Full length article

Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging

Jamie M. Lydersen [a,*], Malcolm P. North [a,b], Eric E. Knapp [c], Brandon M. Collins [a]

[a] USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618, United States
[b] John Muir Institute, University of California, One Shields Ave., Davis, CA 95616, United States
[c] USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, United States

ABSTRACT

Fire suppression and past logging have dramatically altered forest conditions in many areas, but changes to within-stand tree spatial patterns over time are not as well understood. The few studies available suggest that variability in tree spatial patterns is an important structural feature of forests with intact frequent fire regimes that should be incorporated in restoration prescriptions. We used a rare dataset consisting of mapped locations for all trees ⩾10 cm in three 4-ha plots in 1929 before logging and in 2007/2008, 78 and 79 years after logging, to assess changes in three spatial components of forest structure: individual trees, tree clusters and gaps. Comparing 1929 old growth to modern conditions, area in gaps decreased from 20% to zero, the percentage of stems that were single trees from 6% to 2% and in small or medium clumps (2–9 trees) from 28% to 9%, while trees in large clumps (⩾10 trees) increased from 66% to 89%. Concurrent with these changes, canopy cover increased from 45% to 62%, and the average number of trees in a clump increased from 11 to 26, resulting in much more homogenous conditions across the stand. These changes also altered tree size and species associations within different structural groups (i.e., single tree, small, medium and large clumps). In an effort to account for the alteration of the fire regime that had already taken place in 1929 (the last fire recorded in tree rings was in 1889) we also analyzed spatial patterns of 1929 conditions removing all trees <25 cm. In this analysis, 35% of the plot area was in gaps and canopy cover averaged 36%. Tree clusters had an average of 5.2 trees per clump, with 13% of trees being singles, 30% in small clumps, 24% in medium clumps and 33% in large clumps. Our results provide metrics that quantify spatial patterns and composition of individual trees, tree clumps, and gaps under the historical fire regime that may be useful to forest managers. Our study demonstrates that the contemporary forest is more homogeneous than it was historically, and variability that likely provided diverse microclimate and habitat conditions and fostered resilience to a variety of stressors and disturbances such as fire, insects and drought has been lost. Future management may benefit from restoring these structural components.

Published by Elsevier B.V.

1. Introduction

A number of studies have documented considerable changes over the past century in structure and composition of forest types historically associated with frequent low- to moderate-severity fire (e.g., Parsons and Debenedetti, 1979; Laudenslayer and Darr, 1990; Naficy et al., 2010; Scholl and Taylor, 2010; Collins et al., 2011). These changes, frequently attributed to factors such as fire exclusion and past logging practices, include higher tree densities, fewer large trees, and increased proportions of shade-tolerant tree species with corresponding decreases in shade-intolerant species. A

lesser-studied aspect of change in these forest types is the spatial pattern of trees. Changes in tree spatial patterns are more difficult to study due to both a general lack of spatially-explicit information for historical/reference forests and the complexity of quantifying meaningful spatial patterns. Recently, several papers have been published using new analytical techniques to examine tree spatial patterns from reconstructed and mapped historical tree data, producing management-relevant metrics (Abella and Denton, 2009; Sánchez Meador et al., 2011; Larson and Churchill, 2012; Larson et al., 2012; Churchill et al., 2013). These studies demonstrate a fairly consistent historical pattern of tree groups, gaps and a matrix of low-density, often large, fire-resistant species in forest types associated with frequent fire. This spatial structure has been identified as having greater resilience to both drought and wildfire

* Corresponding author. Tel.: +1 530 759 1767; fax: +1 530 747 0241.
E-mail address: jmlydersen@fs.fed.us (J.M. Lydersen).

(Stephens et al., 2008), as well as reduced crown fire potential (Fule et al., 2001). Additionally, several studies suggest this interspersion of tree groups with high canopy cover, gaps, and low-tree density matrix provides necessary habitat for a range of wildlife species, including several sensitive species (Raphael et al., 1987; Humple and Burnett, 2010; Underwood et al., 2010).

Although the need for greater structural heterogeneity in fire-suppressed forests is widely acknowledged, existing data have been difficult to apply to management prescriptions because local-scale measures of spatial heterogeneity are lacking. Until recently, most studies on tree spatial patterns used global statistical techniques such as Ripley's K (e.g., North et al., 2007) and Moran's I (e.g., Scholl and Taylor, 2010) that calculate the average scale over which tree spacing is aggregated, random or regular across the measured stand (Sánchez Meador et al., 2011; Larson and Churchill, 2012). Marking guidelines, however, often require more local measures such as size of tree groups and gaps, percentage of area that tree canopies occupy within a stand, and species composition and diameter distributions within different tree groups. While recent work begins to address this translation of spatial heterogeneity to silvicultural prescriptions (Churchill et al., 2013), additional spatial analyses from different forest types and geographic settings are needed to provide measures of local tree aggregation and gap structure that can be directly incorporated into restoration prescriptions designed to increase forest heterogeneity.

The objective of this study was to analyze temporal changes in tree spatial patterns in a mixed-conifer forest with a history of frequent fire using spatial metrics amenable to the development of silvicultural prescriptions. We take advantage of a unique dataset consisting of detailed stem maps for three different plots, mapped in 1929, and again in 2007/2008. Having historical and contemporary stem maps of the same plots allows the extent of change in spatial forest structural patterns to be quantified. Specifically, we sought to characterize (1) changes to the distribution of area in openings, single trees, and tree clumps; (2) changes in the average number, density, size and species composition of stems within tree clumps; and (3) distribution of species and size classes among single trees and tree clumps. While local measures of forest spatial structure hold promise for identifying patterns that may be more useful for silvicultural application, no standard metrics of local within-stand structure have been identified or gained acceptance in the literature. Our intent is to develop some metrics to generate further discussion and refinement of these tools.

2. Methods

2.1. Study site

Three permanent "Methods of Cutting" plots were established in 1929 in the Stanislaus Tuolumne Experimental Forest (STEF), located in mixed-conifer forest in the central Sierra Nevada near Pinecrest, California. Plots, hereafter referred to as MC9, MC10 and MC11, are each approximately four ha in size and range in elevation from 1740 to 1805 m. Plots were mapped in 1929 prior to any harvest, recording location, species and diameter at breast height (DBH) for all trees >10 cm. After the initial data collection, each plot received a different logging treatment. MC9 was harvested following standard Forest Service methods for that time, resulting in removal of many of the large overstory trees of all species and maintaining approximately the same proportion of pine as in the original stand. MC10 was harvested using a "light economic selection", in which only the largest pines were removed with an objective of maximizing first-harvest profits. MC11 was logged

according to a standard practice on private forest lands at that time, in which all merchantable trees were removed. The same data was collected in 1929 following logging, and again in 2007 (MC11) or 2008 (MC9 and 10). The mapping in 2007 and 2008 was completed using laser rangefinders.

Fire history studies in this area showed a median fire return interval of five years (range 1–40 years) at the approximate scale of the plots, with the last fire in 1889 (Knapp et al., Unpublished results). Because the last fire recorded occurred forty years prior to forest mapping, it is possible that some ingrowth post-1889 had attained a DBH >10 cm. Therefore the density of especially the smallest tree size classes may not be fully representative of forest conditions under the historical fire regime. To address the potential influence of this fire-free period on tree spatial patterns we created an additional dataset consisting of 1929 pre-harvest trees that excluded those less than 25 cm DBH. Dropping trees between 10 cm and 25 cm resulted in 2400 or 58.9% fewer trees, but these trees comprised just 6.5% of the basal area present in the full 1929 dataset. Restricting the spatial analysis to trees ⩾ 25 cm DBH is also of practical interest because trees smaller than this are often not marked in current thinning prescriptions in the Sierra Nevada. Such a cut-off, however, neglects the role of <25 cm trees, to the extent that these were present in forests with an intact historical fire regime.

The principal species growing in the study area were white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*) and ponderosa pine (*Pinus ponderosa*). Willow (*Salix scouleriana*) and black oak (*Quercus kelloggii*) > 10 cm DBH were present but rare (<0.11% of canopy cover in 1929 and < 0.25% of stems in 2007/2008), and were therefore excluded from the analyses. In addition, data for Jeffrey pine (*Pinus jeffreyi*) were combined with ponderosa pine. Jeffrey pines were uncommon in 2007/2008, representing only 5% of "yellow pines" (encompassing both ponderosa and Jeffrey pine), and Jeffrey pine was either not present or the two species were not differentiated in the 1929 data.

2.2. Detecting tree clumps

For each mapped dataset, forest spatial structure was characterized in terms of open gaps, solitary trees, and clumps of two or more trees, which are typical structural components of fire-dependent forests (Larson and Churchill, 2012). The degree of tree clumping was analyzed in ArcMap 9.3 using a clustering algorithm that assigns trees into clumps or singles based on the presence of adjacent trees within a user-defined distance from the stem location (Plotkin et al., 2002; Larson and Churchill, 2008; Abella and Denton, 2009; Sánchez Meador et al., 2011; Larson et al., 2012). Following methods suggested by Larson and Churchill (2008), we assessed tree clumping at inter-tree distances ranging from 1 to 9 m.

