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**POST-FIRE FOREST SUCCESSION, GROUP-GAP DYNAMICS, AND
IMPLICATIONS FOR FIRE RESILIENCE IN AN OLD GROWTH PINUS
PONDEROSA FOREST**

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by

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ABSTRACT

This research quantifies forest structure and examines how post-fire succession alters pine-oak composition, group-gap spatial structure, and wildfire resilience in an old-growth ponderosa pine (*Pinus ponderosa*) forest that was resilient to recent wildfires and exhibits a heterogeneous forest structure thought to be similar to forests before fire exclusion. To quantify forest structure and spatial patterns, trees were aged, mapped, and measured in the year 2000 – six-years after a wildfire – and in 2016 – 22-years post-fire – in six, 1-hectare, stem map plots in the Beaver Creek Pinery, located in the Ishi Wilderness, Southern Cascades, California. Regeneration – seedlings and saplings – were tallied in 10x10m cells. Rates of tree recruitment, mortality, and growth for the site’s two co-dominant species – ponderosa pine and California black oak (*Quercus kelloggii*) were estimated using demographic models. Local patterns in group structure was quantified using spatial clump algorithms and gap area was quantified using the empty space function. Potential fire behavior and effects were modeled for a range of fuel and weather conditions.

Stand density and basal area in both 2000 and 2016 were within the historical range of variability for pre-fire exclusion ponderosa pine forests. Initially, wildfire promoted California black oak; however, oak abundance and regeneration has declined while pine abundance and regeneration has increased in the subsequent 22 years without fire. In 2000, ~15% of trees were classified as individuals and tree group sizes ranged from 2 to 75 trees. Small tree groups (2-4 trees) consist of similar-aged trees while larger groups are multi-aged. In 2016, the percent of trees classified as individuals decreased by ~30%, and the scale and intensity of clustering increased. The greatest change in spatial patterns occurred in plots with the highest rates of post-fire recruitment. The size and frequency of canopy gaps was similar in 2000 and 2016; however, higher densities of seedlings and saplings were associated with canopy gaps in 2016 which suggests, without future fire, canopy gaps will be infilled. Fire behavior models indicate the Beaver Creek Pinery is still resilient to high severity wildfire. Overall, this research broadens our understanding on the persistent effects of fire on spatial heterogeneity and demonstrates that wildfires can be used to restore resiliency to forests where wildfires have been suppressed for nearly a century.

Keywords: Forest Structure, Group-Gap, Forest Development, Wildfire Resilience, *Pinus ponderosa*, *Quercus kelloggii*

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CHAPTER 1 – Introduction

Historically, fire-frequent forests were characterized by a heterogeneous, group-gap structure. In *Pinus ponderosa* (ponderosa pine) forests, this structure was maintained by complex interactions between fire-generated mortality, seedling establishment, and post-fire survival (Cooper 1961, White 1985, Stephens & Fry 2005). Following wildfire and a good seed crop, dense patches of seedlings establish in canopy gaps with exposed mineral soil and open to intermediate light availability (Cooper 1961, Bonnet et al. 2005). These seedling patches are protected from subsequent wildfire since seedlings produce little surface fuels. However, as the seedlings grow into saplings and small trees, a flammable layer that can carry a surface fire develops. When a surface fire passes through, the smaller trees in patches are less likely to survive, leaving behind a group of evenly aged trees or a single individual (Cooper 1960, 1961). Over time, an overstory group can remain static, can increase in size and become multi-aged when crowns expand into adjacent groups or new trees establish near the existing group, can devolve into a single, fire-resilient, individual, or overstory tree groups can disappear when all individuals of the group die due to a disturbance. Therefore, at any one time, a stand consists of a mosaic of dense regeneration patches, groups of even/uneven aged overstory trees, widely spaced individual trees, and un-occupied canopy openings (Cooper 1960, White 1985, Churchill et al. 2013). This group-gap spatial structure promotes a diverse mosaic of understory plant cover (Dodson et al. 2008, North et al. 2005) and provides a variety of habitats that support a diverse assemblage of bird and small mammal species (Buchanan et al. 2003, Latif et al. 2015). It also promotes resilience – gaps inhibit the spread of intense surface or crown fires (Beaty & Taylor 2007, Stephens et al. 2010) and impede insect outbreaks by disrupting pheromone plumes (Fettig et al. 2007), and the diversity of structural components results in heterogeneous fuel conditions that can provide safe sites for tree regeneration (Fry & Stephens 2010, Fry et al. 2014).

