fire history

Historical fires in the study area were likely of both anthropogenic and non-anthropogenic origin. Lightning fire starts are common in the Sierra Nevada during the dry summer months (van Wagtendonk and Fites-Kaufman, 2006) and the Native Americans that once lived in the area traditionally managed vegetation with fire (Anderson, 2005). To quantify changes in the fire regime and pinpoint the date of the last fire, we sampled stumps with fire scars at three locations within the Stanislaus-Tuolumne Experimental forest in 2006 – one approximately 3 km NW of the MC plots, the second 0.4 km east of the MC plots, and the third 0.3 km south of the MC plots. Between 8 and 17 fire scar samples were collected from stumps and dead snags within an approximately 2 ha search area per location. Sections were removed using a chain saw, and then planed and sanded to a high polish. Fire years were determined by visually cross-dating tree rings (Stokes and Smiley, 1968). We used the COFECHA computer program (Grissino-Mayer, 2001) to help cross-date samples that could not be visually dated. Where possible, we estimated the likely season of the fire by noting the position of the scar within the growth ring relative to the typical seasonal timing of tree-ring growth (Fowells, 1941; Caprio and Swetnam, 1995). In the North American Mediterranean climate region, fire scars at the ring boundary are typically classified as late-summer to early fall (Beaty and Taylor, 2001; Skinner, 2002; Stephens and Collins, 2004). We calculated the median fire return interval (FRI) for the study area and for each individual site. To reduce the chance of including wounding caused by disturbances other than fire, fire years were assigned only when scars were registered on two or more trees.

2.5. Analyses

We compared structural characteristics (tree density, quadratic mean diameter, and basal area) of the three MC plots between measurement intervals and with unlogged control plots in 2012

Fig. 2. Example of an original stem map from Methods of Cutting plot 9 (MC9) on the Stanislaus National Forest. The map was based on a survey of an unlogged old-growth stand by E.A. Wieslander and H.W. Siggins in 1929, with the map drawn by A. A. Hasel in 1933.

using a repeated measures mixed linear model in SAS PROC MIXED. Plots were considered to be random and time fixed. Unequal variance among plot types (MC vs. Control) was accounted for by specifying plot type as grouping variable in the covariance structure. We used Tukey's HSD test for all pairwise comparisons. We did not compare the three logging treatments statistically because treatments were not replicated and the plots were surveyed in their entirety without subsampling.

Because number of tree seedlings, saplings, and herbaceous species were subsampled within quadrats and data for these variables contained numerous zeros and were not normally distributed, we used generalized linear mixed models (SAS PROC GLIMMIX) with the Laplace method of estimation to evaluate differences among the MC plots over time. We tested fit to negative binomial and Poisson distributions both with and without specifying plot × quadrat as a random term in the model, with the best fit determined using Akaike's Information Criteria (AIC). In all cases, the negative binomial distribution and specifying plot × quadrat as a random term provided the best fit.

We analyzed shrub cover as a repeated measures mixed linear model in SAS PROC MIXED, with plot specified as random and time as fixed. Shrub cover data were first transformed with a 0.25 power transformation, which improved the distribution of the residuals. Unequal variance among times was accounted for by specifying time as a grouping variable in the covariance structure. Frequency of shrub and herbaceous vegetation was also broken down by species, but patchiness in occurrence and small sample size, particularly for herbaceous species, precluded meaningful statistical analyses. Individual species frequency data are therefore exploratory and presented mainly for descriptive purposes.

We explored associations between shrub cover and the overstory using a classification and regression tree (CART) analysis in SPlus, with a minimum deviation of 0.07, 30 observations before splitting and a minimum final node size of 60. The regression tree approach is non-parametric and identifies variables and thresholds (nodes) for those variables by repeatedly splitting the data into increasingly homogenous groups. We used number and basal area of trees >10 cm dbh, number and basal area of pines >10 cm dbh, and percentage of trees and basal area composed of pine, all in both a 15 m radius circular plot centered on the midpoint of each quadrat, and in the southern half of a semicircle of the same radius (to better estimate the light environment) as potential explanatory variables. We also tested the same variables for smaller (10 m) and larger (20 m) radii in exploratory analyses, but correlations with shrub cover were not as strong as for the 15 m radius.

3. Results

3.1. Overstory change 1929–2007/08

Average tree density in 2007/08 (739.3 ha^{-1}) was more than twice that found in 1929, prior to logging (314.5 ha^{-1}) ($P = 0.002$) (Table 1). Basal area was also greater ($P = 0.001$) and quadratic mean diameter was lower ($P = 0.009$) over the same time period. These statistical tests have low power (three plots) and do not account for differences resulting from how individual plots were logged in 1929, after initial measurement.

