Spatial dynamics of tree group and gap structure in an old-growth ponderosa pine-California black oak forest burned by repeated wildfires


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A B S T R A C T

Knowledge of how tree groups and gaps are formed and maintained in frequent-fire forests is key to managing for heterogeneous and resilient forest conditions. This research quantifies changes in tree group and gap spatial structure and abundance of ponderosa pine (Pinus ponderosa) and California black oak (Quercus kelloggii) with stand development after wildfires in 1990 and 1994 in an old-growth forest in the Ishi Wilderness, southern Cascades, California. Forest demography and tree group and gap structure were quantified by measuring, mapping, and aging trees in six 1-ha permanent plots in 2000 and 2016. Tree recruitment, mortality, and growth were estimated using demographic models and spatial characteristics including gap structure were identified using an inter-tree distance algorithm and the empty space function. Potential fire behavior and effects in 2016 were estimated to determine if the current forest would be resilient to a wildfire in the near future.

Stand density and basal area in both 2000 and 2016 resembled reference conditions for pre-fire suppression frequent-fire forests in the western United States. Wildfires initially promoted California black oak regeneration via sprouting, but oak regeneration from seed declined relative to ponderosa pine over the post-fire period. In 2000, ~15% of trees were classified as single tree groups and an average tree group had 6 trees (range 2–38) which increased to 9 trees (range 2–240) in 2016. Small groups (2–4 trees) had similar-aged trees while larger groups were multi-aged. By 2016, single tree groups decreased by ~30%, and the size, density, and intensity of clustering within tree groups increased, with an average tree group size of 9 (range 2–240) in 2016. Rates of post-fire regeneration, particularly the high rate for ponderosa pine, drove spatial dynamics in tree group and gap structure. Although the size and frequency of canopy gaps were similar in 2000 and 2016, the density of seedlings and saplings in gaps was higher in 2016, and large gaps were being fragmented by gap filling. Potential fire behavior predicted surface fire and low overstory tree mortality, suggesting the current forest would be resilient to a wildfire. However, burning will be necessary in the future to reduce the demographic pressure of ponderosa pine, promote black oak, and to maintain and create future spatial heterogeneity. Cumulatively, this research demonstrates that wildland fires under certain conditions can maintain and restore fire resilience in ponderosa pine forests reducing the negative ecological consequences related to past fire exclusion.

1. Introduction

Ponderosa pine (Pinus ponderosa) and mixed pine-oak forests in the western USA evolved with frequent fire and were historically resilient to fire. In this context, resilience represents a capacity for forests to reorganize and return to a prior condition after disturbance while absorbing environmental changes such as climate change (Folke et al., 2010; Millar et al., 2007). A characteristic feature of ponderosa pine forests is structural heterogeneity at small-scales which imparts resilience to chronic fire (Churchill et al., 2013). Under a regime of frequent fire, a stand, at any one point in time, consists of a mosaic of groups of even/uneven aged overstory trees, widely spaced individual trees, dense patches of regeneration, and unoccupied canopy gaps (Cooper, 1960; Larson and Churchill, 2012; White, 1985). This group and gap structure promotes understory species and lifeform diversity (Dodson et al., 2008; Laughlin et al., 2011; North et al., 2005) and provides a range of habitats that supports a diverse assemblage of bird and small mammal species (Buchanan et al., 2003; Latif et al., 2015). A
group and gap structure also creates spatially heterogeneous surface and canopy fuel conditions which burn with highly variable effects that inhibit spread of intense surface or crown fire while providing protected sites for tree regeneration (Fry and Stephens, 2010; Taylor et al., 2014).

The structure and resilience of frequent-fire ponderosa pine and pine-oak forests in the western USA was altered significantly by Euro-American settlement in the mid to late 19th century (Covington and Moore, 1994; Taylor, 2004). Logging, grazing, and especially fire exclusion led to an increase in tree density and forest canopy cover, reduction in gap area by infilling of trees, and an increase in both surface and canopy fuel (Knapp et al., 2013; Scholl and Taylor, 2010; Taylor et al., 2014). In logged areas, the largest and most fire-resistant trees were often removed (Laudenslayer et al., 1989; Naficy et al., 2010) resulting in dense stands of intermediate and smaller sized trees. Fire exclusion also shifted species composition of pine-dominated and mixed pine-oak forests toward conifer dominance, and oaks have declined where they have been overtopped by a dense conifer canopy (Cockling et al., 2012, 2014; McDonald and Tappeiner, 2002). Fire-exclusion related forest changes have increased susceptibility of ponderosa pine and pine-oak forests to high-severity fire, insect attacks, drought-induced tree mortality, and climate change (Guarin and Taylor, 2005; Hurteau et al., 2014; Preisler et al., 2017). Fire exclusion, logging and other forest management practices are still prevalent in western landscapes with millions of hectares in need of restoration (Churchill et al., 2013; Hessburg et al., 2015). Creation of forest structures that are both resistant and resilient to fire is central to restoration goals in frequent-fire forests throughout western North America (e.g., Gaines et al., 2010; Roccaforte et al., 2010). The basis for manipulating forest structure to restore resilience is a documented shift away from historic (pre-Euro-American settlement) forest structure and composition and the increased susceptibility of forests to high-severity fire that can shift forest to an alternative stable state of grassland or shrubland through repeated high-severity fire (Airey Lauvau et al., 2016; Coppolleta et al., 2016; Reily et al., 2017).