Sierra Nevada mixed-conifer forests are distinctly clustered (North et al., 2004) and foresters often define tree clumps by crown overlap. Therefore tree patterns were also analyzed using crown radius as the critical distance, defining tree clumps (also commonly referred to as clusters) as a group of two or more trees with touching or overlapping crowns (Meyer et al., 2008). Tree crown radii were estimated using allometric equations developed from on-site field measurements taken in 2012. DBH and two orthogonal crown diameters were measured on 59–70 trees of each of the four principle species, with trees systematically selected by proximity to a set of grid points within each plot. The crown projection was visually estimated using clinometers at the ground level. We then developed linear regression equations in SAS version 9.3 (SAS Institute Inc., 2011) to predict crown radius from DBH. All allometric regressions were significant with

R^2 values varying between 0.67 (white fir) to 0.88 (ponderosa pine), and were nearly identical to previously published allometric equations for these same species developed from statewide data (Gill et al., 2000).

After delineating tree clumps, edge effects were controlled for by applying a 9 m buffer inward from the plot edge. The largest crown radius in any of the datasets was 8.9 m; therefore this width buffer excluded the effect of tree canopies hanging into the plot from stems outside the plot boundary, but allowed for tree canopies within the 9 m buffer to contribute to clump canopy characteristics. Continuous clumps may have extended beyond the plot boundaries, so our analysis reflects the structural characteristics within a discrete area, and thus does not characterize qualities such as absolute maximum number of stems per clump that might be witnessed at larger spatial scales. Tree clumps were categorized as small (2–4 trees), medium (5–9 trees) and large (10 or more trees), the same categories used by Larson et al. (2012) and recommended by (Churchill et al., 2013). Species composition, average nearest neighbor distance, basal area, stem density, quadratic mean DBH (QMD) and the proportions of plot area and trees encompassed were then calculated for single trees and within the various classes of tree clumps. These same attributes, with the exception of proportions of trees and plot area encompassed, were also calculated as stand-level averages to compare against the four different local structural conditions (individual tree, small, medium and large clump).

2.3. Characterization of open space

Forest openings were quantified using the PatchMorph tool in ArcMap 9.3. This tool identifies areas of interest or suitability using two user-specified thresholds: (1) "gap", or maximum pixel size of unsuitable area allowed within a suitable area, and (2) "spur" or minimum width allowed for defining a suitable area (Girvetz and Greco, 2007). Our aim was to describe areas that were not directly under any projected canopy area, and were greater in diameter than most tree crowns and could therefore represent an area comparable in size to the zone of dominance of a large tree in our data. Since all trees in our study had a calculated crown diameter greater than 1.5 m, this was used as the "gap" threshold, thereby preventing overlap of gap space with tree canopy cover and allowing us to uniquely classify all area within the plots as tree clump, single, or opening. The "spur" threshold was 12 m, which resulted in a minimum opening width bigger than all but the largest tree crown diameters in the data, and a minimum area of 112 m^2. Smaller "spur" values allowed for substantial inclusion of narrow intercanopy areas into forest gaps, while larger "spur" values failed to detect sizeable open areas.

Canopy openings were further analyzed using the empty space function (Diggle, 2003; Larson et al., 2012; Churchill et al., 2013). We used this technique to calculate the distance to the nearest canopy edge for all points in a 5 × 5 m grid overlaying the buffered plot area. The 5 m spacing between grid points was chosen using guidelines reviewed in (Diggle, 2003), suggesting that the number of points along each side of the grid should be roughly equal to the square root of the number of observations in the spatial dataset. For comparison, the analysis was also performed using a 1×1 m grid. All values in this analysis were within 1.5% of the values obtained using a 5 × 5 m grid. Plot area not directly under the projected tree canopy was then summarized by distance to nearest canopy edge. In addition to informing on the gap size distribution, this analysis describes the open spaces between trees that are too small (i.e., <112 m^2) to be defined as gaps in PatchMorph.

2.4. Comparisons between datasets and structural groups

We were interested in assessing forest spatial structure prior to logging and fire suppression, and how it has changed over time. Therefore our discussion is focused on analysis of three datasets: (1) 1929 ⩾25 cm, (2) 1929 ⩾10 cm and (3) 2007/2008 (⩾10 cm). We also performed spatial analysis of the 1929 postlogging dataset, showing the immediate effects of the different logging treatments on spatial structure. This information is presented in Appendix A.

To allow for statistical comparisons between the 1929 and the 2007/2008 datasets, the data from the three plots were averaged. Although plots experienced different harvest methods, both the magnitude and variation in structure and composition among plots in the 2007/2008 dataset was minimal and even less than differences among plots prior to logging (Table A1). This suggests that any unique effects of the individual logging treatments had largely disappeared after 79 years, perhaps eclipsed by changes of greater magnitude due to other factors such as fire exclusion.

Repeated-measures mixed model ANOVAs were used to assess differences in structural metrics of the 1929 ⩾10 cm dataset to both the 2007/2008 and 1929 ⩾25 cm datasets within each spatial class (single trees and small, medium and large clumps). Dunnett's test, which is appropriate for making multiple comparisons to one treatment (Dunnett, 1955), was used to compare means to those in the 1929 ⩾10 cm dataset. We did not make statistical comparisons between 1929 ⩾25 cm and 2007/2008 since these datasets differed by multiple confounding factors (time of mapping and minimum diameter cutoff). We also tested for differences in QMD between single trees and small, medium and large clumps within 1929 ⩾10 cm and 2007/2008 using a similar mixed model ANOVA and Tukey's HSD (Honest Significant Difference) test. Homogeneity of variances were checked using plots of residual vs. predicted values and a Levene test (Levene, 1960), and normality of residuals was assessed using the Shapiro–Wilk test (Shapiro and Wilk, 1965). Logarithmic and power transformations were used on most variables (exceptions were canopy cover, stand level basal area, stem density and proportion of trees within clumps) to improve conformation to model assumptions. Contingency analyses were also performed to evaluate the distribution of different tree species and size classes among structural groups. Pearson's chi-squared (χ^2) values were used to compare cell counts in contingency tables to expected distributions. Statistical comparisons were made using SAS software, version 9.3 (SAS Institute Inc, 2011), and an alpha level of 0.05.

2.5. Global pattern analysis

To provide an additional measure of forest spatial structure that would allow comparisons between this study and other previously published papers, Ripley's K point pattern analysis was performed in an exploratory context using version 1.31–1 of the Spatstat package (Baddeley and Turner, 2005) in R version 3.0 (R Core Team, 2013). This method informs on the average clumping of trees within an area. A result of trees being significantly clumped at a certain distance means that on average, trees have more neighbors within that distance than would be expected with a random distribution (Illian et al., 2008). The square-root transformation, or L-function, was calculated for each plot in each dataset, using the default settings in Spatstat, so that spatial aggregation was assessed up to a maximum distance of 45 m (one quarter the length of the shortest plot dimension), over 512 equally spaced intervals. We used the isotropic correction to control for edge effects. Observed values of L(r) were compared to an envelope of complete spatial randomness (CSR) generated with 999 simulations.

Table 1
Structural characteristics of single trees, small, medium and large clumps, and stand level structure, showing mean (and standard deviation) of the three plots. Asterisks denote significant difference from1929 $\geqslant$ 10 cm ($p < 0.05$). Clump basal area and stem densities were calculated using clump canopy projection area.

	1929 $\geqslant$ 25 cm		1929 $\geqslant$ 10 cm		2007/2008	
Single trees						
# Singles ha^{-1}	16.6	(2.9)	18.1	(2.6)	16.9	(3.8)
Proportion of trees (%)	12.6*	(1.5)	5.6	(0.6)	2.3*	(0.8)
% Shade intolerant	30.2	(5.5)	31.5	(10.4)	12.0	(7.1)
Nearest neighbor dist. (m)	8.7*	(0.7)	6.4	(0.3)	4.7*	(0.3)
BA/ha (m^2 ha^{-1})	7.6*	(0.5)	4.8	(0.6)	0.8*	(0.3)
Small clumps (2–4 trees)						
# Clumps ha^{-1}	14.4	(1.8)	14.7	(4.2)	11.4	(0.8)
Proportion of trees (%)	30.4*	(6.8)	13.4	(6)	4.0*	(0.6)
% Shade intolerant	26.3	(5)	24.9	(2.9)	6.7*	(1.7)
Nearest neighbor dist. (m)	3.4*	(0.3)	2.8	(0.3)	1.9*	(0.1)
BA/clump (m^2)	1.2	(0.3)	0.8	(0.3)	0.2*	(0)
BA/ha (m^2 ha^{-1})	133.5*	(15.3)	92.8	(10.9)	66.4*	(3.9)
Stem density ha^{-1}	496.3*	(64)	1000.8	(133.4)	1174.6	(84.6)
Medium clumps (5–9 trees)						
# Clumps ha^{-1}	5.0*	(0.8)	7.2	(0.9)	5.3*	(0.6)
Proportion of trees (%)	23.5[a]	(1.5)	14.8	(3.8)	4.6[a]	(0.5)
% Shade intolerant	23.3	(3)	22.7	(5.9)	8.0*	(3)
Nearest neighbor dist. (m)	3.1*	(0.2)	2	(0.1)	1.7*	(0.1)
BA/clump (m^2)	2.5*	(0.3)	1.2	(0.2)	0.6*	(0.1)
BA/ha (m^2 ha^{-1})	147.1*	(10.9)	100.7	(9.5)	99.2	(19.2)
Stem density ha^{-1}	518.5*	(52)	1172.4	(126.8)	1258.2	(108.9)
Large clumps ($\geqslant$ 10 trees)						
# Clumps ha^{-1}	3.1*	(1.6)	7.0	(2.3)	11.7*	(1.8)
Proportion of trees (%)	33.5*	(8.6)	66.2	(10.3)	89.1*	(25.2)
% Shade intolerant	22.1	(5.8)	16.8	(4.9)	8.8*	(2.4)
Nearest neighbor dist. (m)	3.1*	(0.4)	2	(0.1)	1.6*	(0.1)
BA/clump (m^2)	5.4	(1.4)	4.4	(0.9)	5.6	(1)
BA/ha (m^2 ha^{-1})	151.4[a]	(29.2)	111.7	(7.7)	117.6[a]	(10.4)
Stem density ha^{-1}	525.9*	(146.5)	1112.2	(43)	1292.6	(126)
Stand metrics						
% Canopy cover	36.4	(4.1)	44.8	(5.1)	61.6*	(2.6)
Ave. trees/clump	5.2	(0.6)	11	(3.5)	26.3*	(5.1)
Max. trees/clump	27*	(5.6)	108	(29.8)	542.7*	(309.1)
Gap density ha^{-1}	6.2	(0.8)	5.2	(0.7)	0.2*	(0.2)

[a] Transformations were unable to reduce heterogeneity of variance below threshold of significance; therefore statistical comparisons are not available.