Logging reduced tree stem density of MC9 and MC11 38% and 35%, respectively, while density in MC10, in which mainly the largest pines were cut, was reduced only 10% (Table 1). In the 78 to 79 years since, tree ingrowth has resulted in densities that are 2.6 to 4.2 times higher than after logging. The greatest change since 1929 occurred in MC9, logged using the US Forest Service preferred prescription at the time, while the least change occurred in MC11, which was logged the heaviest (Table 1). Logging reduced basal area by 70% in MC9, 28% in MC10, and 76% in MC11, but as with tree density, basal area was substantially higher in all plots in 2007/08 than in 1929 prior to logging (Table 1). Despite major differences in the amount of basal area removed in 1929, all plots contained nearly the same basal area in 2007/08 (67.5–71.6 m^2 ha^{-1}).

The greatest increase in density occurred among the small to intermediate sized trees, with significantly more trees in 2007/08 than in 1929 prior to logging in all size categories between 10 and 75 cm dbh (Table 1). Larger trees (>90 cm dbh) were still in deficit compared with the 1929 pre-logging data, with the difference statistically significant for both the 90–105 cm and 120+ cm categories (Table 1). Percentage-wise, trees in the 30–45 cm and 45–60 cm categories were the most over-represented, and trees in the >120 cm category were the most under-represented, compared with historical (1929) conditions (Table 1). The deficit of large trees was least pronounced in MC10, where large white fir and incense cedar were not removed in the logging.

The contemporary (2012) unlogged control plots were significantly denser ($P < 0.001$), contained more basal area ($P = 0.003$) and had a lower quadratic mean diameter ($P < 0.001$) than the MC plots in 1929, prior to logging. Conversely, the 2012 unlogged control plots were similar to the contemporary MC plots, 78 and 79 years after logging, in tree density, basal area, and quadratic mean diameter (Table 1). Breaking the tree density numbers down by size category showed that the contemporary plots (logged (MC)

Table 1
Live tree density by diameter size class and quadratic mean diameter (QMD) in 1929 prior to logging (1929 after logging in parentheses), and in 2007 or 2008 (78 or 79 years after logging) within three plots established in the central Sierra Nevada as part of a "Methods of Cutting" (MC) study. Averages of the three MC plots in 1929 (prior to logging) and 2007/08 were also compared with each other and with data collected in an adjacent unlogged "control" stand in 2012. Values within a column followed by different letters were statistically significant from each other ($P < 0.05$).

Plot	Date	Size class (cm)										QMD (cm)	BA (m^2 ha^{-1})
		10–20	20–30	30–45	45–60	60–75	75–90	90–105	105–120	120+	Total density		
		(Trees ha^{-1})											
9	1929	125.6 (85.7)	42.4 (32.8)	31.7 (27.1)	24.6 (16.6)	18.2 (8.0)	16.4 (4.8)	11.2 (1.6)	6.6 (0.5)	8.0 (0.0)	284.6 (177.1)	49.5 (34.2)	54.7 (16.3)
9	2008	417.2	174.6	127.6	62.9	28.7	12.8	5.0	2.5	1.6	832.9	32.1	67.5
10	1929	139.3 (127.5)	44.9 (41.0)	23.3 (23.1)	10.8 (10.8)	9.0 (8.7)	12.6 (12.3)	11.3 (9.5)	7.7 (6.2)	10.0 (3.3)	268.8 (242.4)	49.3 (44.0)	51.4 (36.9)
10	2008	306.0	160.5	131.8	62.6	24.1	9.0	6.2	6.2	5.1	711.4	35.8	71.6
11	1929	197.0 (141.2)	69.9 (59.0)	49.6 (42.6)	20.4 (8.0)	14.7 (1.6)	14.2 (1.3)	8.0 (0.0)	6.7 (0.3)	9.4 (0.5)	389.9 (254.6)	42.6 (25.9)	55.7 (13.5)
11	2007	260.2	148.2	133.7	70.7	33.8	21.4	3.8	1.6	0.0	673.4	36.0	69.0
9-11	1929	154.0[a]	52.4[a]	34.9[a]	18.6[a]	14.0[a]	14.4[a]	10.2[b]	7.0[a]	9.1[b]	314.5[a]	47.1[a]	53.9[a]
9-11	2007/08	327.8[b]	161.1[b]	131.0[b]	65.4[c]	28.9[c]	14.4[a]	5.0[a]	3.4[a]	2.2[a]	739.3[b]	34.6[b]	69.4[b]
Unlogged control	2012	347.6[b]	182.0[b]	111.2[b]	43.6[b]	16.5[b]	12.4[a]	9.1[ab]	5.8[a]	11.5[b]	739.7[b]	37.8[b]	78.2[b]

Table 2
Tree basal area by species and percentage of basal area composed of pine in 1929 prior to logging (1929 after logging in parentheses), and in 2007 or 2008 within three plots established as part of a "Methods of Cutting" study in 1929.