Before fire suppression, interactions between frequent fire and stand structure maintained a gap and tree group structure in mixed ponderosa pine-California black oak (Quercus kelloggii, hereafter black oak) forests in lower montane forests in the Sierra Nevada, southern Cascade, and Klamath Mountains in California (Skinner et al., 2018a; Skinner et al., 2018b; van Wagendonk et al., 2018). Ponderosa pine and black oak are both well adapted to wildfire. Ponderosa pine has thick insulating bark, is fire-resistant, and regenerates from seed; black oak has a thinner bark, sprouts from the base and crown after being injured or top-killed by fire, and also regenerates from seed (Barton, 2002; Hammett et al., 2017; Nemens et al., 2018). Mixtures of pine and black oak within a stand are thought to increase forest resilience to fire (Skinner, 1995). Black oak litter is highly flammable and promotes rapidly spreading, low-intensity, surface fire (Engber and Varner, 2018), and black oak in mixed stands breaks up crown fuel continuity thereby reducing crown fire spread (Skinner et al., 2018a). The tree group and gap structure is also thought to be important for regeneration and persistence of black oak, particularly large diameter trees, as establishment and growth of this species benefit from high-light environments (Long et al., 2016). With fire exclusion, ponderosa pine has increased and black oak has declined, altering fire-vegetation interactions and the potential to restore a resilient group and gap structure in highly affected forests (Cockling et al., 2014, 2012; Nemens et al., 2018).

Managed wildfire has been proposed as a key restoration tool to increase structural heterogeneity and fragment fuels in frequent-fire forests altered by fire suppression (Larson et al., 2013; Naficy et al., 2010; North et al., 2012). Use of managed wildfire is particularly appropriate in large remote tracts of forest where use of mechanical fuel treatment to alter fire behavior is constrained by cost, access, terrain, and legal or regulatory requirements (Larson et al., 2013; North et al., 2015). In designated wilderness, fire (prescribed, managed wildfire) is the primary tool available for vegetation and fuels management (USDI, 1998), and there evidence that reintroduction of fire has successfully restored pre-settlement conditions exists for select contemporary forests with restored fire regimes and limited anthropogenic disturbance (Larson et al., 2013; Parks et al., 2015; Harris and Taylor, 2015). Yet, there is also increasing concern and mounting evidence that in areas where forest structure has been dramatically altered, re-introducing wildfire could exacerbate the problem (Thompson and Spies, 2010, Crotteau et al., 2013, Coppolleta et al., 2016, Harris and Taylor, 2017). The initial effects of a re-entry burn (the first fire following a period of fire exclusion) strongly influence fire effects in subsequent burns (Harris and Taylor, 2017; Parks et al., 2015; Walker et al., 2018). High-severity fire effects in recent re-entry burns have led to high-severity fire effects in burns that can initiate long-term shifts from forest to vegetation types such as grassland or shrubland (Coppolleta et al., 2016; Guiterman et al., 2018; Savage and Mast, 2005). In more anthropogenically-disturbed, fire-suppressed areas, active management – such as prescribed burning or mechanical thinning – can help restore a negative feedback and may be needed before re-introducing wildland fire back on the landscape (Ritchie et al., 2007; Harris and Taylor, 2017).

Contemporary reference sites that can guide active management of western forests are rare (Stephens and Gill, 2005; Larson et al., 2013). These sites are valuable, since they allow for quantitative measures of forest structure (Barbour et al., 2009) and provide important insights into healthy ecosystem processes (Binkley et al., 2007; Stephens et al., 2008). The Beaver Creek Pinery, an old-growth forest in the Ishi Wilderness, may serve as an important contemporary reference site for ponderosa pine-black oak forests. Due to limited anthropogenic disturbances in the 20th century and a history of frequent, low-moderate severity fire, this forest was resilient to two wildfires in the 1990s. Further, these fires preserved a resilient forest structure by thinning ingrowth resulting from fire exclusion, promoting tree regeneration, and generating spatially heterogeneous tree patterns thought to be similar to forests before fire suppression (Taylor, 2010). Here, we characterize changes in this resilient tree group and gap structure over a 22-year period.

Specifically, our objectives were to: (1) quantify post-fire tree recruitment, mortality, and growth for ponderosa pine and black oak during stand development; (2) quantify the spatial and structural attributes of tree groups and gaps and how they have changed since the wildfires; (3) determine if historic tree group development was predominantly even or uneven aged; and (4) evaluate whether the current forest structure is resilient to fire by estimating potential fire behavior and effects. To fulfill our objectives, we used repeat measurements of forest characteristic in six large (∼1 ha) permanent plots that were sampled in 2000 and 2016.

2. Method

2.1. Study site

Our study was conducted in the Beaver Creek Pinery, an ∼100 ha forest on a plateau in the Ishi Wilderness, in the southern Cascades, California (Fig. 1). The elevation of the Beaver Creek Pinery is 850 m. Ponderosa pine and black oak are the canopy dominants. Common understory shrubs include Arctostaphylos manzanita subsp. rooffi, A. viscella, Ceanothus integerrimus, C. prostratus, C. lemmonii, Franagua californica, Mahonia aquifolium, and Toxicodendron diversilobum. The Beaver Creek Pinery is underlain by Cohassett gravelly loam soil (USDA Web Soil Survey) and average annual temperature and precipitation in Cohasset (800 m, 20 km southwest) is 16°C and 145 cm, respectively. Most precipitation occurs between October-April. The Yana (Yahi) tribe lived in the region for 3000 years prior to European settlement in the mid-19th century, and Ishi, the last tribal member living in what is now the Ishi wilderness, emerged from the area in 1911 (Kroeger, 1961). The Yana used fire to promote plant growth for food, fiber, and game.
mapped new tree recruitment, and recorded tree mortality. In both sample years, we counted saplings (<5 cm dbh and >1.4 m tall) and seedlings (0.2–1.4 m tall) in 10 m × 10 m grid cells in each plot, and recorded if oaks had established from seed or sprout. Oak regeneration was assumed to be from seed unless stems were highly aggregated or in close proximity to the remains of a top-killed oak. We also estimated canopy cover above each cell (open 0–33%, intermediate 33–66%, closed >66%) and estimated ground cover of shrubs, forbs, and grasses (0%, <1%, 1–5%, 5–25%, 25–50%, 50–75%, and 75–100%).