In addition to creating this group-gap structure, frequent wildfire promoted oaks (*Quercus* spp) as an important associate species in *P. ponderosa* forests. In western dry forests, *Quercus kelloggii* (California black oak) provides forage and nesting habitat for wildlife and is culturally valued by local Native American tribes (Anderson 2005, Purcell

et al. 2008, 2009; Long et al. 2016ab). Both *P. ponderosa* and *Q. kelloggii* are adapted to wildfire; however, they have different life history characteristics that influence their response to fire. In forests adapted to frequent, low to moderate severity fire, *P. ponderosa* is “fire-resistant” while *Q. kelloggii* is “fire-resilient” (Barton 1999, 2008). *Pinus ponderosa* regeneration – seedlings and saplings – has thin bark and is highly prone to fire damage; however, over time, *P. ponderosa* individuals exhibit positive bark allometry and as they age, they develop thicker, fire-resistant bark which allows *P. ponderosa* to survive (“resist”) frequent fire. While *Q. kelloggii* also exhibits positive bark allometry, they typically have thinner bark than *P. ponderosa* at both sapling and adult life-stages (Jackson et al. 1999). Consequently, *Q. kelloggii* is more susceptible to damage from wildfire; however, *Q. kelloggii* is resilient following disturbance as it can resprout after being top-killed (McDonald 1969, Barton 1999, 2002, Fulé et al. 2000, Hammett et al. 2017). Maintenance of a mixture of pine and oak within a stand is thought to increase forest resilience to fire (Skinner 1995, Knapp et al. 2009). *Quercus kelloggii* litter is highly flammable and promotes low intensity, surface fire (Engber & Varner 2012). As *Q. kelloggii* go dormant, they allow sunlight to dry fuels in the fall and winter. In turn, fires can occur later into the season, which shortens the fire-free interval in which fuels can accumulate (Knapp 2009); additionally, having areas of dry fuels under dormant oaks and shaded areas that are too wet to burn under pines creates a fine-scale fuel mosaic that, after fire, leaves behind safe places for regeneration (Stephens & Fry 2010, Knapp et al. 2009). Further, the absence of leaves on oaks during fall and winter permits heat from fires to dissipate and lowers the potential for crown scorch (Skinner 1995). Finally, *Q. kelloggii* crowns within mixed stands break up crown fuel continuity compared to conifer-only stands and therefore reduce potential for crown fire (Skinner et al. 2006).

The group-gap structure of *P. ponderosa* forests that developed with frequent fire was dramatically altered following Euro-American settlement in the 19th century (Covington et al. 1994, Skinner 1995, Taylor 2004, Collins et al. 2011, Lyderson et al. 2013, Fry et al. 2014). Logging, grazing, and especially fire exclusion led to a large increase in tree density and forest canopy cover, infilling of gaps with trees, and an

accumulation of both surface and canopy fuel (Scholl & Taylor 2010, Knapp et al. 2013). In logged areas, the largest, most fire-resistant, trees were often removed (Laudenslayer et al. 1989; Naficy et al. 2010) leading to dense forests of intermediate and smaller sized trees. Moreover, the absence of fire disturbance has shifted the proportional abundance of conifers and hardwoods in mixed forests towards conifers (McDonald & Tappeiner 2002, Cocking et al. 2012, 2014). Consequently, fire exclusion, logging, and other land use changes have replaced historical group-gap structure that was once resilient to climatic variation, insects and disease outbreaks, and wildfire with contemporary forest structures that are prone to high severity fire, insect attacks and drought-induced tree mortality (Stephens et al. 2008).