3. Results

3.1. Stand level structure

Comparing stand characteristics of the 1929 $\geqslant$ 10 cm (pre-logging) and 2007/2008 datasets for trees located inside of the 9 m buffer, there was a decrease in the percent pine (from 20.8 to 10.7% by stem count), QMD (from 47.3 to 34.6 cm), standard deviation of diameter (from 32.1 to 19.1 cm), and an increase in tree density (from 328.1 to 754.8 ha^{-1}) and basal area (from 56.6 to 70.5 m^2 ha^{-1}) over time, despite the substantial harvest of overstory trees after the initial survey in 1929. Estimated canopy cover changed from 45% in 1929 to 62% in 2007/2008. Average and maximum number of trees per clump also increased, and the number of forest openings decreased over time (Table 1). All stand-level metrics (percent pine, QMD, standard deviation of diameter, basal area, stem density, canopy cover, gap density, average and maximum number of trees per clump, and area of plot in gaps) in 2007/2008 were significantly different from those in the pre-harvest data.

After excluding trees <25 cm DBH in 1929, 25.1% of stems were pine species, QMD was 71.7 cm, standard deviation of diameter was 33.8 cm, tree density was 133.4 stems ha^{-1} and basal area was 52.8 m^2 ha^{-1}. In general, these stand-level results were more similar to the 1929 $\geqslant$ 10 cm dataset than results from the 2007/

2008 dataset. Between 1929 $\geqslant$ 25 cm and 1929 $\geqslant$ 10 cm, the only significant differences were in maximum number of trees per clump, proportion pine species, QMD and stem density (Table 1).

3.2. Clump detection algorithm at multiple inter-tree distances

Varying the inter-tree distance used in the tree clump detection algorithm at regular intervals gave different proportions of trees allocated into structural groupings for each dataset (Fig. 1). In the 1929 $\geqslant$ 25 dataset, virtually all trees were in clumps containing ten or more trees at a distance of 8 m. This threshold was reached much more quickly in the other two datasets, occurring at 5 m for the 1929 $\geqslant$ 10 cm dataset, and at 3 m for the 2007/2008 dataset. Results of the relative proportion of trees in each structural group at an inter-tree distance of 3 m were most similar to results obtained using crown radius as the critical distance.

3.3. Forest openings

Substantial differences in the proportion of plot area in gaps and open space were found between the three datasets. This was largely due to differences in the area covered by tree clumps containing ten or more trees (Fig. 2). A similar amount of open space occurred within 3 m of a tree canopy projection in all datasets, but in the 2007/2008 forest only a small percent-
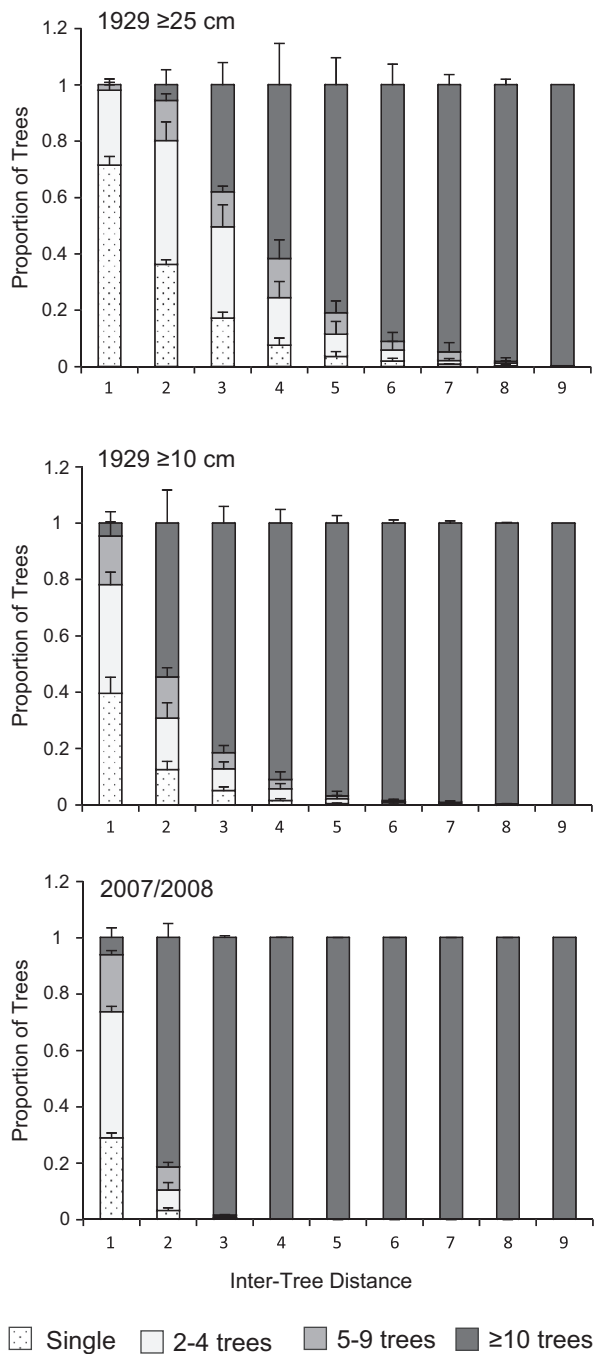
Fig. 1. Proportion of trees in each structural group at a range of inter-tree distances. Data for the three plots are averaged in each dataset; error bars show the standard deviation of each group.

age of the plot was more than 3 m from the nearest canopy projection (Table 2). Similarly, the distribution of gap sizes varied between the three datasets (Fig. 3). In the 1929 $\geqslant$25 cm dataset, gaps of all sizes were common components of the landscape. While small gaps were more frequent, the greatest proportion of gap area was in larger openings. In the 1929 $\geqslant$10 cm dataset gaps were also common, but including all trees in the analysis resulted in fewer gaps in the 250–500 m^2 and $\geqslant$1000 m^2 size classes compared to using a 25 cm tree size cutoff. In 2007/2008 small gaps (<250 m^2) were very infrequent, and larger gaps were absent.

3.4. Local characteristics of tree spatial structure

3.4.1. Changes over time, assessing trees $\geqslant$10 cm DBH

Over time there were substantial changes to the characteristics of single trees and tree clumps (Table 1). Both datasets contained a range of tree clump sizes (Fig. 4). The majority of trees were found in large tree clumps in both datasets, however the spatial pattern changed over time such that the modern forest had a lower proportion of trees as singles and in small clumps, and a greater proportion in large clumps. The density of single trees and small tree clumps did not vary significantly over time, but there was an increase in the density of large clumps and a decrease in the density of medium clumps. Consistent with the stand level averages, both percent pine and nearest neighbor distance were significantly lower in all structural groups in the contemporary forest compared to 1929. QMD was lower in all structural groups, with the exception of large tree clumps (Fig. 5). Correspondingly, basal area (both per ha and per clump) decreased within singles and small clumps, despite an increase at the stand level, reflecting the shift in stand structure caused by loss of widely spaced large diameter trees and a greater prevalence of smaller diameter trees. Basal area within large clumps did not change over time (Table 1).

3.4.2. Comparisons between 1929 $\geqslant$25 cm and 1929 $\geqslant$10 cm

Comparing the 1929 $\geqslant$25 cm to the 1929 $\geqslant$10 cm dataset, a greater proportion of trees were singles, corresponding to a greater proportion of plot area in this structural group. There was also a lower proportion of trees and plot area in large clumps, and a greater proportion of trees in small clumps in the 1929 $\geqslant$25 cm dataset. All clump sizes had greater BA ha^{-1} on average, and significantly lower stem densities. Nearest neighbor distance was also significantly greater in all structural groups. There were no significant differences in species composition in any structural group.

3.4.3. Associations of tree species and diameter within structural groups

QMD for trees $\geqslant$10 cm varied between structural groups as well as between 1929 and 2007/2008 (Fig. 5). In 1929, QMD was significantly smaller for trees in large clumps than for singles or trees in small clumps. Trees in medium clumps were also significantly smaller than trees in small clumps. In contrast, in 2007/2008, solitary trees had a significantly smaller QMD than trees in medium or large clumps.