2.3. Stand characteristics and development

To characterize post-fire stand development and tree population dynamics, we estimated rates of recruitment, mortality, and loss/gain of basal area for ponderosa pine and black oak between 2000 and 2016. Recruitment and mortality were estimated following Condit et al., 1995, 1993:

\[
\text{mortality rate (year}^{-1}) = \frac{\ln(N_t) - \ln(N_{t-1})}{t} \times 100
\]

\[
\text{recruitment rate (year}^{-1}) = \frac{\ln(N_{t+1}) - \ln(N_t)}{t} \times 100
\]

where \(N_t, N_{t-1}\) and \(N_{t+1}\) are the number of trees (≥5 cm DBH) alive in 2000, total number of trees living in 2016, and the number trees surviving between 2000 and 20016, respectively; \(t\) is the time interval (16 years).

Basal area (BA) lost or gained by recruitment or mortality was identified using the following equations:

\[
\text{BA loss rate (year}^{-1}) = \frac{\text{BA}_{t-1} - \text{BA}_t}{t} \times 100
\]

\[
\text{BA gain rate (year}^{-1}) = \frac{\text{BA}_t - \text{BA}_{t-1}}{t} \times 100
\]

where \(\text{BA}_t, \text{BA}_{t-1}\), \(\text{BA}_0\) and \(\text{BA}_4\) are the basal area values for trees that died during the census period, trees alive at the beginning of the study, trees recruited during the census period, and trees that survived during the census period, respectively.

Changes in the populations for trees and BA were inferred from the population growth rate (\(\lambda\)) (Condit et al., 1999) using data for both sampling dates:

\[
\lambda_{\text{trees}} (\text{year}^{-1}) = \frac{\ln(N_{\text{trees}_{2000}}) - \ln(N_{\text{trees}_{2000}})}{t} \times 100
\]

\[
\lambda_{\text{BA}} (\text{year}^{-1}) = \frac{\ln(N_{\text{BA}_{2000}}) - \ln(N_{\text{BA}_{2000}})}{t} \times 100
\]

where \(N\) and \(\text{BA}\) are the number of trees or the basal area of species at each time point.

Comparisons in density, basal area, and rates of recruitment and mortality between species over the census period were made using paired t-tests (density, basal area) or non-parametric Kruskal-Wallis H tests (recruitment, mortality). We used a relaxed probability of significance (\(p = 0.1\)) for comparisons because the number of plots was small (\(n = 6\)).

The influence of density and distance from focal tree to competitors on tree mortality was identified by calculating the H index (Hegyi, 1974). This tree-to-tree index assumes that relative dbh and distance between the focal and competitor tree(s) describes their competitive interaction and is commonly used to assess competition where spatial data for each tree is recorded (Contreras et al., 2011; Vernon et al., 2018). Competition was assessed for three populations: trees alive in 2000 that survived to 2016, trees alive in 2000 that did not survive to 2016, and trees alive in 2016. The H index was calculated using the following equation:

Fig. 1. Location of the Beaver Creek Pinery in northern California in the Ishi Wilderness, within Lassen National Forest (Top inset), the location of the six stem map plots (Top and Bottom) measured in 2000 and 2016 and severity of the 1990 Campbell fire (Top) and 1994 Barkley fire (Bottom) as identified by the Monitoring Trends in Burn Severity Program (http://www.mtbs.gov/).
\[
\sum_{i=1}^{n} \frac{D_i}{\text{Dist}_{ij}}
\]

where \(D_i\) is the diameter of the competitor, \(D_{ij}\) is the diameter of the focal tree, and \(\text{Dist}_{ij}\) is the distance between the focal and competitor tree. Competitor trees were defined as any tree within 12 m of the focal tree and we applied a 12 m buffer to avoid artificially low competition indices for trees near the plot edges. Competition effects (measured by the \(H\) index) on trees that survived the census period vs trees that died during the census period were compared using a \(t\)-test. Competition was also compared for trees that survived the census period.

2.4. Spatial patterns and dynamics

2.4.1. Group characteristics

Tree group and gap structure and dynamics were determined by quantifying the spatial structure of tree populations within plots in 2000 and 2016. Tree group characteristics were identified using an inter-tree distance (\(d\)) algorithm over a range of spatial scales. Trees were assigned to a group within a given radius \(\leq d\), while trees at distances > \(d\) were considered single tree groups (Plotkin et al., 2002). Since edge effects have been shown to be minimal in identifying clumping patterns (Churchill et al., 2013; Plotkin et al., 2002; Yamada and Rogerson, 2003), an edge correction was not used. Tree group sizes were identified for five functional categories for ponderosa pine forests identified by Churchill et al. (2017): (1) individual (1 tree); (2) small (2–4 trees); (3) medium (5–9 trees); (4) large (10–15 trees); and (5) extra-large clump (≥16 trees) at inter-tree distances of 1–12 m. We compared tree group frequency for both 2000 and 2016 using a 6-m inter-tree distance, a distance that corresponds with the average crown radius of trees in mature and old growth ponderosa pine forests (Abella and Denton, 2009; Churchill et al., 2013; Sánchez Meador et al., 2011). Characterization at this distance also permitted direct comparison with group characteristics in ponderosa pine forests in the Pacific Northwest (Churchill et al., 2013, 2016, 2017), the Southwest (Abella and Denton, 2009; Sánchez Meador et al., 2011, 2009; Schneider et al., 2016) and the Rocky Mountains (Brown et al., 2015; Clyatt et al., 2016).

In addition to quantifying tree group spatial characteristics using local spatial metrics, they were also quantified using a global statistic, Ripley’s K. Ripley’s K is based on point pattern analysis, and we used the standardized L-function to identify the type, scale, and intensity of pattern for trees in 2000 and 2016. Ripley’s L-function was calculated for trees in each plot using the Spatstat package (Baddeley and Turner, 2005) in R version 3.3.2 (R Core Team, 2013) and spatial patterns were assessed at 1 m intervals up to a maximum radius (\(r\)) of one quarter the length of the shortest plot dimension. An envelope of complete spatial randomness (CSR) was generated using 999 simulations and values of \(L\) (\(r\)) above the envelope denote clumping, values below signify a uniform pattern, values within the envelope represent a random pattern. Analyses were performed for all six plots for populations of at least 15 trees in the following categories: (1) all trees alive in 2000 and 2016; (2) ponderosa pine alive in 2000 and 2016; (3) black oak alive in 2000 and 2016.