Reintroducing fire to restore a heterogeneous structure within the historical range of variability has been advocated for many fire-suppressed forests in the western United States to reduce their susceptibility to severe wildfire and promote forest health and ecosystem services (Allen et al. 2002, North et al. 2009, Webster and Halpern 2010, Franklin & Johnson 2012). Yet, fire suppression policies and land use practices that have dramatically altered western dry forest structure are pervasive across the western landscape and millions of acres are in need of restoration. As such, the area in need of restoration exceeds the current capacity of prescribed burn programs (North et al. 2012; Ryan et al. 2013); further, prescribed burning cannot be implemented in remote and wilderness areas, is difficult to implement at landscape scales, and is seasonally-restricted to mild weather conditions (Knapp et al. 2009, North et al. 2009). Therefore, managing naturally ignited wildfires has been proposed as a means of restoring remote and large tracts of fire suppressed forests (Naficy et al. 2010, North et al. 2012, Larson et al. 2013). Since fire-frequent forest structure can be maintained by a negative feedback with wildfire (whereby, fires consume fuels and limit subsequent fire severity) (Agee 2005, McKenzie et al. 2011), un-logged, fire-excluded forests are thought to possess a latent resilience to reintroduced fire (Naficy et al. 2010, Larson et al. 2013). For example, Larson et al. 2013 provide empirical evidence which shows that two wildfires – in 2000 and 2011 – restored stand conditions to within the historical range of variability for ~115 hectares of unlogged, fire-excluded *P. ponderosa* forest in Bob Marshall Wilderness,

Montana. At a landscape scale, reintroduction of fire to restore historical-like conditions has been successful in some contemporary forests with restored fire regimes and limited anthropogenic disturbance (Collins et al. 2009, Lydersen & North 2012, Parks et al. 2014, Harris & Taylor 2015, Estes et al. 2017). Yet, there is increasing concern and mounting evidence that forest structure has been so dramatically changed, reintroducing wildfire into these structurally-altered forests could exacerbate the problem (Thompson & Spies 2010, Crotteau et al. 2013, Coppoletta et al. 2016, Harris & Taylor 2017). Reintroducing fire into previously harvested/grazed, fire suppressed forests can create a positive feedback where an initial high severity wildfire, due to the over-accumulation of fuel or increasingly extreme weather conditions from climate change, leads to high severity reburns and a shift into an alternative state, such as a forest to shrubland conversion (Coppoletta et al. 2016; Harris et al. 2017). Active management – such as prescribed burning or mechanical thinning – in more anthropogenically-disturbed, fire-suppressed areas can help restore a negative feedback and might be needed before re-introducing wildland fire back on the western landscape (Ritchie et al. 2007; Harris et al. 2017). However, contemporary reference sites that can guide such active management are rare (Stephens & Fulé 2005; Larson et al. 2013). These sites are valuable, however, since they allow for quantitative measures of forest structure (Barbour et al. 2002) and provide important insights into healthy ecosystem processes (Binkley et al. 2007; Stephens et al. 2008).

Here, we quantify the group-gap structure in an old-growth *P. ponderosa* forest that was resilient to recent wildfires and exhibits a heterogeneous forest structure thought to be similar to forests before fire exclusion. We also determine how stand development influences structural heterogeneity and potential fire behavior to understand the consequences of post-fire structural changes on the forest's potential resilience to future wildfire. Specifically, objectives of this research were to:

- 1) Characterize forest development and population dynamics for *P. ponderosa* and *Q. kelloggii* in an old growth forest
- 2) Quantify the spatial arrangement of tree groups and canopy gaps and how they have changed post-fire

- 3) Determine if within-group age structure of supports an even-aged group model of stand development (Cooper 1960, White 1985)
- 4) Identify the relationship between canopy cover and tree regeneration abundance
- 5) Estimate potential fire behavior after 22 years of post-fire succession

This research broadens our understanding on the persistent effects of fire on spatial heterogeneity and provides spatially-explicit structural information to guide management efforts to restore resiliency in forests where wildfires have been suppressed for nearly a century.