Contingency analysis of species and size class distributions within the different structural groups deviated significantly ($p \leqslant 0.0001$) from the expected distribution in all three datasets (Table 3). Species associations were similar in both 1929 datasets, but removal of trees 10–25 cm DBH from the analysis resulted in some changes to associations, and overall a less pronounced pattern of local structuring. In particular, in the 1929 $\geqslant$10 cm dataset ponderosa pine was more likely to be single and white fir were less likely to be single or in small groups. Another notable pattern in the 1929 $\geqslant$10 cm dataset was that intermediate size trees (50–100 cm DBH) were more likely to be in small or medium tree groups. Size class and species associations with different structural groups differed greatly in 2007/2008 from that in either 1929 dataset. In particular, small rather than large trees occurred disproportionately as singles in 2007/2008.

3.5. Global point pattern analysis

The spatial point pattern of trees identified by Ripley's K analysis indicated that trees were significantly clustered between 1 and 45 m in all datasets (Fig. 6). In all plots in each dataset there was an initial downward spike in the observed L(r). In both the 1929 $\geqslant$25 cm and 2007/2008 datasets, this spike was small enough that
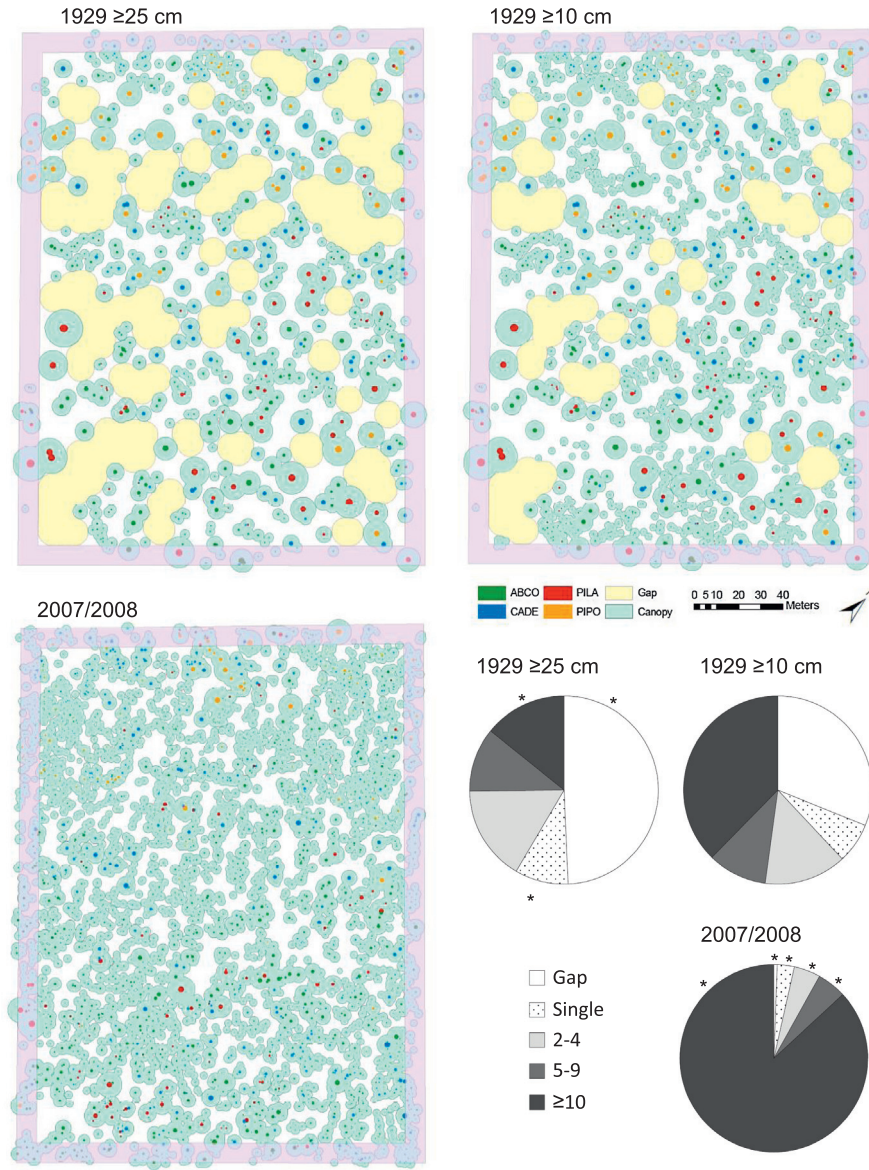
Fig. 2. Spatial composition of MC9 plot area in the three datasets, showing analysis of tree clustering and gaps. The purple colored zone is the 9 m buffer on the inside edge of the plot. Pie charts show the relative proportion of plot area in each structural group, including gaps but not open space smaller than the minimum gap size. Asterisks by pie charts denote significant difference from 1929 ⩾ 10 cm (*p* < 0.05). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Empty space distribution calculated from a systematic grid of sample points (5 × 5 m spacing) across each plot.

	1929 ⩾25 cm	1929 ⩾10 cm	2007/2008
%<3 m	37.8 (3.2)	39.6 (2.3)	37.0 (2.6)
%3–6 m	17.8 (3.4)	12.5 (4)	1.3 (0.5)
%6–9 m	6.0 (2.3)	2.8 (2)	0.0 (0)
%⩾9 m	1.6 (1.3)	0.5 (0.6)	0.0 (0)
Total % in open	63.2 (4)	55.4 (4.7)	38.3 (3.1)

trees were not different from CSR at distances of less than 1 m in each plot. In the 1929 ⩾10 cm dataset, this spike was sufficiently large that the point pattern was regularly spaced at very small distances. The observed L(r) for all plots in all datasets had a quick increase following this initial downward spike, indicating that the clustered pattern was most pronounced at smaller distances (approximately <10 m in both 1929 datasets, and approximately <3 m in 2007/2008). In both 1929 datasets, maximum clustering in MC9 and MC10 was observed between 10–20 m, while MC11
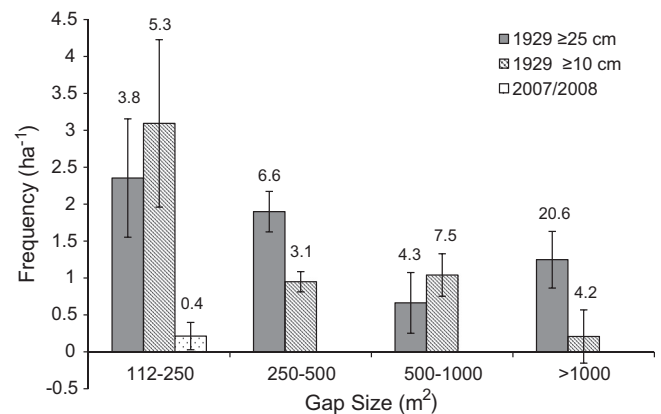
Fig. 3. Frequency distribution of gap sizes identified by the PatchMorph tool (see Methods), averaged across the three plots. Error bars correspond to standard deviation, and numbers above bars are the average percent of plot area encompassed in each gap size class.
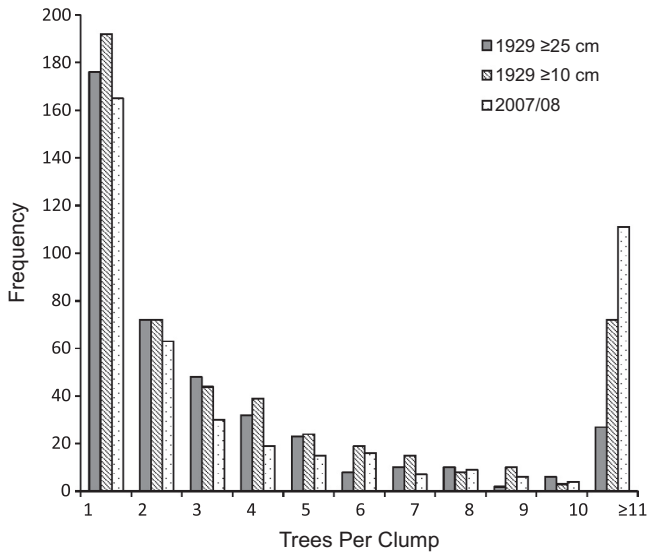
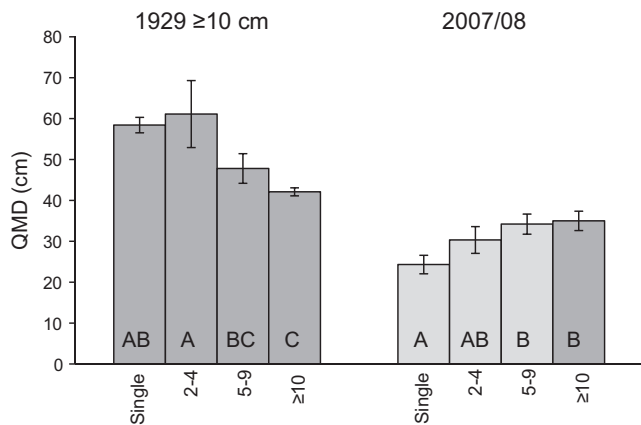**Fig. 4.** Frequency distribution of singles and tree clump sizes for all plots in the three datasets.

Fig. 5. Quadratic mean DBH for each structural group in 1929 ⩾10 cm and 2007/2008. Error bars correspond to standard deviation. Different shading refers to statistically significant differences between time points within a structural group, and letters refer to Tukey's HSD groupings for comparisons between structural groups within each time point.

continued to slowly increase with greater values of r. In the 2007/2008 dataset, all plots had a sharp increase until around 2.5 m, and then gradually increased with larger values of r.