To assess if historical tree group development followed an even- or uneven-age model of group development, we identified the age structure of trees in the tree group sizes in 2000. A narrow range of tree ages within groups would support an even-aged model whereas a wide range in ages would indicate groups were comprised of multiple age classes. We used a 20 year age range as a cutoff for even-aged (≤20 years) and un-even aged (>20 years) groups to account for variation in the number of years to reach coring height. The proportion of even and uneven aged groups was calculated for each tree group size except for the individual trees.

2.4.2. Gap characteristics

Gap characteristics (frequency, area) in 2000 and 2016 were quantified using the empty space function \(F(t)\) to calculate distances to nearest tree (Diggle, 2013) from each cell in a 0.5 m × 0.5 m grid in each plot. Distances were pooled in 3 m classes to create a gap size and total open canopy area distribution for 2000 and 2016. We tested for differences in the shape of these distributions using a Kolmogorov-Smirnov two-sample test. Gaps were identified using a threshold distance of 9 m from a tree stem, as suggested by Churchill et al. (2017) and Clyatt et al. (2016), since this distance is beyond the influence of the canopy and tree root systems and should permit successful ponderosa pine regeneration and growth (Simard et al., 2012; York et al., 2004). We followed Clyatt et al. (2016) in quantifying gaps where gaps were ≥9 m from the nearest tree and then buffered by 5 m to account for tree crown extension into openings. Areas 9 m or closer to plot edges were also removed to prevent overestimation of gap area. Open area in each plot for each sample year was calculated by subtracting crown area from plot area. Differences in mean gap size and open area in 2000 and 2016 were identified using separate paired \(t\)-tests and a relaxed probability of significance (\(p = 0.1\)) because the number of plots was small (\(n = 6\)).

Gap dynamics were identified by estimating rates of crown extension by the overstory, gap infilling from newly established trees, and gap creation from tree mortality with the following equations:

\[
\text{infilling}_{\text{regrowth}} \left(\%\text{year}^{-1}\right) = \frac{(\text{Gap}_{2000} - \text{Gap}_{2016})/\text{Gap}_{2000}}{t} \times 100
\]

\[
\text{creation} \left(\%\text{year}^{-1}\right) = \frac{(\text{Gap}_{2016} - \text{Gap}_{2000})/\text{Gap}_{2016}}{t} \times 100
\]

\[
\text{crown extension} \left(\%\text{year}^{-1}\right) = \frac{(\text{CD}_{2016} - \text{CD}_{2000})/\text{CD}_{2000}}{t} \times 100
\]

where \(\text{Gap}_{2000}\) is gap area in 2000, \(\text{Gap}_{2000}\) is the gap area that remained open between 2000 and 2016, \(\text{Gap}_{2016}\) is gap area in 2016, \(\text{CD}_{2000}\) is the portion crown diameters from trees in 2000 extending into Gapboth (i.e. unoccupied gap area), \(\text{CD}_{2016}\) is overlap between Gapboth and 2016 crown diameters of surviving trees, and \(t\) is the time interval (16 years). Crown diameter for this analysis was estimated using species-specific diameter-crown width equations (Keyser, 2008) calibrated with field measurements.

2.4.3. Regeneration and gap characteristics

The relationship between canopy cover and abundance of tree regeneration was identified by comparing seedling and sapling density in 10 m × 10 m cell canopy cover classes in 2000 and 2016. Comparisons were made using a non-parametric Kruskal-Wallis test with a Dunn’s post-hoc test. Infilling of regeneration into gaps between 2000 and 2016 was also graphically assessed by mapping regeneration density of ponderosa pine and black oak in each cell and calculating the area occupied by density class in each plot. Changes in seedling and sapling abundance were identified using paired \(t\)-tests and a relaxed probability of significance (\(p = 0.1\)) because the number of plots was small (\(n = 6\)).

2.5. Potential fire behavior

Potential fire behavior following 22 years of post-fire succession after the 1994 wildfire was determined for each plot using Crown Mass in the Fuel Management Analyst Plus software (FMA, Carlton, 2004). Crown Mass uses tree lists from each plot to estimate potential fire behavior (i.e. rate of spread, flame length, fire type) and fire effects (i.e. probability of mortality, percent crown scorch) under specified burning conditions. Potential fire behavior depends on several factors including the type and quantity of fuel, fuel moisture content, and fire weather conditions (Rothermel, 1983; Ryan and Reinhardt, 1988). To account for potential variability in fire behavior estimates, we ran simulations.
for three fire weather conditions: the 50th, 90th, and 98th percentile values of the energy release component (ERC) during the fire season (May 1–September 31) (Table A1). ERC is sensitive to variation in fuel moisture values and how they influence potential fire intensity. Temperature, wind speed, and fuel moistures for ERC percentiles were extracted using Fire Family Plus (Main et al., 1999) (Table A1). Daily ERC percentiles and weather variables from the nearby (20 km southwest, elevation 800 m) Cohasset remote automated weather station were used to derive potential fire behavior estimates. Surface fuel characteristics in each plot were estimated using photo-series (Bonsl and Schramel, 1981), and photo-series values were used by FMA to estimate a standard fuel model. Photo-series estimates were most similar to Timber Litter model 08 (TL08, Scott and Burgan, 2005), so this surface fuel model was used for estimating potential fire behavior in all plots (Table A2). A standard fuel model was used for potential fire behavior estimates rather than field measurements because standard fuel models have been calibrated with fire behavior under conditions similar to those used in this study. Canopy fuel variables were estimated by FMA from the diameters and crown ratios of trees in the tree list of each plot (van Wagner, 1993, 1977) (Table A2).