Plot	Year	Abies concolor	Calocedrus decurrens	Pinus lambertiana	Pinus ponderosa	Pine basal area
		(m² ha⁻¹)				(%)
9	1929	17.5 (6.0)	14.6 (4.4)	13.6 (4.3)	9.1 (1.5)	41.5 (36.0)
9	2008	30.6	22.0	8.2	6.7	22.1
10	1929	23.7 (23.0)	11.1 (10.6)	12.3 (3.1)	4.3 (0.3)	32.2 (9.2)
10	2008	35.6	23.0	10.8	2.1	18.1
11	1929	25.5 (9.2)	9.6 (2.2)	15.0 (1.8)	5.6 (0.2)	37.3 (14.5)
11	2007	35.4	18.5	10.1	5.0	21.8

Table 3
Statistical significance (P) of the effects of logging treatment (plot) and time on tree seedling and sapling density (total and pine), shrub cover and herbaceous species richness within quadrats in three Methods of Cutting plots, as determined with repeated measures mixed linear models. Tree variables were analyzed for three time periods (1929 pre logging, 1929 post logging, and 2008), while shrub cover was analyzed for four time periods (1929 pre logging, 1929 post logging, 1931, and 2008).

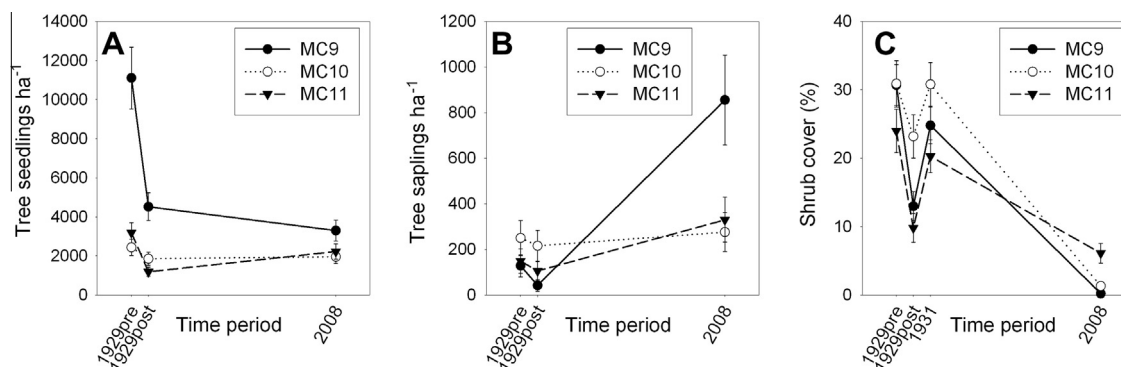| Effect	Tree				Understory	
	Seedling density	Pine seedling density	Sapling density	Pine sapling density	Shrub cover	Herbaceous species richness
	P					
Plot	<0.001	0.435	0.378	0.997	0.557	0.020
Time	<0.001	0.002	<0.001	0.975	<0.001	0.009
Plot × time	<0.001	0.684	<0.001	0.838	<0.001	0.322

Fig. 3. Density of tree seedlings (A), tree saplings (B) and shrub cover (C) in three "Methods of Cutting" plots on the Stanislaus National Forest in 1929 (prior to logging), in 1929 (immediately after logging), and in 2008. For shrubs, cover in 1931 is also shown. Bars show the standard error.

and unlogged (Control)) both contained substantially more small and intermediate sized trees, relative to the 1929 pre-logging condition (Table 1). However, the unlogged control (2012) was most over-represented in the smallest tree size categories (10–30 cm dbh), while the 2007/08 MC plots instead contained significantly more trees in the intermediate tree size categories (45–75 cm dbh). The logged MC plots in 2007/2008 contained significantly fewer trees in the largest size category (>120 cm) than either the unlogged 1929 MC plots or the 2012 unlogged control. Density of the largest trees in the unlogged control was not significantly different from the historical 1929 density, showing that in the absence of logging, the large tree component was maintained over time.

Prior to logging in 1929, the tree species composition, in terms of basal area, was 41% white fir (*Abies concolor*), 25% sugar pine (*Pinus lambertiana*), 22% incense cedar (*Calocedrus decurrens*), and 12% ponderosa/Jeffrey pine (*P. ponderosa*/ *P. jeffreyi*), averaged across plots (Table 2). All logging treatments removed a greater proportion of the basal area of pine than white fir or incense cedar. The favoring of white fir and incense cedar among leave trees was especially pronounced in MC10, where harvest focused exclusively on pine and the only loss of white fir and incense cedar was the result of logging damage. The logging treatment in MC9 (USFS cut)

retained the most pine. In 2007/08, the tree species composition (basal area) was 49% white fir, 31% incense cedar, 14% sugar pine, and 7% ponderosa/ Jeffrey pine, averaged across plots (Table 2). Percentage of the basal area composed of pines, which averaged 37% in 1929 prior to logging, dropped to 21% in 2007/08, with little difference among plots despite the variation in selection among species in the logging treatments (Table 2).