# 4. Discussion

4.1. Overview

Historical fires in Sierra Nevada mixed-conifer forests are believed to have been predominantly low- to moderate-severity (Scholl and Taylor, 2010), occasionally producing patches of high severity, and this variability in part resulted in a highly heterogeneous forest structure (Show and Kotok, 1924; Beaty and Taylor, 2008). A challenge to managers restoring spatial and compositional structure similar to what would be produced by an intact fire regime is translating this historical heterogeneity into prescriptions and marking guidelines. Our study documents the spatial and structural homogenization following a single-entry harvest and more than 100 years of fire exclusion. In 1929, forest conditions were heterogeneous, consisting of varying sizes of tree clusters and gaps, with single trees interspersed throughout. Much of this heterogeneity was lost in the contemporary forest, where gaps had almost disappeared, likely substantially reducing or eliminating areas with sufficient light to support pine regeneration (Bigelow et al., 2011) and most shrub species that once occurred in canopy openings (Nagel and Taylor, 2005). This loss of spatial heterogeneity carries with it a loss of certain microclimate and habitat features that some wildlife species depend on (White et al., in press).

We caution that our analysis has several limitations. First, excluding small trees gives an incomplete characterization of forest conditions under the historical fire regime. Due to the patchy nature of historical fires (Show and Kotok, 1924), smaller trees would not have been eliminated from stands, even with an active fire regime, and stems in the smaller size classes (<10 or <25 cm) were likely present. Therefore, the use of either diameter cut-off underestimates smaller diameter tree spatial conditions. Second, our data is limited to three plots in close proximity to each other and does not encompass a broader range of geographic or topographic settings that can strongly influence active-fire forest conditions (Lydersen and North, 2012), and thus may underrepresent the full scale of variability present across a landscape. Finally, the plots in our study all received a different logging treatment in 1929. While some of the differences in forest structure created by the logging treatments may still be apparent today, we found that the variation among plots in the 2007/2008 dataset was minimal (Table A1), and therefore treat the plots as replicates in statistical analyses. The current lack of significant structural differences between the different logging treatments may in part be due to STEF's high site productivity. In all three plots forest conditions have converged to a similar state of dense understory trees and an increased prevalence of shade-tolerant species. Many western US forests have a similar history of logging and fire exclusion,

Table 3
Contingency analysis of the distribution of tree species and size classes among structural groups. Cells with "+" symbols contained more counts than expected, those with "−" symbols contained fewer than expected. The number of symbols denote the magnitude of a cell's contribution to the overall χ^2 value, with three symbols for those contributing >10, two for those between 3.5 and 10, one for those between 1.5 and 3.5, and 0 for those <1.5. The cell values for contribution to the overall χ^2 value are included as supplemental material in Appendix B.

	1929 ⩾25 cm				1929 ⩾10 cm				2007/2008			
	Single	Small	Medium	Large	Single	Small	Medium	Large	Single	Small	Medium	Large
White fir	0	0	0	+	− −	− −	−	+ +	− −	0	0	0
Incense-cedar	0	+	+	− −	0	+	+ +	− −	+ +	+ +	+	0
Sugar pine	+	−	0	0	+ +	− −	0	0	− −	0	0	0
Ponderosa pine	0	+ +	−	−	+ +	+ + +	0	− − −	+ + +	− −	−	0
10–50	0	−	0	+	− −	−	−	+ +	+	0	0	0
50–100[a]	− −	0	0	0	0	+ + +	+ +	− − −	− − −	−	0	0
>100	+ +	+	0	− −	+	−	0	0				

[a] In the 2007/2008 dataset all trees >50 cm DBH were included in this size class because too few were in the largest size category.
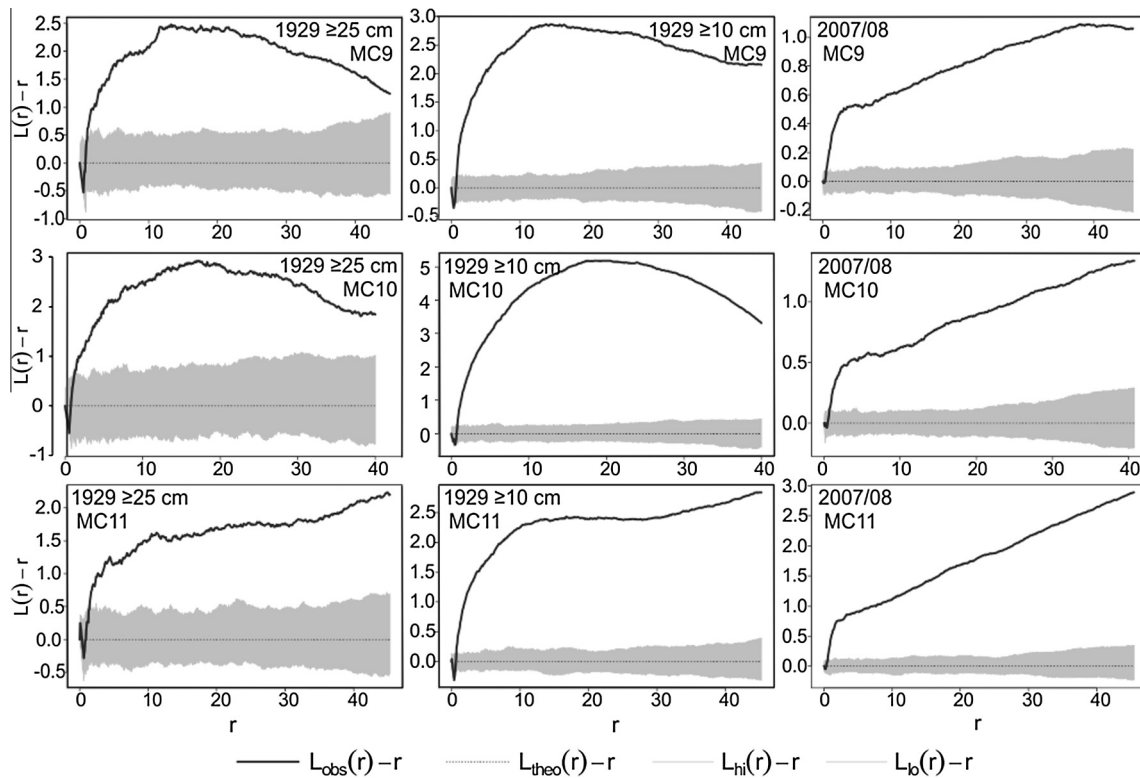
Fig. 6. Global tree spatial patterns for each plot in the three datasets, at inter-tree distances of *r*. Values above the gray zone (CSR) indicate a clumped pattern and values below indicate regular spacing.

but the legacy of logging effects may be more pronounced in more xeric forests with slower growth and recovery from overstory tree removal. Despite these limitations our results help quantify the dominant within-stand spatial patterns in historical and contemporary Sierra Nevada mixed-conifer forests. Using mapped plots with both historical and contemporary measurements helps overcome a substantial limitation of tree-ring based reconstructions: the loss of evidence over time.

4.2. Comparison of methods

The results of the Ripley's K analysis were typical of those using global pattern techniques to assess spatial structure in fire-dependent western forests, in that most studies have demonstrated tree spatial aggregation at distances of less than 20 m (Larson and Churchill, 2012). For example, (North et al., 2007) found significant clustering at distances of <70 m in reference conditions, and at all distances tested in an untreated control. The initial downward spike in the observed L(r) we noted has also been reported for large trees (Lutz et al., 2012). However (Lutz et al., 2012) did not see a downward spike at small distances when the spatial pattern of all size classes was considered. They attributed this spatial pattern to physical attributes of large trees preventing overlap within 3 m distances. Our study supports this finding as this spike was least pronounced in the 2007/2008 data that had fewer large trees.

Assessing local spatial conditions, our study site exhibited more tree clustering at smaller inter-tree distances than has been reported in other studies using the same clump detection algorithm on data from historical and contemporary forests. This was particularly noticeable when comparing to work done in forests with a much lower overall stem density. For example Churchill et al. (2013) found that the majority of trees in a reference ponderosa pine-Douglas-fir forest in the eastern Cascades were classified as singles up to an inter-tree distance of 5 m, and even at a distance of 10 m their site still had nearly a third of trees as singles. The

smallest proportion of trees was in clumps of five or more trees at any inter-tree distance. Conditions in a mixed-conifer forest in the northern Rockies that had similar tree densities to those at our study site were somewhat closer to our findings (Larson et al., 2012). However, trees were still less clumped, with over two thirds of the trees in reference conditions classified as single at an inter-tree distance of 3 m, and just over half the trees in clumps of ten or more trees at a distance of 9 m. In contrast, in 1929 our site had either 5 or 17% of trees as singles at an inter-tree distance of 3 m (considering trees >10 cm or >25 cm DBH, respectively), and 100% of trees in clumps of ten or more at an inter-tree distance of 9 m (Fig. 1). Comparing contemporary conditions, at an inter-tree distance of 3 m, Larson et al. (2012) found that pre-treatment sites generally had most trees in clumps of 2–4 trees, while 99% of trees at our site were in clumps of ten or more trees at that inter-tree distance. This may reflect the high productivity of our study site and that infilling trees may not yet have reached sufficient density to trigger widespread competitive mortality (i.e., stem-exclusion phase (O'Hara et al., 1996)).