3. Results

3.1. Stand characteristics and development

3.1.1. Overstory trees

On average, tree density and basal area for ponderosa pine and black oak were similar (p > 0.1) in 2000 to 2016 (Table 1), but there were important demographic differences between species (Table 2). Ponderosa pine had higher rates of recruitment and lower rates of mortality than black oak (p < 0.05) over the study period. On average, the number of living stems (L alive) of ponderosa pine increased (3.7% yr⁻¹) while those of black oak decreased slightly (−0.01% yr⁻¹) (Table 2). As expected, ingrowth of both ponderosa pine and black oak were concentrated in the smallest size-classes (5–15, 15–25 cm, saplings) as saplings recruited into the tree size classes. Mortality was size-dependent and not evenly distributed among size-classes. Mortality rates for ponderosa pine were highest for small (5–15 cm) and large (100–120 cm) diameter trees. In contrast, mortality rates for black oak were highest for larger diameter trees (65–75 cm) (Fig. 2).

Basal area remained relatively stable due to limited overstory mortality and large increases in tree density (Table 3). On average, the rate of basal area increase (0.29% yr⁻¹) was higher for ponderosa pine than black oak (−0.79% yr⁻¹) and plots with the highest rates of basal area increase in ponderosa pine experienced the greatest rates of basal area loss for black oak (Table 3). Competition influenced tree mortality over the study period. Trees that died over the census period experienced greater competition as measured by the H index than those that survived to 2016 (H = 3.06 vs 2.01, p = 0.04), while surviving trees had similar levels of competition in 2000 and 2016 (H = 2.01 vs 1.97, p = 0.37).

3.1.2. Seedlings and saplings

From 2000 to 2016, the density of ponderosa pine seedlings and saplings increased (p < 0.1) while for black oak, seedlings decreased and sapling density did not change (p ≥ 0.1) (Table 1). In 2000, 87% of black oak regeneration was from seedling establishment rather than sprouts and this percentage decreased to 35% by 2016 suggesting lower survival of oak seedlings compared to oak sprouts.

3.2. Spatial patterns

3.2.1. Tree group characteristics and dynamics

The proportion of trees in group sizes at different inter-tree distances varied between 2000 and 2016. On average, the proportion of individual and small tree groups at inter-tree distances of 1–3 m declined, while those in medium tree groups increased, and the proportion of extra-large tree groups increased at all inter-tree distances (1–12 m) (Figs. 3 and 4). Average tree group size was 5.5 trees per group in 2000 and 9.2 trees in 2016. Maximum group size increased from 38 trees to 240 trees as post-fire regeneration grew into the tree size class. Although the proportion of group types changed over time at the 6-m inter-tree distance, the frequency of group types was statistically similar in both years (p = 0.77, Kolmorov-Smirnov two sample test) (Fig. 5). The average number of groups per plot was 18 ha⁻¹ (range 11–27 ha⁻¹) and 22 ha⁻¹ (range 15–30 ha⁻¹) in 2000 and 2016, respectively (Table A3).

The age range of trees varied with group size (Fig. 6). Using the criteria of ≤20 years of age between trees for an even-aged group, ~70% of small tree groups were even-aged while fewer medium (30%), and no large (0%) or extra-large tree groups (0%) were even-aged.

The global spatial statistic, Ripley’s L(r) revealed a significant pattern of clumping in all plots in 2000 and 2016; however, the scale and intensity of tree clumping differed among plots, by species, and by year. For plots 1, 3, and 6 the clump intensity for all trees and ponderosa pine trees increased from 2000 to 2016 (Fig. 7). For plots 2, 4, and 5 the intensity of clumping was similar but the scale of clumping was smaller in 2016. In plots with both species, black oak was more intensely clumped than ponderosa pine, except in plot 4.

Table 1

<table>
<thead>
<tr>
<th>Plot</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
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<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>Ponderosa pine</td>
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<td>12.64</td>
<td>28.20</td>
<td>27.47</td>
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<tr>
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<td>2.93</td>
<td>1.88</td>
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<tr>
<td>Seedlings (ha⁻¹)</td>
<td>Snags</td>
<td>82</td>
<td>410</td>
<td>103</td>
<td>106</td>
<td>65</td>
</tr>
<tr>
<td>Saplings (ha⁻¹)</td>
<td>Live</td>
<td>17</td>
<td>13</td>
<td>16</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>Average Shrub Cover (%)</td>
<td>5.1</td>
<td>16.4</td>
<td>21.2</td>
<td>34.9</td>
<td>19.0</td>
<td>37.1</td>
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<tr>
<td>Average Herb Cover (%)</td>
<td>43.3</td>
<td>22.9</td>
<td>24.4</td>
<td>11.2</td>
<td>27.6</td>
<td>30.4</td>
</tr>
</tbody>
</table>
3.2.2. Gap characteristics and dynamics

On average, the rate of gap filling from tree regeneration (1.44% yr⁻¹) and crown extension into gaps (1.05% yr⁻¹) exceeded rates of new gap creation (0.58% yr⁻¹).

Despite the higher rate of filling, there was no difference in the frequency distribution and sizes of gaps in 2000 and 2016 (p > 0.05) (Figs. 3 and 8); however, total gap area (> 9 m from tree was greater between the two times (p = 0.07) than in 2000.

3.2.3. Gap characteristics and regeneration dynamics

Area occupied by regeneration increased between 2000 and 2016 (Fig. 9) and this was mainly due to the increase of ponderosa pine. There was a decline in area occupied by black oak regeneration (Table 1). In 2016, both ponderosa pine and black oak seedlings were more abundant beneath canopy gaps (< 33% cover) than in either intermediate or closed canopy conditions (p < 0.05, Kruskal Wallis H-test). The same pattern was observed for ponderosa pine, but not black oak saplings.