3.2. Understory change 1929–2008

The time × plot interaction was statistically significant ($P < 0.001$) for both tree seedlings (between 10 and 137 cm tall) and saplings (>137 cm tall and <10 cm dbh) (Table 3). The loss of seedlings between 1929 prior to logging and 1929 after logging was 53% in MC9, 24% in MC10, and 62% in MC11 (Fig. 3). Tree seedling numbers changed relatively little between post-logging in 1929 and 2008. Saplings were also reduced by logging but have since increased above 1929 pre-logging levels in MC9 and MC11. This increase was especially pronounced in MC9, with 128 and 856 saplings ha⁻¹ recorded in 1929 and 2008, respectively. Density of pine (sugar, ponderosa, and Jeffrey) seedlings declined significantly over time (Table 3), with 766 ha⁻¹ in 1929 prior to logging, 368 ha⁻¹ in 1929 after logging, and only 68 ha⁻¹ in 2008. There were no

Table 4
Frequency of the most common understory plant species in quadrats in the old-growth condition in 1929 (pre-logging), 1929 (post-logging), 1931, and 2008. Frequency of shrubs and subshrubs were based on 300 quadrats and herbs were based on 30 quadrats. All species listed occurred in ⩾5% of quadrats in at least one measurement year. Graminoid = members of the Poaceae and Cyperaceae families.

Taxa	Growth habit	Annual/perennial	Frequency (%)			
			1929 pre	1929 post	1931	2008
Apocynum androsaemifolium	Herb	P	0	0	16.7	13.3
Arctostaphylos patula	Shrub – tall	P	7.7	4.3	10.3	0
Ceanothus cordulatus	Shrub – tall	P	27.0	17.0	27.0	0
Ceanothus integerrimus	Shrub – tall	P	11.0	7.3	13.0	0.3
Ceanothus parvifolius	Shrub – tall	P	15.0	9.7	20.0	0
Chamaebatia foliolosa	Shrub – short	P	42.3	30.3	52.7	0.3
Chrysolepis sempervirens	Shrub – tall	P	17.3	13.3	21.7	13.7
Disporum hookeri	Herb	P	10.0	6.7	10.0	10.0
Epilobium sp.	Herb	A	16.7	6.7	6.7	0
Fritillaria pinetorum	Herb	P	6.7	6.7	6.7	0
Gayophytum diffusum	Herb	A	3.3	3.3	16.7	3.3
Graminoid	Herb	P	20.0	16.7	26.7	13.3
Hieraceum albiflorum	Herb	P	23.3	20.0	20.0	0
Iris hartwegii	Herb	P	10.0	6.7	23.3	16.7
Kelloggia galioides	Herb	P	0	0	13.3	6.7
Lilium washingtonianum	Herb	P	10.0	6.7	6.7	10.0
Osmorrhiza sp.	Herb	P	10.0	10.0	6.7	0
Pyrola picta	Herb	P	0	0	3.3	16.7
Smilacina sp.	Herb	P	13.3	10	13.3	3.3
Viola sp.	Herb	P	20.0	16.7	26.7	23.3
Rosa gymnocarpa	Subshrub	P	3.7	2.6	53.0	21.0
Symphoricarpos mollis	Subshrub	P	0.7	0.7	6.7	7.7

significant differences in the density of pine saplings among plots or over time (Table 3). Among seedlings, incense cedar showed the greatest increase in abundance and sugar pine the greatest decrease in abundance, relative to other tree species. Percentage of incense cedar rose from 33.7% of all seedlings in 1929 (pre-logging) to 56.8% in 2008, while percentage of sugar pine seedlings dropped from 12.4% to 3.0% over the same period.

Prior to logging in 1929, cover of shrubs was patchy and similar across all three plots, averaging 28.6% (Fig. 3). Shrubs were most commonly found in small canopy gaps (Fig. 2). The time × plot interaction for shrub cover was significant (Table 3), with logging resulting in a greater short-term loss of cover in MC9 and MC11 than in MC10 (Fig. 3). Shrub cover recovered to or approached pre-logging levels in all plots in 1931. By 2008, cover had declined to 0.2% in MC9, 1.3% in MC10, and 6.1% in MC11 (Fig. 3). The most common shrub species found in higher light environments within the forest in 1929 (*Arctostaphylos patula*, *Ceanothus cordulatus*, *C. integerrimus*, *C. parvifolius*, and *Chamaebatia foliolosa*) were mostly eliminated from the plots by 2008 (Table 4). Classification and regression tree analysis showed that prior to logging in 1929, shrub cover averaged 53.5% in quadrats containing four or fewer trees within a 15 m radius semicircle facing south, whereas shrub cover averaged only 7.4% in quadrats containing ten or more trees in this semicircle (Fig. 4). For plots with an intermediate number of nearby trees (five to nine), average shrub cover was higher when those trees were small (low basal area). Nearly 29% of the quadrats contained four or fewer trees and 35% of the quadrats contained more than nine trees in 1929. The percentages in the same quadrats in 2008 were 0 and 98%, respectively (Fig. 4).