CHAPTER 2. – Study Area

Post-fire forest development in old-growth *P. ponderosa*-*Q. kelloggii* forests was studied in the Beaver Creek Pinery (BCP) in the Ishi Wilderness within Lassen National Forest, in the southern Cascades, California (Figure 2.1).

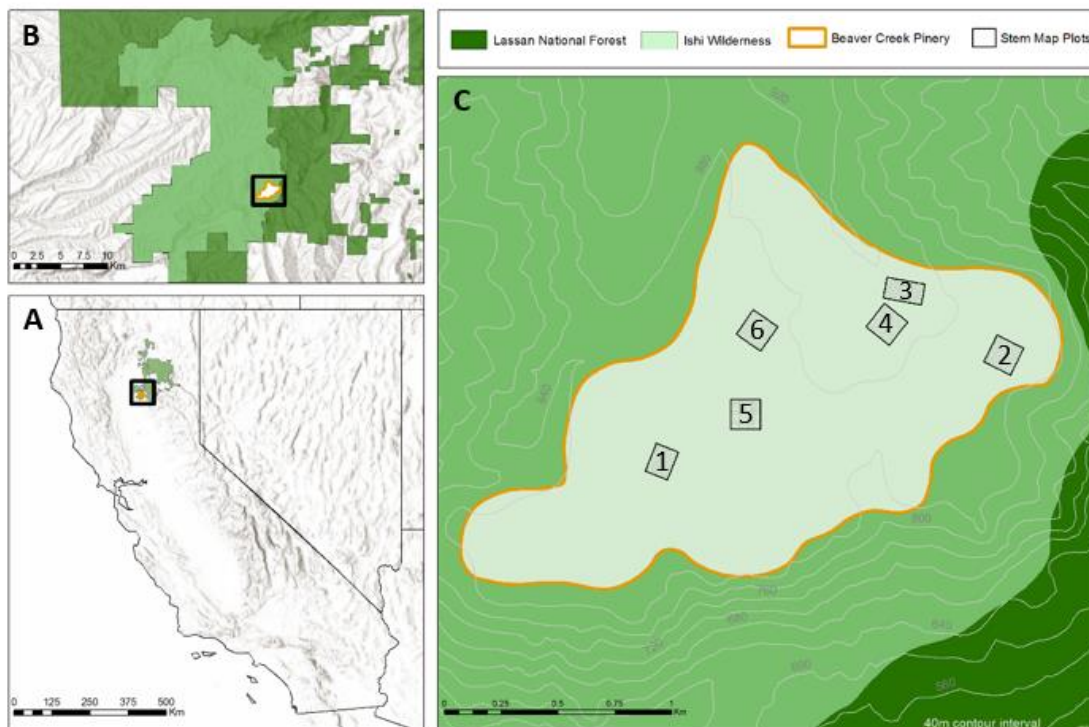


Figure 2.1. Location of the Beaver Creek Pinery in northern California (A), in the Ishi Wilderness, within Lassen National Forest (B), and the location of the six stem map plots measured in 2000 and 2016 (C)

BCP is ~100 ha in size and is located on a plateau at an elevation of ~850 meters. Two tree species, *Pinus ponderosa* (ponderosa pine) and *Quercus kelloggii* (California black oak), are the canopy dominants. Common understory species include *Ceanothus prostratus*, *C. lemmonii*, *Mahonia aquifolium*, *Stipa lemmonii*, and *Carex multicaulis*. BCP is underlain by Cohasset gravelly loam soil (USDA Web Soil Survey) and the average annual temperature and precipitation in Cohasset (800m elevation and 20km southwest) is 16°C and 145 cm, respectively (www.ncdc.noaa.gov). Most precipitation occurs between October – April. The Yana (Yahi) tribe lived in the region for 3,000 years prior to European settlement in the 19th century and the last member of the tribe surviving in the wild emerged from the area in 1911 (Schulz 1954). The Yana used fire to maintain

browse habitat for game species and to promote plant growth for food and fiber (Schulz 1954, Elsasser 1981, Anderson 1996, 2005). In particular, prescribed fires were set to promote *Quercus* growth and acorn production (Elsasser 1981, Anderson 2006). BCP has no history of logging, and fires have not been as uniformly suppressed due to rugged terrain and designation as Wilderness, as compared to other areas in the Lassen National Forest (Taylor 2010).