3.3. Potential fire behavior

Fire behavior modeling predicted potential flame lengths < 1 m under all weather conditions (Table 4). Plots with passive crown fire and the highest flame lengths had the highest density of small diameter trees (< 15 cm dbh). Average probability of mortality was highest (100%) for saplings (< 5 cm dbh, > 1.4 m tall) and lowest (1.1%) for large trees (> 30 cm dbh) (Table 4). The low probability of mortality and low crown scorch (11%) for large trees, even under extreme weather conditions, masks species differences – the probability of top-kill was higher for black oak (21.5%) than ponderosa pine (7.3%).

4. Discussion

4.1. Stand characteristics

Repeat low- and moderate-severity wildfires in the Beaver Creek Pinery in the 20th century preserved and reinforced a tree group and gap structure. Fires in 1901 and 1924 were recorded by fire scars throughout the Beaver Creek Pinery and the presence of 80–250 year old trees in each plot suggest these fires were low to moderate in severity (Taylor, 2010). After a 66 year period without fire, the Beaver Creek Pinery burned again in 1990 and 1994. Six years after the last fire, the forest was comprised of tree groups of different sizes consisting of mainly intermediate and large diameter trees, interspersed with gaps. Live tree density and basal area after the fires averaged 126 trees ha⁻¹ and 26.3 m² ha⁻¹. These values fell within the range of values for tree

Table 2
Number of living trees (stems ≥ 5 cm) on each census date and the rate (%) of mortality and recruitment over the study period (2000 to 2016).

<table>
<thead>
<tr>
<th>Plot</th>
<th>1</th>
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<td>83</td>
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<td></td>
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Fig. 2. Diameter class distribution (bars) of all non-surviving trees in six 1 ha plots in 2016 and size-specific mortality rates (lines) for ponderosa pine (dark green) and California black oak (light green) trees (≥ 5 cm) that died during the study period (2000–2016). Mid-point values for each 10 cm class are shown on the x-axis.
density (48–315 trees ha$^{-1}$) and basal area (16–53.9 m$^2$ ha$^{-1}$) recorded from historic and contemporary reference forests in California (Scholl and Taylor, 2010; Stephens et al., 2015; Taylor et al., 2014), Oregon (Flagmann et al., 2013) and pine-oak forests in the southwest (52–166 trees ha$^{-1}$, 8.0–17.6 m$^2$ ha$^{-1}$) (Fulé et al., 2002; Moore et al., 2004; Rodman et al., 2017). Twenty-two years after the last fire, average tree density (226 trees ha$^{-1}$) and basal area (27.5 m$^2$ ha$^{-1}$) were still within the range of reference forest values indicating that wildfires in the Beaver Creek Pinery maintained conditions similar to forests before fire suppression (Oliver, 2001; Skinner et al., 2018b). In contrast, current density and basal area in the Beaver Creek Pinery are at, or below, the average density (343–757 trees ha$^{-1}$) and basal area (27.2–69.9 m$^2$ ha$^{-1}$) of living trees in other conifer and pine-oak forests that have not burned since the late 19th or early 20th century or historical reference stands (Collins et al., 2011; Knapp et al., 2013; North et al., 2007; Taylor et al., 2014). This reduced density and basal area is

<table>
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<td>25.7</td>
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<td>16.0</td>
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<td>0.66</td>
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<td>0.09</td>
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<td><em>Quercus kelloggii</em></td>
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<td>2.88</td>
<td>1.00</td>
<td>2.05</td>
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<td>0.51</td>
<td>1.91</td>
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<tr>
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<td>0.35</td>
<td>0.19</td>
<td>1.46</td>
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<tr>
<td>$\lambda_{BA}$ (% year$^{-1}$)</td>
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<td>0.95</td>
<td>−0.4</td>
<td>−2.21</td>
<td>−3.06</td>
<td>−0.43</td>
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</tbody>
</table>

Table 3

Basal area (m$^2$ ha$^{-1}$) of living trees (stems ≥ 5 cm) on each census date and the rate of basal area loss (from mortality) and gain (from growth and recruitment) over the study period.

Fig. 3. Maps of tree groups and canopy gaps in 2000 (top row) and 2016 (bottom row) in six 1 ha stem map plots in the Beaver Creek Pinery. Background shading indicates the distance to the nearest tree (empty space function) and regions > 9 m away from any tree are outlined. Darker green circles represent ponderosa pine and light green circles California black oak.
likely the direct result of multiple recent fires.

Post-fire forest development reveals different demographic responses by ponderosa pine and black oak. Fires initially promoted black oak regeneration from seed and via sprouting, a pattern observed for black oak after other fires (Crotteau et al., 2013). By 2016, many post-fire sprouts had grown into small trees while seedlings that established from seed decreased by ∼75%, and the number and area occupied by black oak seedlings declined over the census period. Post-fire height growth rates of black oak sprouts are high, and faster than height growth rates of conifers, providing an initial advantage to oaks in early stand development under open conditions (Crotteau et al., 2013; Hammett et al., 2017; Nemens et al., 2018). In contrast, there was a large increase in ponderosa pine regeneration by 2016, with seedlings five-fold and saplings 200-fold more abundant than in 2000. Average annual percentage population growth rates for ponderosa pine were also three-fold higher than for black oak. Ponderosa pine basal area also increased over the study period, while black oak basal area declined. Tree mortality rates for both species were size-dependent, a pattern identified for other conifer and deciduous forest species in temperate forests in North America and East Asia (Canham and Murphy, 2017; Nakashizuka et al., 2000; Runkle, 2000; Taylor et al., 2004; van Mantgem et al., 2009). Size-dependent mortality in these forests appears to be related to competitive effects from neighboring trees. Tree mortality rates were higher for focal trees at closer distances to other trees and for the smallest and largest diameter stems. Other mortality agents such as insects and pathogens, and warming temperatures may have contributed to the higher rates in these size-classes though specific causes of tree death were not determined. The overall demographic response since the wildfires has been a strong increase in ponderosa pine and a small decline in black oak, leading to greater dominance by ponderosa pine.