Herbaceous species richness differed significantly over time (Table 3), with an average of 1.50 species noted per quadrat in 1929 prior to logging, 1.01 in 1929 after logging, 1.96 in 1931, and 1.00 in 2008. Herbaceous species richness in 2008 was significantly less than in 1931 (two years post- logging) ($P = 0.022$), but was not significantly different from 1929 prior to logging ($P = 0.315$). The herbaceous understory was dominated by dicots, with graminoids (grasses and sedges) found in only 20% of quadrats in 1929 and 13% of quadrats in 2008 (Table 4). The three herbaceous taxa having the most total stems in 1929 (*Epilobium* sp.,

Hieracium albiflorum, and *Fritillaria pinetorum*) had disappeared from the quadrats in 2008. Several species not noted in the 1929 surveys (e.g. *Apocynum andosaemifolium*, *Kelloggia gallioides*, and *Pyrola picta*) were found in 2008.

3.3. Fire history

We cross-dated 431 fire scars on samples from 39 trees (22 incense cedar, 10 ponderosa pine, and 7 sugar pine) from the three collection sites. The earliest recorded fire-scar date was 1336 while the earliest on at least two trees was 1492. Because the number of samples and records of fires decline rapidly before 1600 and no fires were recorded in the twentieth century, we constrained our analyses of the fire history to the period from 1600 to 1900. Considering only fires that scarred at least two trees, the median fire interval for the three fire scar collection areas combined was 3 years, with a minimum and maximum of 1 and 23 years, respectively (Fig. 5). At the scale of individual approximately 2 ha fire scar collection areas, the median fire return interval ranged from 5 to 9 years (mean = 6.3), with a minimum and maximum of 1 and 40 years between fires. The last fire recorded in the area occurred in 1889, 40 years prior to establishment of the MC plots. This length of time without fire was similar to the longest fire-free period from 1600 to 1900. Position of the scar within the annual ring could be determined for 61% of the scars – 2.7% of these occurred within the early-early wood, 10.0% occurred in the middle-early wood, 21.8% occurred in the late-early wood, 59.4% occurred in the late wood, and 6.1% occurred at the ring boundary (dormant).

4. Discussion

4.1. Reference conditions

Due to relatively low fuel loading, historical forests of the Sierra Nevada prior to significant alteration of the fire regime were thought to burn with predominantly low-severity effects, but with occasional patches of moderate to high severity (Sudworth, 1900; Show and Kotok, 1924). Data from reference forests at that time
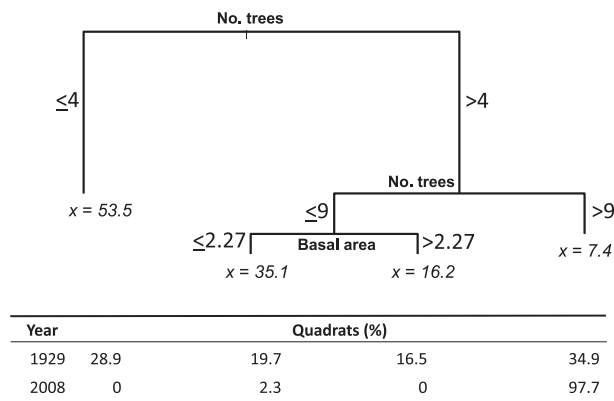
Fig. 4. Classification and regression tree (CART) output showing variables most strongly associated with shrub cover within 218 quadrats in 1929 prior to logging. Number of trees (>10 cm dbh) and basal area were summed within the southern half of a 15 m radius semicircle centered on each quadrat. The length of the line from each split is proportional to the total sum of squares explained by that variable. Below are the percentage of quadrats within each split in 1929, and the percentage that would be under 2007/08 stand conditions.

Fig. 5. Fire history of three locations within the Stanislaus-Tuolumne Experimental Forest near MC plots 9-11. Samples denoted with "STR" were collected along Old Strawberry Road, approximately 3 km NW of the MC plots, samples denoted "ST" were collected east of Sheering Creek, 0.4 km east of the MC plots, and plots denoted "STC" were collected along FS road 4N10, 0.3 km south of the MC plots. Each horizontal line represents a record from a single tree. Bold vertical lines are years where a fire was recorded and the composite at the bottom shows the year of fires recorded by at least two trees.

therefore provide one possible example of a composition and structure likely to be resilient to wildfire. However, to evaluate how representative the 1929 pre-logging data might be of "reference" conditions, it is important to consider the extent to which the forest may already have been altered by changes to the fire regime or other impacts associated with Euro-American settlement.

While the median historic fire return interval at the spatial scale of the MC plots was 6 years, the longest recorded time without a fire between 1600 and 1889 was 40 years – the same length of time as between the last fire (1889) and the plot establishment (1929). Thus the fire interval departure in 1929 appears to have been at the very upper end but still within the range of historical fire intervals. It is probable that some fires had been missed. These missed fires could have resulted in higher numbers of small trees in the 1929 pre-logging data set than would have been expected with a fully intact fire regime. However, seedling growth information from nearby plots (Stark, 1965) suggest that the average tree in the 1929 pre-logging data set establishing more than 6 years after the last fire (i.e. post-1895), would not yet have reached the 10 cm diameter cut-off of the smallest tree size class in our survey. Nevertheless, because tree seedling growth rates in actual stands are highly variable (Schubert, 1956), it is possible that some ⩾10 cm trees established post-1895. A larger minimum size cut-off (e.g. 20–25 cm dbh) may be appropriate if a more conservative estimate of reference conditions is desired.