Fire was a frequent disturbance in BCP and the mean and median composite fire return interval for the BCP forest, identified using fire scar dendrochronology, are 16 and 12 years, respectively, and most burns occurred late in the growing season (Taylor 2010). In the 20th century, the BCP experienced five wildfires, the most recent being in 1990 (Campbell) and 1994 (Barkley) (www.mtbs.gov, Figure 2.2).

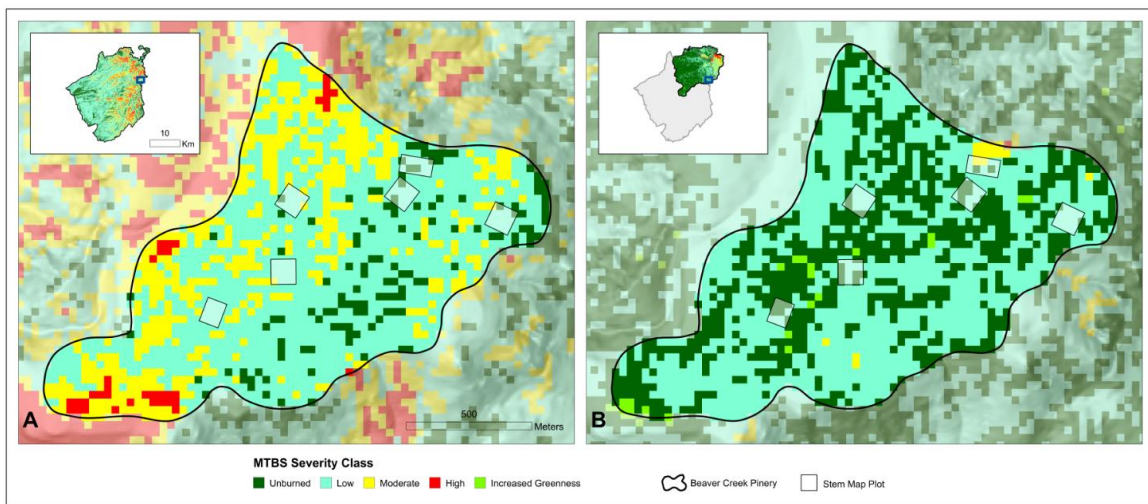


Figure 2.2. Severity of the 1990 Campbell fire (A) and 1994 Barkley fire (B) in the Beaver Creek Pinery, as measured using relative normalized burn ratio (rNBR) from the Monitoring Trends in Burn Severity

Despite burning in hot conditions (Campbell ignition date: Aug 06, 1990, 43.9°C maximum temperature, 11% mean min relative humidity; Barkley ignition date: Sept 18, 1994, 36.1°C maximum temperature, 13% mean min relative humidity), the Campbell and Barkley fires burnt through BCP with low and moderate severity (Figure 2.2). These fires killed groups of smaller diameter trees to create canopy gaps and shift tree diameter distributions towards larger diameter trees (Appendix Figure 1); surviving trees in the overstory were aggregated in similar aged groups at scales $< 225\text{m}^2$, which resulted in an uneven age structure at larger spatial scales (Taylor 2010).

CHAPTER 3 – Methods

Field Sampling

Old growth *P. ponderosa* forests were initially sampled six years post-fire (2000) in six ~1 ha plots (Figure 2.1). Plot locations were selected based on the presence of large diameter trees (>100 cm dbh), homogeneous site conditions, and stand characteristics which represent a range of post-fire structural conditions. Forest change since 2000 was identified by resampling the plots in June 2016, 22 years post-fire.