The post-fire demographic responses of ponderosa pine and black oak in the Beaver Creek Pinyon are consistent with longer term compositional shifts observed in mixed stands that have not burned for several decades or even a century (Cocking et al., 2014, 2012). Shade tolerant, fire-intolerant and fast growing conifers such as Douglas-fir (Pseudotsuga menziesii), white fir (Abies concolor), and incense-cedar (Calocedrus decurrens) have established abundantly in black oak woodlands and mixed pine-oak forests during long fire-free periods and these species can overtop and replace black oak (Cocking et al., 2014, 2012; Hammett et al., 2017). Re-entry burns after long periods of fire suppression can have highly variable effects on pine-oak regeneration and dominance. Higher severity fires reduce conifer dominance and stimulate black oak regeneration through resprouting and new establishment (Cocking et al., 2014, 2012), and there is high survival of black oak sprouts after top kill in high-severity burns (Hammett et al., 2017; Nemens et al., 2018). Compositional shifts leading to increased dominance of oaks has been observed in burns and reburns of moderate- and high-severity in California, the southwest and northern Mexico and is characteristic of sprouting species in mixed pine-oak forests (Barton and Poulos, 2018; Cocking et al., 2014, 2012; Fulé et al., 2000). Shifts in relative dominance are more muted after low-severity fire (Cocking et al., 2014) and response patterns in the Beaver Creek Pinyon were consistent with a low-severity fire pattern. Yet, the robust post-fire demographic response of ponderosa pine suggests that more frequent (< 22-year intervals) low-severity fires may be necessary to retain black oak in these old-growth stands by reducing ponderosa pine establishment.

Fig. 4. Mean proportion of trees (stems ≥ 5 cm dbh) in different tree group sizes at 1–12 m intertree distances for six ~ 1 ha plots in the Beaver Creek Pinery. Data shown in this figure are reported in Table A3.

Fig. 5. Pooled frequency of individual, small, medium, large, and extra-large tree groups in 2000 (left panel) and 2016 (right panel) at a 6 m intertree distance.
4.2. Spatial patterns and dynamics

A spatial structure comprised of individual trees, tree groups, and canopy gaps is a hallmark of historical reference conditions in frequent-fire ponderosa pine and pine-oak forests. The two low-moderate severity wildfires in the Beaver Creek Pinyon in the 1990s re-enforced a tree group and gap structure generated by the 1924 and earlier fires that has some characteristics similar to reference forests despite forest changes caused by decades of fire suppression. The average (global) spatial pattern of trees in the Beaver Creek Pinyon was clumping at scales < 0.4 ha with local variability in clump size, a spatial structure identified in other frequent-fire old-growth pine-oak and pine-dominated forests in the western United States (Fry et al., 2014; Larson and Churchill, 2012; Taylor, 2004; White, 1985).

4.2.1. Group and gap characteristics

Average tree group size in the Beaver Creek Pinyon was similar to historic and contemporary reference conditions, but maximum tree group size was larger (Beaver Creek Pinyon = 38–240 trees group$^{-1}$). Maximum values for trees group$^{-1}$ were only 40 in the eastern Cascades (Churchill et al., 2017, 2013), 25 in the southwest (Abella and Denton, 2009; Sánchez Meador et al., 2011), and 26 in the Rocky Mountains (Brown et al., 2015). Moreover, compared to the Beaver Creek Pinyon, proportions of trees in large (10–15) and extra-large (≥16 trees) groups at a 6-m inter-tree distance was also smaller (e.g. Churchill et al., 2017; Larson and Churchill, 2012; Sánchez Meador et al., 2011). Some of these differences among studies could be related to variation in the minimum tree size cutoff.

Site productivity and fire frequency may explain the high maximum trees group$^{-1}$ in the Beaver Creek Pinyon (Churchill et al., 2017; Clyatt et al., 2016; Lydersen et al., 2013). Frequent-fire forests growing on highly productive sites tend to support higher tree density and basal area, and larger tree groups than on less productive sites (Churchill et al., 2017). Soil type (Cohasst Loam), rapid height-gain, and basal area gain rates in the Beaver Creek Pinyon between 2000 and 2016 indicate the site is productive. Fire suppression effects on stand structure would also contribute to high tree density in the extra-large tree group.

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Canopy cover increased after 22-years of post-fire forest development, with gap creation rates lower than rates of infilling and canopy extension. Gap areas in the Beaver Creek Pinyon decreased slightly from 2000 to 2016 and infilling of gaps by trees was evident, causing fragmentation of large gaps (> 600 m$^2$) into smaller gaps (< 600 m$^2$) (e.g. Fig. 3, plot 1, 6; Fig. 8). Nevertheless, gaps in the Beaver Creek Pinyon were larger compared to frequent-fire forests that have experienced a century or more of fire suppression, Forests that have not burned for a century or more have mainly small gaps (< 250 m$^2$) and more continuous forest cover because gaps have been filled by trees (Fry et al., 2014; Lydersen et al., 2013; Skinner, 1995).

Creating and maintaining a diverse pattern of canopy gaps and tree groups in both relatively even-aged, single cohort stands and un-even aged stands with few older trees remaining, can create natural fuel breaks that reduce fire risk, thin out undesirable overstory species, promote understory diversity, and over time create a more heterogeneous age-structure (Churchill et al., 2013). In many western forests, particularly those impacted by past management and fire-suppression, active forest management is needed to restore or promote structural heterogeneity. In these cases, the values reported here and in the supplemental information for a contemporary ponderosa pine-black oak reference site can assist managers in identifying specific thresholds for the size and frequency of tree groups and canopy gaps. The results of our study also suggest that, once stand structure is restored, multiple, successive low-moderate severity fires can be used to maintain heterogeneity and resiliency.