The shrub, herbaceous understory, and tree seedling data, while providing some of the best quantitative information currently available about forests of that time, are possibly less reflective of conditions prior to Euro-American settlement than the tree data. Changes to these components may occur more rapidly. In addition, the Sierra Nevada experienced an unusually moist period early in the twentieth century (Hughes and Brown, 1992; Cook et al., 2011). Combined with the absence of fire and approximately 40 years of heavy sheep grazing starting in the 1860s, these factors may have substantially influenced understory vegetation and tree recruitment dynamics (McKelvey and Johnston, 1992). Although the MC plots were fenced after establishment in 1929 to exclude livestock, the legacy of past grazing still needs to be considered. Historical observations of Leiberg (1902) and Sudworth (1900) indicated that large numbers of tree seedlings established after sheep were removed, possibly due to the reduced competition with understory grasses and forbs. Because changes in grazing, fire regime, and climate occurred simultaneously, individual effects of each on vegetation cannot be fully separated.
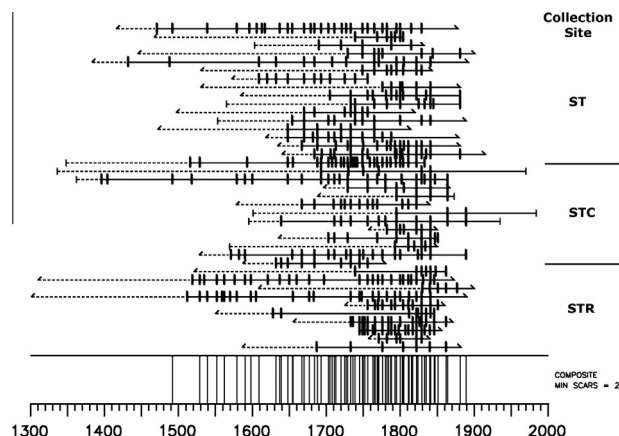
The average historical tree density and basal area values prior to logging in the 1929 MC plots are higher than those reported for several nearby studies (Scholl and Taylor, 2010; Collins et al., 2011). These differences exist for comparisons using the same minimum tree size cut-off and for both small and larger tree size classes, suggesting that discrepancies are most likely explained by site differences rather than time elapsed since the previous fire. The plots studied by Scholl and Taylor (2010) and Collins et al. (2011) covered a broad range of aspects, slope positions, and elevations. It is well understood that historical structure of dry forests throughout the western US was exceedingly variable (Scholl and Taylor, 2010; Collins et al., 2011; Williams and Baker, 2012), reflecting these topographic gradients, as well as variability in the fire regime and site productivity (Lydersen and North, 2012). Both the overstory and understory data from this study are therefore likely most representative of highly productive, relatively moist, mid-slope locations containing deep soils.

4.2. Forest change – overstory

Our data demonstrate that dramatic changes have occurred in these forests over the study period – changes that potentially influence important characteristics such as the habitat suitability for different wildlife species as well as fire hazard. Change within the MC plots from 1929 to 2007/08 is unequivocal because the existence of plot corner stakes and tree tags allowed the same area to be measured both times, and the entire plot area was surveyed, eliminating the possibility of sampling error. Comparisons using historical data also lack uncertainties associated with studies of change based on forest reconstruction techniques (Huffman et al., 2001). These changes can be attributed to a combination of factors, including fire exclusion, past logging practices, and possibly climate.

For the small and intermediate sized trees (<60 cm), which can act as ladder fuels and increase the probability of crown fire (Agee and Skinner, 2005), past logging did not appear to be a major factor. Density in the small and intermediate size categories was nearly identical in the logged 2007/08 MC plots and the unlogged contemporary "control" stands, with over three times as many trees compared to historic (1929) conditions. In addition, 78+ years after logging, the three MC plots had strikingly similar densities of

trees in these size classes, despite major differences in how heavily they were logged. Densification over the long-term therefore appears to have been influenced more strongly by factors shared by all plots such as the exclusion of fire and possibly climate change.