For assessing within-clump characteristics, most other studies selected an inter-tree distance of 6 m, corresponding to the average crown diameter of a mature ponderosa pine (Abella and Denton, 2009; Larson et al., 2012; Churchill et al., 2013). Sánchez Meador et al. (2011) used a similar approach to that employed in this study, defining tree clumps based on individual crown radii, with resulting inter-tree distances ranging from 5.3 to 6.6 m. Our study site had a greater range of variability in crown size (0.9–8.9 m in 1929, 0.9–6.5 m in 2007/2008). Therefore, the choice to define tree clumps ecologically based on overlapping crowns (Larson and Churchill, 2012) rather than using a single inter-tree distance such as 6 m likely had a greater impact on the results of our analysis, particularly since the average crown size was different in 2007/2008 than in 1929. Although use of actual crown radii potentially makes the results more ecologically meaningful, the use of a variable inter-tree distance may prove to be more challenging to

implement in marking prescriptions compared with the use of a single distance (Churchill et al., 2013).

4.3. Changes in spatial structure over time, assessing trees ⩾ 10 cm DBH

4.3.1. Canopy openings

The distribution of gaps and open space was very different between the historical and current forest. There was a similar amount of open space within 3 m of canopy in both time points, but the contemporary forest had a complete loss of gaps >250 m^2 and far fewer small (<250 m^2) gaps. This loss of open space has coincided with a decrease in shrub cover and diversity (Knapp et al., Unpublished results). Definitions of gap sizes in experimental and observational studies are often larger than those identified in our analysis. For example, York et al. (2007) generated gaps ranging from 0.1 to 1 ha in size, and Skinner (1995) used a minimum cutoff of 0.1 ha when identifying gaps from aerial photographs. Piirto and Rogers (2002) suggest that gaps in giant sequoia groves were typically 0.04–0.8 ha prior to fire exclusion. We found that at the scale of our study plots, openings within the 1929 forest ranged from 0.01 to 0.4 ha, with gaps smaller than 0.05 ha being a common structural element. This difference in gap size between our study and those defined in other studies could be due to several factors: (1) how we chose to define gaps, (2) the scale of the study (4 ha), and/or (3) the specific conditions of our study site (e.g., site productivity). Despite these potential influences, our results suggest that a distribution of gap sizes, consisting of many small gaps with fewer large gaps, may be an inherent fine-scale pattern in Sierran mixed-conifer forests. Silvicultural treatments aimed at restoring historical forest structure and pattern could incorporate a similar gap size distribution to restore heterogeneity.

4.3.2. Local spatial patterns of trees

The number of single trees did not change over time, but the size and composition among single trees varied greatly between the contemporary forest and 1929. Single trees in the historical forest were more likely to be large trees and pine species. This presence of widely spaced, fire-resistant pines and other large diameter trees, interspersed with gaps, likely contributed to the rarity of crown fire in historical forests (Show and Kotok, 1924). Nearest neighbor distance decreased significantly between times, so that in the contemporary forest the frequency distribution of single trees with size was reversed, with large trees less likely to occur as singles and small trees more likely. High tree densities may have caused this association in 2007/2008, because for a tree to have an isolated canopy, it generally had to have a small crown. In the contemporary forest, ponderosa pines were still more likely to occur as single trees than other species. This may reflect the association of ponderosa pine with harsher microsites where overall tree density would be expected to be somewhat lower, even in a dense forest.

The stem density within tree clumps was similar in 1929 and 2008 when considering all trees ⩾ 10 cm, but the nearest neighbor distance did decrease over time. In addition, the space taken up by large tree clusters increased with time such that large tree clumps in the contemporary forest occupied more than twice the amount of space within the stand as compared to 1929, and encompassed a larger proportion of stems. The maximum number of trees per clump also increased fivefold between 1929 and 2007/2008. These shifts represent a homogenization of the stand structure, to one where the majority is composed of large clumps of very closely spaced trees. Large tree clusters are often proposed as good options to maintain habitat for wildlife species reliant on closed canopy (North et al., 2009). These areas are important components of the forest, yet are at risk of loss from crown fire under current conditions (Hessburg et al., 2005). Dense clumps of trees may also experience increased mortality from moisture stress (Lutz et al., 2009), particularly in a warming climate (van Mantgem and Stephenson, 2007).

4.4. Reference conditions

All reconstruction methods have limitations (White and Walker, 1997), and an inferred "reference condition" really encompasses a range of possible stand structures depending on sample scale and methods used. One potential shortcoming of our characterization of historical forest conditions is the lack of information on small trees. Small trees in particular may have varied in density depending on recent fire frequency and severity, as they are more susceptible to fire induced mortality. For example, in a Jeffery pine mixed-conifer forest with a relatively intact fire regime, one study found that wildfires killed 30–60% of pole sized trees (Minnich et al., 2000) and another found that half of trees <20 cm died after a fire (Stephens et al., 2008). Even if more complete information on the historical patterns of small trees was available, it would be confounded by the impacts of fire suppression, as the last fire recorded in tree rings was 1889. We believe that the range of conditions captured by two different minimum tree diameters may encompass what likely occurred when fire had an active influence on forest structure.

While the overarching pattern of open spaces, singles and tree clumps is a consistent finding in frequent-fire western forests, the characteristics of local patterns appears to vary by forest type. The distributional range of trees among the different structural groups in this study was on the same order as that reported for reference conditions in a mixed-conifer forest in western Montana (Larson et al., 2012), although there were generally fewer trees in small and medium clumps and a greater proportion in large clumps at our study site. However, our finding that larger diameter pines occurred disproportionately as single trees and in small groups is similar to other spatial studies of frequent-fire forests (e.g., Pielou, 1960; Sánchez Meador et al., 2011). Perhaps the dominance of shade-tolerant species at our site contributed to the lower proportions of single trees and small clumps. Compared to local spatial structure of reference conditions for ponderosa pine forests in Northern Arizona, our study had a greater proportion of trees in clumps and a greater maximum number of trees per clump, even when excluding the smaller trees (Abella and Denton, 2009; Sánchez Meador et al., 2011). As noted by Larson et al. (2012), the difference in proportion of trees in clumps is likely due to the mixed-conifer sites having higher productivity that may support greater tree density than the ponderosa pine sites in Northern Arizona, a finding also supported by the greater maximum clump size in this study.

While restoration guidelines often include a target stand-level canopy cover (North and Sherlock, 2012), metrics of average canopy conditions do not capture the high variability in canopy cover noted in historical forests. Within the 1929 plots, there was high structural variability in how canopy cover was allocated due to the presence of different sizes of tree clumps, widely-spaced single trees and openings. Low density areas of large solitary trees with low average canopy cover are an important structural component of many reference forests (Larson and Churchill, 2012). The historical data from our study showed that pine species and larger diameter trees occurred disproportionately as singles and in small groups. The historical structure also contained patches of high tree density forming large areas of contiguous canopy cover. These larger tree clumps were more likely to be dominated by white fir and small trees, suggesting that restoration of contemporary mixed-conifer stands could maintain some larger groups of similar composition to provide such habitat, in addition to creating more open

Table A1
Structural characteristics in 1929 post-harvest and 2007/2008 for each of the three plots.

	1929 Post-harvest			2007/2008		
	MC9	MC10	MC11	MC9	MC10	MC11
Single trees						
# Singles ha^{-1}	28.1	15.6	23.2	13.7	15.9	21.1
Proportion of trees (%)	15.3	6.2	8.8	1.6	2.2	3.1
% Shade intolerant	22.3	28.0	22.4	20.0	9.8	6.3
Nearest neighbor dist.(m)	6.7	7.4	5.9	4.4	4.8	4.8
BA/ha (m^2 ha^{-1})	3.3	4.5	2.4	0.5	0.9	1.0
Proportion of plot area (%)	4.6	3.8	3.3	1.3	1.8	2.4
QMD (cm)	38.7	60.8	36.5	21.9	26.3	24.8
Small clumps						
# Clumps ha^{-1}	19.4	13.1	19.9	10.7	11.2	12.2
Proportion of trees (%)	28.6	14.8	20.0	3.4	3.8	4.6
% Shade intolerant	14.4	11.5	20.8	6.4	5.1	8.6
Nearest neighbor dist.(m)	2.1	2.5	2.1	1.8	2.0	1.9
BA/clump (m^2)	0.2	0.7	0.2	0.2	0.2	0.2
BA/ha (m^2 ha^{-1})	58.1	104.3	56.4	63.6	70.8	64.9
Stem density (ha^{-1})	1202.6	1018.0	1211.5	1270.6	1110.9	1142.4
Proportion of plot area (%)	5.5	6.2	5.0	2.4	2.9	3.1
QMD (cm)	31.9	55.7	28.7	27.1	33.6	30.3
Medium clumps						
# Clumps ha^{-1}	4.9	6.5	6.6	5.7	4.7	5.6
Proportion of trees (%)	15.3	17.5	17.1	4.4	4.3	5.2
% Shade intolerant	7.3	20.7	19.3	5.1	7.9	11.1
Nearest neighbor dist.(m)	1.7	2.0	1.4	1.7	1.5	1.8
BA/clump (m^2)	0.4	1.2	0.3	0.5	0.7	0.6
BA/ha (m^2 ha^{-1})	70.7	108.8	61.1	81.9	119.8	95.8
Stem density (ha^{-1})	1458.1	1216.2	1610.5	1243.0	1373.9	1157.7
Proportion of plot area (%)	17.5	5.6	3.0	3.3	2.8	3.3
QMD (cm)	29.8	47.1	22.8	31.6	36.5	34.5
Large clumps						
# Clumps ha^{-1}	4.6	4.4	7.1	10.7	10.6	13.8
Proportion of trees (%)	40.8	61.5	54.1	90.5	89.8	87.1
% Shade intolerant	20.6	11.3	18.6	6.3	9.1	11.1
Nearest neighbor dist.(m)	1.8	1.8	1.6	1.5	1.7	1.6
BA/clump (m^2)	1.4	4.0	1.0	5.9	6.5	4.4
BA/ha (m^2 ha^{-1})	89.0	105.7	67.0	107.2	127.9	117.6
Stem density (ha^{-1})	1185.7	1290.1	1426.5	1437.9	1213.6	1226.3
Proportion of plot area (%)	7.0	14.0	10.1	56.4	55.1	49.8
QMD (cm)	33.6	38.0	24.8	32.3	36.3	36.4
Stand						
Canopy cover (%)	34.6	29.6	21.3	63.5	62.6	58.6
% Shade intolerant	18.1	17.1	20.8	10.1	9.7	12.2
QMD (cm)	33.4	44.3	26.5	31.9	36.1	35.8
DBH St. Dev. (cm)	18.8	29.8	13.8	17.8	21.0	18.6
BA/ha (m^2 ha^{-1})	16.2	38.6	14.6	67.9	75.4	68.0
Stem density (ha^{-1})	184.2	250.1	263.7	847.9	738.6	677.9
Ave. trees/clump	5.4	9.8	7.2	30.8	27.3	20.8
Max. trees/clump	40	126	45	584	829	215
Number of gaps/ha	2.7	5.0	2.5	0.3	0.0	0.3