In each plot, the stem location (x,y) of each tree (≥ 5 cm dbh) was mapped and saplings (<5cm dbh and >1.4 m tall) and seedlings (0.2-1.4m tall) were counted in 10x10m cells. The diameter (dbh) of each tree was measured and classified by relative height class – emergent, dominant, co-dominant, intermediate, or suppressed. Canopy cover was estimated above each 10x10m cell by cover class (open 0-33% canopy, intermediate 33-66%, and closed >66%) and ground cover of shrubs, forbs, and grasses was also estimated in each cell by cover classes (0%, <1%, 1-5%, 5-25%, 25-50%, 50-75%, and 75-100%). In 2000, all living overstory trees were cored; cores were cross-dated and trees were aged to the innermost tree ring that hit the pith (Taylor 2010).

Demography

To characterize stand development and population dynamics between 2000 and 2016, rates of recruitment, mortality, and loss/gain of basal area were estimated for the two co-dominants in BCP: *P. ponderosa* and *Q. kelloggii*. Recruitment and mortality were estimated using a logarithmic model (Condit et al. 1995, 1999):

$$\text{mortality rate (\% year}^{-1}\text{)} = \frac{\text{Ln}(N_b) - \text{Ln}(N_s)}{t} \times 100$$

$$\text{recruitment rate (\% year}^{-1}\text{)} = \frac{\text{Ln}(N_e) - \text{Ln}(N_s)}{t} \times 100$$

Where N_b , N_e , and N_s are the number of trees alive at the beginning of the study, total number of trees living at the end of the study, and the number surviving to the end of the census period, respectively; t is the time interval (16 years).

Basal area (BA) lost or gained in mortality and recruitment was identified using the following equations (Taylor et al. 2004):

$$BA \text{ loss rate } (\% \text{ year}^{-1}) = \frac{(BA_l / BA_b)}{t} \times 100$$

$$BA \text{ gain rate } (\% \text{ year}^{-1}) = \frac{((BA_r + BA_g) / BA_b)}{t} \times 100$$

Where BA_l , BA_b , BA_r and BA_g are the basal area values for trees dying during the census period, trees living at the beginning of the study, trees recruited during the census period, trees surviving through the census period, respectively.

Changes in the populations for trees and BA were inferred from the population growth rate (λ) (Condit et al. 1999) using data for 2000 (beginning of census period) and 2016 (end of census period):

$$\lambda_{trees} (\% \text{ year}^{-1}) = \frac{\ln(N_{2016}) - \ln(N_{2000})}{t} \times 100$$

$$\lambda_{BA} (\% \text{ year}^{-1}) = \frac{(BA_{2016} - BA_{2000}) / BA_{2000}}{t} \times 100$$

Where N and BA are the number of trees or the basal area of species at each time point.

To characterize competition, the H index (Hegyi 1974) was calculated for three populations – trees alive in 2000 that survive to 2016, trees alive in 2000 that did not survive to 2016, and trees alive in 2016 – using the following equation:

$$\sum_{j=1}^n \frac{D_j}{Dist_{ij}}$$

Where D_j is the diameter of the competitor, D_i is the diameter of the focal tree, and $Dist_{ij}$ is the distance between the focal tree and competitor tree. A competitor tree was defined as any tree within 12m of the focal tree. Competition indices six years post-fire, in 2000, for surviving and non-surviving trees were compared using a t-test; additionally, competition indices for living trees in 2000 and 2016 were compared using a paired t-test.

Spatial Patterns

I. Group Characteristics

To quantify group-gap structure of these forests and how it has changed post-fire, we characterized forest structure in both 2000 and 2016. To identify group characteristics, an intertree distance (d) based algorithm over a range of spatial scales (distances) was used. This algorithm assigns trees within a given radius $\leq d$ to the same cluster while trees at locations $> d$ are considered single tree clumps (Plotkin et al. 2002). Since edge effects have been shown to be minimal in identifying clumping patterns, an edge correction was not used (Plotkin et al. 2002; Yamada and Rogerson 2000; Churchill et al. 2013). We identified tree groups for intertree distances of 1-12m for five functional categories of clump (group) size in *P. ponderosa* 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). For both years, tree group frequency and size were characterized for an intertree distance of 6m since this distance corresponds with the average crown radius for trees in mature and old growth ponderosa pine forests (Abella & Denton 2009, Sánchez Meador et al. 2011, Churchill et al. 2013). Using this distance also permitted direct comparison of our results with other *P. ponderosa* forests in Oregon (Churchill et al. 2013, 2017), the southwest (Sánchez Meador et al. 2009, 2011, Abella & Denton 2009, Schneider et al. 2016) and the Rocky Mountains (Brown et al. 2015, Clyatt et al. 2016). Trees were also clustered using a second, crown diameter-based method to evaluate any differences in group-gap structure related to use of a standard crown radius (Sánchez Meador et al. 2011, Lydersen et al. 2013). Crown area in this analysis was estimated using diameter-crown width equations for *P. ponderosa* and *Q. kelloggii* (Keyser 2008) and trees with overlapping crowns were grouped together and summarized as described above.