While the role of climate in the three-fold increase in density of small and intermediate sized trees cannot be ruled out, much of this dramatic change is likely the result of fire exclusion. Early observers of forest structure in the Sierra Nevada believed the number of trees that could establish was limited by frequent fire (Sudworth, 1900; Leiberg, 1902; Show and Kotok, 1924). While weather conditions favorable to germination and early growth can increase the probability of seedling survival (Stark, 1965), seedlings typically establish in large numbers in many years on relatively moist N-facing aspects and in deeper soils like those in this study (Fowells and Schubert, 1951; Stark, 1965). Stand reconstruction studies in the Sierra Nevada suggest a steady input of trees rather than distinct pulses associated with periods of favorable and unfavorable climate (Scholl and Taylor, 2006, 2010). Furthermore, even in other drier forest types where pulses of regeneration have been attributed to periods of favorable climate, the association between regeneration and climate has mainly been shown for periods where fire was excluded (Mast et al., 1999), with thinning of seedlings and young trees by repeated fires breaking down these associations over time.

Our finding of similar densities of small to medium sized trees in adjacent logged and unlogged plots was shared by Dolph et al. (1995) in a 50 year study of plots where 0–95% of the volume was removed, but differs from Naficy et al. (2010) who reported greater densities in logged areas than in unlogged areas in the northern Rockies. This suggests that there may be regional differences in the long-term responses to logging and fire exclusion across dry forest types of the Western US.

For the larger (>90 cm) tree size categories, which are frequently preferentially used for nesting, resting, or roosting by wildlife species (Bond et al., 2004; Zielinski et al., 2004) and are generally the most resistant to fire due to thicker bark and higher height to live crown (Peterson and Ryan, 1986), the 2007/08 MC plot data show a deficit relative to the 1929 data and the contemporary unlogged control stands. This suggests that for the largest trees, past logging remains responsible for the departure from historic conditions.

The majority of studies investigating long-term change in forests of the western US with a history of frequent fire have also found dramatic increases in tree density in the absence of fire over time (Parsons and DeBennedetti, 1979; Moore et al., 2004; Scholl and Taylor, 2010; Collins et al., 2011; Hagmann et al., 2013). Magnitude of the tree density increase in the MC plots was similar (Scholl and Taylor, 2010; Hagmann et al., 2013), to somewhat or substantially less (Moore et al., 2004; Collins et al., 2011) than that reported for other such forests.

The shift in species composition from less shade tolerant to more shade tolerant species we noted in the MC plots is in line with other studies in mixed conifer forests of the western US with a history of frequent fire (Parsons and DeBennedetti, 1979; Taylor, 2000; Scholl and Taylor, 2010). Interestingly, even though the logging treatment in MC9 retained a much higher percentage of pine than in MC10 and MC11, the compositional differences were not maintained over time. This suggests that over the long term, factors other than the logging may be playing a larger role in shaping species composition. Indeed, for the plots in our study, the proportion of pine among the smaller tree size classes (10–45 cm dbh) was lowest in the contemporary unlogged control plots, despite the presence of an overstory of large seed-bearing pines. This suggests that the lack of sites suitable for seedling establishment may be exerting more influence on pine recruitment in these forests than lack of seed. Low level of pine recruitment in dense contem-

porary stands has been noted by others (Ansley and Battles, 1998; van Mantgem et al., 2004; Bigelow et al., 2011). Pines generally require higher light environments than more shade tolerant species such as fir and incense cedar, and benefit more from bare mineral soil (Ansley and Battles, 1998; Moghaddas et al., 2008). It is also possible that the introduced white pine blister rust pathogen (*Cronartium rubicola*) may be causing substantial mortality of young sugar pine trees (van Mantgem et al., 2004).

4.3. Forest change – understory

Shrubs were the dominant understory growth form in the 1929 MC plots prior to logging, and the over 11-fold decline in cover over time is likely related to the increase in forest density and infilling of small gaps where shrubs were most commonly found. In spatial analyses using tree diameter: canopy radius equations in the same MC plots, Lydersen et al. (2013) estimated that canopy cover increased from 45% to 62% and the percentage of plot area in canopy gaps $\geqslant 112$ m^2 in size dropped from 20.1% to 0.4% between 1929 and 2007/08. Furthermore, CART analysis showed that tree density in a 15 m radius south-facing semicircle was the variable that best distinguished between quadrats with high and low shrub cover. The semicircle was a better predictor than the full 15 m radius circle, suggesting that light, rather than competition for water and underground resources may be most limiting to shrub establishment and survival. The CART analysis indicated that most shrubs occurred in quadrats with $\leqslant 9$ trees in the southern semicircle. Fully 65% of quadrats had a tree density below this threshold in 1929, prior to logging, but only 2% of quadrats remained below the same threshold in 2008. Furthermore, the species composition shifted from dominance by shrubs typical of higher light environments (*Arctostaphylos patula*, *Ceanothus* sp., and *Chamaebatia foliolosa*) to species more tolerant of shade (e.g. *Chrysolepis sempervirens*). These results are consistent with studies in contemporary forests which generally demonstrate an inverse relationship between shrub abundance and overstory canopy cover (Kie, 1985; North et al., 2005), and an increase in shrub abundance following stand thinning treatments (McConnell and Smith, 1970).