conditions to favor pines and shrubs. This heterogeneous pattern produced by different species associations among structural groupings contributed to variation in canopy closure (a point-level measure of canopy conditions sensu (Jennings et al., 1999)) across the stand.

Comparisons between the 1929 >>25 cm and 1929 ⩾10 cm datasets show where trees may have arisen during the initial forty years of fire suppression, comparable to a quiescent period in the fire record. Trees 10–25 cm DBH grew within forest openings, so that the 1929 ⩾10 cm dataset had a higher proportion of small gaps (<0.05 ha), and larger gaps (>0.1 ha) were rare. Stand-level average canopy cover ranged from 36% (when considering trees ⩾25 cm) to 45% (when considering trees ⩾10 cm). Thus approximately 9% of the canopy cover was contributed by trees between 10 and 25 cm DBH-a size class frequently targeted for removal in standard "thinning from below" prescriptions. These small trees were predominantly shade-tolerant species (82%) that generally occurred in large, dense patches, reflecting the dense and highly clustered nature of tree regeneration (Stephens and Fry, 2005; Larson and Churchill, 2012). In the 1929 ⩾10 cm dataset, basal area per clump was greater, while basal area ha^{-1} within clumps was lower, indicating that in addition to growing within open areas, the trees that arose near the onset of fire exclusion grew near larger trees. This infilling of small trees generates a more competitive environment which can put trees at greater risk of mortality (Das et al., 2011), and increase the risk of crown fire due to ladder fuels carrying fire into the canopy.

In both 1929 datasets, gaps were typically sinuous, rather than round, in shape (Fig. 2). While other studies have suggested that a relatively high amount of light (>41% of full sun) is needed to favor regeneration of shade-intolerant pines (Bigelow et al., 2011), these somewhat narrow breaks in the canopy likely provided sufficient light to support shrub patches and pine regeneration in forests when fire played an active role. Shrub patches are less common in fire-suppressed forests, but provide important habitat and are associated with higher small mammal (Coppeto et al., 2006) and

bird (Raphael et al., 1987; Humple and Burnett, 2010) species diversity.

5. Management recommendations

Foresters often focus on measuring, marking and managing trees at the scale of a stand, which Oliver and Larson (1996) describe as "a spatially continuous group of trees and associated vegetation having similar structures and growing under similar soil and climatic conditions". Spatial descriptions of active-fire forest conditions presented here and in other regions (Larson and Churchill 2012) suggest fine-scale within stand patterns and their influence on ecological processes may be important to consider in management practices. While more traditional even spacing may maximize tree growth rates, the resulting structure may not have been a common historical condition.

In mixed-conifer forests similar to those found at STEF, marking prescriptions designed to restore within-stand heterogeneity might focus on creating tree groups, gaps and individual trees roughly in proportion to our 1929 ⩾25 cm data (Figs. 1 and 3 and Table 1). The high variability in tree clumps in the historical data, with larger clumps consisting of between 10 and 33 trees, suggests that managers may wish to create a range of tree cluster sizes rather than emphasizing the groups of 3–6 trees that are often marked (authors pers. obs.; Churchill et al., 2013). When marking trees to leave as a larger clump, thinning some smaller trees within the clump may be appropriate when within-clump densities exceed those present in the reference forest, if it can be done without excessive damage to residual trees. Groups of trees may be identified by focusing on the attributes that make them potential wildlife habitat such as the presence of large, old trees and higher levels of canopy closure (North et al., 2009). Other characteristics that may enhance habitat value include live trees with dead tops or broken branches, evidence of heart rot organisms, mistletoe brooms, or other "defects" associated with preferred habitat for some species (North and Sherlock, 2012). The reference forest also contained abundant single trees and small tree clumps, comprised of a greater proportion of large trees and pines. In areas where large neighboring pines remain, a more aggressive thinning of shade-tolerant species may be appropriate to create an open environment to favor shrub habitat and pine regeneration.

What may be more difficult is creating a range of gap sizes, including gaps >0.05 ha. Current standards and guides in the Sierra Nevada emphasize meeting target canopy cover conditions of 40 or 50% depending on potential use by the California spotted owl (*Strix occidentalis occidentalis*) (USDA, 2004). Marking crews may be reluctant to create these large gaps, particularly when the removal of larger trees would result (Churchill et al., 2013). Larger gaps in our reference forest were sinuous. This could provide some guidance on the width of larger gaps and help overcome this obstacle, allowing for large gaps to be created while minimizing larger diameter stem removal. The resulting high microsite variability in canopy closure may not compromise target canopy cover, a stand-level average measure (North and Stine, 2012).

Restoration of heterogeneous spatial structure in western fire-dependent forests can potentially increase ecosystem resilience to drought and wildfire, without compromising forest habitat for species associated with closed canopy conditions (North et al., 2010; Underwood et al., 2010). Measures of local spatial structure of active-fire forests can help inform managers by providing information that is more easily translated to tree marking guidelines, but descriptions of within-stand characteristics are new and will benefit from further development. The most difficult practical concept suggested by our research is that management and marking avoid downscaling stand-level targets if the objective is to increase fine-scale forest heterogeneity. There may not be a single, optimal marking method to create the spatial patterns suggested by the historical structure data, but flexible response to existing conditions and applying the general principles outlined here should put a stand on a trajectory towards such heterogeneity.

Acknowledgements

Appendix A

Even though the three plots were harvested using different cutting methods, some generalizations can be made about the 1929 post-harvest data as compared to the other time points
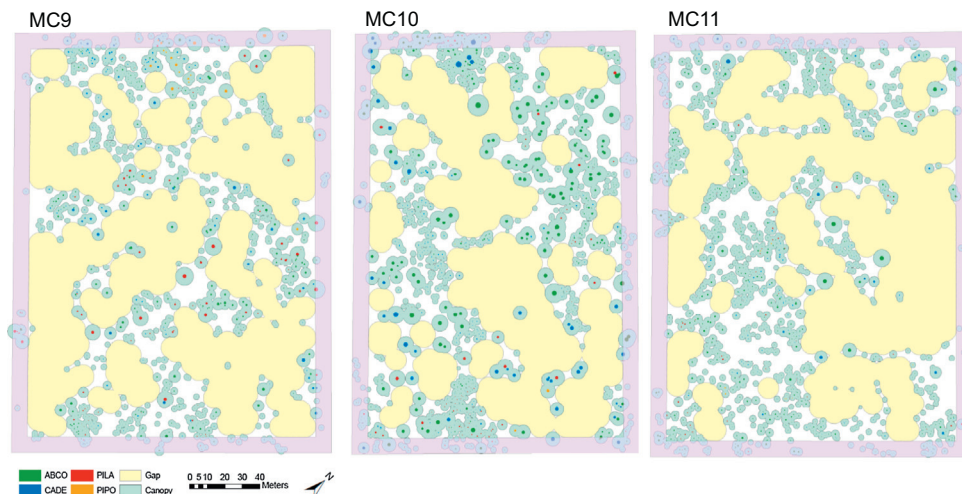
Fig. A1. Stem maps are of MC9, MC10 and MC11 post-harvest in 1929, showing spatial composition of plot area and analysis of tree clustering and gaps. The purple colored zone is the 9 m buffer on the inside edge of the plot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Appendix B. Supplementary Material 1

Cell contributions to the overall χ^2 value for contingency analysis of the distribution of tree species and size classes among structural groups.

	1929 $\geqslant$ 25 cm				1929 $\geqslant$ 10 cm				2007/2008			
	Single	Small	Medium	Large	Single	Small	Medium	Large	Single	Small	Medium	Large
White fir	2.95	1.37	1.31	0.00	5.68	6.34	4.28	2.92	0.44	4.20	1.01	0.33
Incense-cedar	7.67	0.16	2.78	1.51	4.89	0.63	3.15	7.21	1.21	4.60	5.09	1.70
Sugar pine	0.52	2.48	1.78	0.28	0.06	5.87	3.75	0.05	0.27	5.92	0.14	0.07
Ponderosa pine	1.69	0.01	7.68	2.09	19.50	6.29	70.96	0.05	0.17	15.01	9.22	2.90
10–50	2.38	0.79	2.95	0.37	4.00	3.78	3.32	2.12	0.14	2.39	0.42	0.00
50–100[a]	0.07	6.18	1.33	0.72	10.78	0.07	24.94	7.18	1.01	16.76	2.97	0.00
>100	5.51	5.63	1.54	0.06	0.16	1.80	1.88	0.19				

[a] In the 2007/08 dataset all trees >50 cm DBH were included in this size class.