The age of trees in tree groups provides insights into pattern-process relationships and mechanisms of group development. Trees were more likely to be even-aged in small groups (2–4 trees) and uneven-aged in larger groups (≥5 trees). These results support findings by White (1985), and spatial analyses of tree ages in other forests that show large tree groups consisting of overlapping groups of even-aged trees (Beaty and Taylor, 2007; Scholl and Taylor, 2010). In frequent-fire forests, even-age groups of seedlings often establish on bare mineral soil where
overstory tree(s) have been killed by fire (Cooper, 1961, 1960). Partial seedling and sapling mortality in subsequent fires and additional recruitment would create large uneven-aged tree groups comprised of small even-aged groups (Beaty and Taylor, 2007; Scholl and Taylor, 2010). Interestingly, half of the extra-large (≥16 trees) tree groups in the Beaver Creek Pinery had a majority of trees in a single 20-year age class that established after 1920. This is likely related to the relatively large numbers of trees that established during the 1924 to 1990 fire-free period near pre-existing individual trees creating large uneven-aged groups with a high percentage of trees in a single age-class.

4.3. Potential fire behavior

Twenty-two years after the wildfires, fuels and vegetation in the plots were predicted to support low-severity fire under moderate and extreme weather conditions. Surface and canopy fuel loads in 2016 were still moderate, and only saplings and small trees (<30 cm dbh) had high probabilities of mortality; large trees (>30 cm dbh) were fire-resistant under modeled fire behavior. The low-moderate fire severity effects predicted for the Beaver Creek Pinery are consistent with potential fire behavior predicted for pine dominated frequent-fire forests in the western US before fire exclusion (Hessburg et al., 2005; Taylor et al., 2014; Van de Water and North, 2011) and demonstrates a relatively long-lasting effect of wildfire on forest structures that influence potential fire behavior. This suggests that if managers initially invest time and resources towards restoring heterogenous structure, these restored forests may retain resilience to fire for an extended period of time, thereby extending the maintenance interval of these sites beyond historical fire frequencies. If management generated a similar degree of heterogeneity across a greater proportion of historically frequent-fire
western forests wildfire, burning under moderate weather conditions may become a more feasible management strategy for more than just unharvested forests in remote wilderness areas (Larson et al., 2013, North et al., 2012; Calkin et al., 2015).

4.4. Conclusions

At present, forest conditions within the Beaver Creek Pinery plots are within the historical range of variability for frequent-fire forests in the western U.S. These conditions have been created and reinforced by repeated wildfires that occurred in the recent past and earlier in the 20th century. The fire effects experienced in the Beaver Creek Pinery were, in part, be due to the particular weather and fuel moisture conditions, as well as the heterogeneous stand structure present at the time of these wildfires. Our results support a perspective that wildfire can maintain and restore resiliency by preserving latent structure (such as legacy trees and canopy openings) in forests with relatively limited anthropogenic disturbances (Larson et al., 2013). Old-growth forest structures were resilient to fire despite nearly 70 years of fire exclusion; once restored, a tree group and gap forest structure will likely persist for an extended period following the last wildfire. Modeling of potential fire behavior for a fire that may occur in the near future also suggests that large, old, overstory trees are currently resilient to fire but seedlings, saplings and small diameter trees would be killed. Maintaining relatively frequent and variable fire intervals into the future with wildfire or prescribed fire, in this Wilderness and elsewhere, will be needed to reduce the demographic pressure of ponderosa pine, promote black oak, and to maintain and create future spatial heterogeneity in vegetation and fuels (Ryan et al., 2013). Cumulatively, this research demonstrates that wildland fires, under certain conditions, can maintain and restore fire resilience in unmanaged ponderosa pine and pine-oak forests and reduce the negative ecological consequences associated

Fig. 8. Pooled frequency of gap sizes in 2000 (white) and 2016 (black) for six ~1 ha stem map plots in the Beaver Creek Pinery.

Fig. 9. Maps of regeneration density for both ponderosa pine and California black oak seedlings and saplings in 2000 (top row) and 2016 (bottom row) in six ~1 ha stem map plots in the Beaver Creek Pinery. Darker shading represents higher density of regeneration. Overstory tree groups are gray and partially transparent.
Table 4
Potential fire behavior and fire effects for saplings (< 5 cm dbh, > 1.4 m tall), small trees (5–30 cm dbh), and large trees (> 30 cm dbh) under different weather conditions in six ~ 1 ha plots in the Beaver Creek Pinyon. Surface fuels in each plot were constant (TL08, Scott & Burgan 2005) in all simulations.

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<tr>
<td>Crown</td>
<td>Passive</td>
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<td>Crown</td>
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<td>Crown</td>
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<td>Average Probability of Mortality (%)</td>
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<td>Small Trees (5–30 cm)</td>
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<td>3</td>
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<td>81.2</td>
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<td>82.8</td>
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<tr>
<td>3</td>
<td>84.9</td>
<td>85.4</td>
<td>86.4</td>
</tr>
<tr>
<td>Large Trees (&gt; 30 cm)</td>
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<td>2</td>
<td>3</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>2</td>
<td>0</td>
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<tr>
<td>3</td>
<td>0.1</td>
<td>0.3</td>
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<tr>
<td>Crown Scorch (%)</td>
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<tr>
<td>Saplings (&lt; 5 cm, &gt; 1.4 m)</td>
<td>1</td>
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</tr>
<tr>
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<td>100</td>
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</tr>
<tr>
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</tr>
<tr>
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<tr>
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<tr>
<td>Large Trees (&gt; 30 cm)</td>
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<td>3</td>
</tr>
<tr>
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<td>10.9</td>
</tr>
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<td>9.1</td>
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<tr>
<td>3</td>
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<td>13.7</td>
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| with past fire exclusion (Franklin and Johnson, 2012; Naficy et al., 2016; North et al., 2012; Taylor et al., 2016).

Acknowledgements
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Appendix A. Supplementary material
Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.016.

References


van de Water, K., North, M., 2011. Stand structure, fuel loads, and fire behavior in riparian and upland forests, Sierra Nevada Mountains, USA; a comparison of current and reconstructed conditions. For. Ecol. Manage. 262, 215–228.