Changes to the herbaceous understory vegetation in the MC plots over time were less pronounced. The high degree of variation in the herbaceous frequency among plots in 1929, low number of quadrats measured (only 10 per MC plot vs. 100 per MC plot for shrubs), and lack of replication all limit the robustness of the herbaceous vegetation data. Still, the loss of some species typically found in higher light and/or with disturbance (e.g. *Epilobium* sp.) and gain of species typical of shaded environments with deep duff layers (e.g. *Pyrola picta*), are consistent with expectations with forest densification and the absence of fire disturbance (Wayman and North, 2007). Other studies suggest that the relationship between overstory change and the understory community may be weaker and of a different trajectory for herbaceous species than for shrubs. Jules et al. (2008) noted a steep decline in shrub abundance, but a gradually increasing herbaceous cover with stand age in a 420-year chronosequence since stand replacing disturbance in southern Oregon, and others have suggested that in seasonally dry environments, herbaceous species richness may be more strongly associated with below ground resources such as soil moisture than overstory canopy cover (Riegel et al., 1995; North et al., 2005). Stem counts or presence/absence data may also not fully capture the ecological significance of changes to the herbaceous community. We noted that many herbaceous species in the 2008 survey existed as a single leaf or non-flowering stems. Long lag times with environmental change and the ability of herbs to persist without flowering under unfavorable conditions has been noted by others (Lindh, 2005). The lack of flowering limits sexual reproduction as well as a source of nectar and pollen for insects and birds. Extent

of flowering was not recorded in the original 1929 survey, however.

4.4. Management implications

Restoring conditions more conducive to natural regeneration of pines and with an understory of patchy shrubs and herbs will likely require a substantial reduction in stand density and the creation of small gaps, like those present in the historical stands (Bigelow et al., 2011; Lydersen et al., 2013). Because pine seedlings prefer bare mineral soil (Cooper, 1960; Stark, 1965; Kilgore, 1973), restoration will also benefit by removing much of the litter, duff and woody fuels that have accumulated during the modern 120+ year period without a recorded fire. Historically, such a forest structure and the presence of areas with bare mineral soil were maintained by frequent low to mixed-severity fire.

Would simply reintroducing fire be sufficient to restore structure and function? Fire burning in stands today following 120+ years of fire exclusion could result in very different outcomes than historic fire. Prior to 1889, fire burned through these stands at a median interval of every 6 years, keeping surface fuels at low levels and thinning out young tree seedlings and saplings. Small trees are easily killed with relatively low-intensity fire, and much of the thinning of stands was therefore likely accomplished at the young regeneration stage (van Wagtendonk and Fites-Kaufman, 2006; Battaglia et al., 2009). After a long fire-free period, many of the encroaching trees have now reached much more fire-resistant sizes (Collins et al., 2011).

Our data suggest that fire-only approaches to restoring forest structure may be more likely to meet objectives in unlogged than in previously logged stands. Unlogged stands retained more of the largest overstory trees, which have the thickest bark and greater canopy base height, potentially making them more resistant to fire. In addition, while tree density was nearly the same in both unlogged and logged stands, more of the excess trees were still in smaller size classes in unlogged stands, presumably because ingrowth established under a forest canopy and therefore grew more slowly. Smaller trees have thinner bark, lower canopy base height, and are more readily killed by fire. The larger average size of ingrowth in second growth stands may require higher intensity fire to fully restore forest structure (Miller and Urban, 2000; Fulé et al., 2004). However, if intensity is much greater than the historical norm, fire could also kill the largest trees that managers with to retain, and may have detrimental effects to other components of the ecosystem less resilient to such fire (Battaglia et al., 2009).

Mechanical thinning, prior to burning, may have some advantages for reducing density when the excess trees are the size of those in our study, particularly in areas where proximity to homes and other infrastructure limits the use of higher-intensity prescribed fire. In addition, once encroaching trees have attained an intermediate size, mechanical thinning may be the best means of substantially altering species composition towards pine, from fir and incense cedar. Beyond the small tree stage, fir and cedar have been shown to be nearly as or even more resistant to fire than pines (Regelbrugge and Conard, 1993; van Mantgem et al., 2013), meaning that after a long fire-free period, fire alone may do little to shift the compositional balance.

Whatever methods are used, evidence suggests that if the structure and function associated with the historical forest are restored, the understory should follow (Dodson and Peterson, 2010; Webster and Halpern, 2010). Shrub species that have disappeared are often still abundant in the seed bank (Quick, 1956; Knapp et al., 2012) and seeds of Ceanothus sp. and Arctostaphylos sp. are stimulated to germinate by heat (Quick and Quick, 1961; Kauffman and Martin, 1991) or smoke/charate from fire (Keeley, 1987). In addition, many of the herbaceous species present in 1929 are perennial and still persist in the understory, even if less robust and non-flowering. The association that has been shown between overstory density or basal area and sexual reproduction in forest herbs (Lindh, 2005) suggests that management action that does not kill the underground stems and rhizomes and results in more light hitting the forest floor should allow these species to again flower and perhaps recapture their historical ecological importance.

Acknowledgements

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