(Table A1). The average number of trees per clump and the distribution of stems amongst the structural classes were more similar to the 1929 pre-harvest data than to contemporary conditions, with a relatively low number of trees per clump, the greatest proportion of stems in large clumps, and a substantial number of trees occurring in small clumps and singles. Nearest neighbor distance was similar to that immediately prior to harvest, and stem density within clumps was similar to the contemporary data. BA ha^{-1} of single trees was lower after harvest, but still greater than in the contemporary forest. As expected, the proportion of plot area in each structural group was generally lower than prior to harvest, corresponding to a decrease in canopy cover. Compared to contemporary conditions there was a greater proportion of plot area in singles and small clumps, but a much lower proportion in large clumps. The number of gaps per hectare was similar to 1929 $\geqslant$ 10 cm, but the average gap size and the proportion of plot area in gaps were greater than in other time points (see Fig. A1).

Appendix B

Supplementary data 1. Cell contributions to the overall χ^2 value for contingency analysis of the distribution of tree species and size classes among structural groups.

References

Abella, S.R., Denton, C.W., 2009. Spatial variation in reference conditions: historical tree density and pattern on a Pinus ponderosa landscape. Canadian Journal of Forest Research 39, 2391–2403.

Baddeley, A., Turner, R., 2005. Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12, 1–42.

Beaty, R.M., Taylor, A.H., 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. Forest Ecology and Management 255, 707–719.

Bigelow, S.W., North, M.P., Salk, C.F., 2011. Using light to predict fuels-reduction and group-selection effects on succession in Sierran mixed-conifer forest. Canadian Journal of Forest Research 41, 2051–2063.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291, 442–457.

Collins, B.M., Everett, R.G., Stephens, S.L., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere, vol. 2, art51.

Coppeto, S.A., Kelt, D.A., Van Vuren, D.H., Wilson, J.A., Bigelow, S., 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. Journal of Mammalogy 87, 402–413.

Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. Forest Ecology and Management 261, 1203–1213.

Diggle, P.J., 2003. Statistical Analysis of Spatial Point Patterns. Arnold, London, UK.

Dunnett, C.W., 1955. A multiple comparison procedure for comparing several treatments with a control. Journal of the American Statistical Association 50, 1096–1121.

Fule, P.Z., Waltz, A.E.M., Covington, W.W., Heinlein, T.A., 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. Journal of Forest 99, 24–29.

Gill, S.J., Biging, G.S., Murphy, E.C., 2000. Modeling conifer tree crown radius and estimating canopy cover. Forest Ecology and Management 126, 405–416.

Girvetz, E.H., Greco, S.E., 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. Landscape Ecology 22, 1131–1142.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211, 117–139.

Humple, D.L., Burnett, R.D., 2010. Nesting ecology of yellow warblers (Dendroica petechia) in montane chaparral habitat in the northern Sierra Nevada. Western North American Naturalist 70, 355–363.

Illian, J., Penttinen, A., Stoyan, H., Stoyan, D., 2008. Statistical Analysis and Modelling of Spatial Point Patterns. John Wiley & Sons, Ltd., The Atrium, Southern Gate, Chichester, West Sussex PO19 8SQ, England.

Jennings, S.B., Brown, N.D., Sheil, D., 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72, 59–73.

Knapp, E.E., Skinner, C.N., Estes, B.L., North, M.P., Unpublished results. Long-term Forest and Understory Change with Recovery from Logging in the Absence of Fire.

Larson, A.J., Churchill, D., 2008. Spatial patterns of overstory trees in late-successional conifer forests. Canadian Journal of Forest Research 38, 2814–2825.

Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267, 74–92.

Larson, A.J., Stover, K.C., Keyes, C.R., 2012. Effects of restoration thinning on spatial heterogeneity in mixed-conifer forest. Canadian Journal of Forest Research 42, 1505–1517.

Laudenslayer, W.F., Darr, H.H., 1990. Historical effects of logging on forests of the Cascade and Sierra Nevada Ranges of California. Transactions of the Western Section of the Wildlife Society, 12–23.

Levene, H., 1960. Robust tests for equality of variances. In: Olkin, I. (Ed.), Stanford Studies in Mathematics and Statistics. Stanford University Press, Palo Alto, California, pp. 278–292.

Lutz, J.A., van Wagtendonk, J.W., Franklin, J.F., 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. Forest Ecology and Management 257, 2296–2307.

Lutz, J.A., Larson, A.J., Swanson, M.E., Freund, J.A., 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS ONE, 7.

Lydersen, J., North, M., 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. Ecosystems 15, 1134–1146.

Meyer, K.M., Wiegand, K., Ward, D., Moustakas, A., 2008. Determining patch size. African Journal of Ecology 46, 440–442.

Minnich, R.A., Barbour, M.G., Burk, J.H., Sosa-Ramirez, J., 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. Journal of Biogeography 27, 105–129.

Naficy, C., Sala, A., Keeling, E.G., Graham, J., DeLuca, T.H., 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications 20, 1851–1864.

Nagel, T.A., Taylor, A.H., 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. Journal of the Torrey Botanical Society 132, 442–457.

North, M., Sherlock, J., 2012. Marking and assessing forest heterogeneity. In: North, M. (Ed.), Managing Sierra Nevada forests. PSW-GTR-237. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 95–105.

North, M., Stine, P., 2012. Clarifying concepts. In: North, M. (Ed.), Managing Sierra Nevada forests. PSW-GTR-237. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 149–164.

North, M., Chen, J.Q., Oakley, B., Song, B., Rudnicki, M., Gray, A., Innes, J., 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. Forest Science 50, 299–311.

North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Canadian Journal of Forest Research 37, 331–342.

North, M., Stine, P., Zielinski, W., Stephens, S., 2009. An ecosystem management strategy for Sierran mixed-conifer forests. USDA Forest Service. Pacific Southwest Research Station, Albany, CA, p. 49.

North, M., Stine, P., O'Hara, K.L., Stephens, S., 2010. Harnessing fire for wildlife. Wildlife Professional 4, 30–33.

O'Hara, K.L., Latham, P.A., Hessburg, P., Smith, B.G., 1996. Technical commentary: a structural classification for inland northwest forest vegetation. Western Journal of Applied Forestry 11, 97–102.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. Wiley, New York.

Parsons, D.J., Debenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2, 21–33.

Pielou, E.C., 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology 48, 575–584.

Piirto, D.D., Rogers, R.R., 2002. An ecological basis for managing giant sequoia ecosystems. Environmental Management 30, 110–128.

Plotkin, J.B., Chave, J.M., Ashton, P.S., 2002. Cluster analysis of spatial patterns in Malaysian tree species. American Naturalist 160, 629–644.

R Core Team, 2013. A Language and Environment for Statistical Computing. In: R Foundation for Statistical Computing, Vienna, Austria.

Raphael, M.G., Morrison, M.L., Yoderwilliams, M.P., 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. Condor 89, 614–626.

Sánchez Meador, A.J., Parysow, P.F., Moore, M.M., 2011. A new method for delineating tree patches and assessing spatial reference conditions of ponderosa pine forests in northern Arizona. Restoration Ecology 19, 490–499.

SAS Institute Inc., 2011. SAS 9.3. In. SAS Institute Inc., Cary, NC.

Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20, 362–380.

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.

Show, S.B., Kotok, E.I., 1924. The role of fire in the California pine forests. USDA, Government Printing Office, Washington, DC, USA, p. 80.

Skinner, C.N., 1995. Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. Landscape Ecology 10, 219–228.

Stephens, S.L., Fry, D.L., 2005. Spatial distribution of regeneration patches in an old-growth Pinus jeffreyi-mixed conifer forest in northwestern Mexico. Journal of Vegetation Science 16, 693–702.

Stephens, S.L., Fry, D.L., Franco-Vizcaino, E., 2008. Wildfire and spatial patterns in forests in northwestern Mexico: the United States wishes it had similar fire problems. Ecology and Society 13, 12.

Underwood, E.C., Viers, J.H., Quinn, J.F., North, M., 2010. Using topography to meet wildlife and fuels treatment objectives in fire-suppressed landscapes. Environmental Management 46, 809–819.

USDA, 2004. Sierra Nevada forest plan amendment: final environmental impact statement. In: U.S. Department of Agriculture, F.S., Pacific Southwest Research Station (Ed.), Vallejo, CA, USA.

van Mantgem, P.J., Stephenson, N.L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecology Letters 10, 909–916.

White, P.S., Walker, J.L., 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5, 338–349.

White, A.M., Zipkin, E.F., Manley, P.N., Schlesinger, M.D., in press. Simulating avian species and foraging group responses to fuel reduction treatments in coniferous forests. Forest Ecology and Management, http://dx.doi.org/10.1016/j.foreco.2013.04.039.

York, R.A., Battles, J.J., Heald, R.C., 2007. Gap-based silviculture in a Sierran mixed-conifer forest: effects of gap size on early survival and 7-year seedling growth. In: Powers, R.F. (Ed.), Restoring Fire-adapted Ecosystems: Proceedings of the 2005 National Silviculture Workshop. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 181–191.