To examine if stand development follows an even- or uneven-age model, age structure within trees groups in 2000 was quantified. Small ranges in tree ages within groups would support an even-aged model, whereby groups of trees establish episodically in canopy openings and a mosaic of even-aged patches is maintained by frequent fire (Cooper 1960, 1961); alternatively, a wide range in ages within a group would indicate an uneven structure whereby groups contain multiple age classes (White 1985). A 20-year

range in ages was used as the cutoff between even-aged (≤ 20 years) and un-even aged (> 20 years) groups to account for uncertainty in aging tree cores. The proportion of even and uneven aged groups was calculated for each clump size: small (2-4 trees), medium (5-9 trees), large (10-15 trees), and extra-large (≥ 16 trees).

In addition to quantifying spatial characteristics and changes using local spatial metrics, changes in the spatial characteristics of trees were also quantified using a global statistic, Ripley's K. Ripley's K is based on point pattern analysis and the standardized version, or L-function, was used to identify the type, scale, and intensity of pattern in tree populations 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, 2017). Spatial aggregation was assessed up to the 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 observed values of $L(r)$ above this envelope denote significant spatial clustering while values below signify a regular pattern. Analyses were conducted for six populations with a minimum size ≥ 15 trees: 1) all trees alive in 2000, 2) all *P. ponderosa* alive in 2000, 3) all *Q. kelloggii* alive in 2000, 4) all trees alive in 2016, 5) all *P. ponderosa* alive in 2016, and 6) all *Q. kelloggii* alive in 2016.

II. Gap Characteristics

To quantify gap characteristics (frequency, size) in 2000 and 2016, the empty space function, $F(t)$ was used to calculate the distances to nearest tree (Diggle 2013) from each cell in a 0.5 x 0.5m grid established in each plot. Distances were pooled in 3m classes to create a distribution of gap size and total open canopy area in 2000 and 2016. Differences in these distributions were tested using a Kolmogorov-Smirnov two sample test. A threshold distance of 9m from a tree stem, as suggested by Churchill et al. 2017 and Clyatt et al. 2016, was used to identify gaps, since this distance is beyond the influence of tree root systems and their mycorrhizae network (Simard et al. 2012), far enough beyond shade of the existing canopy to permit successful *P. ponderosa* regeneration and growth (York et al. 2004), and wide enough to inhibit the spread of active crown fire except under very extreme fire weather (Beaty & Taylor 2007; Stephens et al. 2010). In quantifying gap characteristics, we followed Clyatt et al. 2016 who

identify gaps as being $\geq 9\text{m}$ from the nearest tree and then buffered that area by 5m to account for extension of tree crowns into openings. Areas within 9m of the plot edge were also removed to prevent overestimation of gap area. Open area in each plot in 2000 and 2016 was calculated by subtracting tree crown area from plot area. Mean gap size in 2000 and 2016 and mean open area in 2000 and 2016 were compared using separate paired t-tests.

To characterize gap dynamics from 2000 to 2016, the rate of crown extension from the overstory, gap infilling from tree regeneration, and gap creation from tree mortality was calculated using the following equations:

$$\text{crown extension } (\% \text{ year}^{-1}) = \frac{(CD_{2016} - CD_{2000})/CD_{2000}}{t} \times 100$$

$$\text{infilling}_{\text{regen}} (\% \text{ year}^{-1}) = \frac{(Gap_{2000} - Gap_{\text{both}})/Gap_{2000}}{t} \times 100$$

$$\text{creation } (\% \text{ year}^{-1}) = \frac{(Gap_{2016} - Gap_{\text{both}})/Gap_{2016}}{t} \times 100$$

Where Gap_{2000} is the area that was classified as a gap ($\geq 9\text{m}$ from tree) in 2000, Gap_{both} is area that remained a gap through the census period, Gap_{2016} is the area classified as a gap in 2016, CD_{2000} is the area of overlap between Gap_{both} and 2000 crown diameters of trees that survived the census period, CD_{2016} is the area of overlap between Gap_{both} and 2016 crown diameters of trees that survived the census period, and t is the time interval (16 years).

III. Regeneration and Gap Characteristics

To identify the relationship between canopy cover characteristics and tree regeneration abundance, we compared density of seedlings and saplings by cover class in the 10x10m cells in 2000 and 2016. A non-parametric Kruskal-Wallis test with a Dunn's post-hoc test was used for comparisons since the data were not normally distributed. We also graphically assessed infilling of regeneration into gaps between 2000 and 2016 by mapping density of regeneration (*P. ponderosa*, *Q. kelloggii*) in the 10x10m cells and calculating the area of each density class in 100m² intervals.

Fire Behavior

To characterize potential fire behavior after 22 years of post-fire succession, fire behavior was simulated in each plot using Crown Mass in the Fuel Management Analyst Plus software (FMA, Carlton 2004). Tree lists of living trees, their diameters and crown ratios, were entered into Crown Mass, which then estimates both potential fire behavior – rate of spread, flame length, crowning index, torching index, and fire type – and some first-order fire effects – probability of mortality, scorch height, percent crown scorch – from the stand level data. Potential fire behavior depends on several factors including the type and quantity of fuels, fuel moisture content, and fire weather conditions (Reinhardt & Crookston 2003) and fuel type and abundance varies, even at small spatial scales (Stephens et al. 2004; Keane et al. 2012). To capture a range of potential fire behavior due to variation in fuels and weather, potential fire behavior was modelled under four weather conditions using three different models of surface fuel structure and abundance. Fire weather conditions - temperature, wind speed, and fuel moistures – for the fire season (May 1 – September 31) were calculated for the 80th, 90th, 95th, and 98th percentile weather conditions using Fire Family Plus (Main et al. 1999, Table 3.1) and daily weather observations from the Cohasset remote automated weather station (RAWS), located 20km southwest of BCP at an elevation of 800m.

Table 3.1. Climate and surface fuel variables generated in Fire Family Plus and used to model potential fire behavior in the Beaver Creek Pinery. Variables were derived from RAWS data from the Cohasset California weather station.

<i>Weather & Fuel Variables</i>	<i>Weather Percentile</i>			
	80 th	90 th	95 th	98 th
Dry Bulb Temperature (C)	33	34	36	38
Min relative humidity (%)	14	11	9	8
Max relative humidity (%)	76	93	100	100
20' Wind Speed (km/h)	16	18	21	24
1 Hour Fuel Moisture (%)	3.23	2.75	2.41	2.06
10 Hour Fuel Moisture (%)	3.79	3.27	2.96	2.62
100 Hour Fuel Moisture (%)	5.39	4.88	4.45	4.13
1000 Hour Fuel Moisture (%)	6.54	6.13	5.84	5.48
Live Woody Fuel Moisture (%)	50.00	50.00	50.00	50.00
Foliar Moisture (%)	30.00	30.00	30.00	30.00

Surface (time-lag) fuel characteristics in each plot were estimated in two ways - first, from eight planar fuel transects following Brown's fuel inventory methods (Brown et al. 1982) collected at four points in and adjacent to each plot and second, using estimates for each plot using photoseries (Blonksi 1981, Taylor et al. 2014). Fuel estimates were then entered into FMA, which compares similarities of field estimates to values for standard fuel models (Anderson 1982, Scott & Burgan 2005). Based on these comparisons, models TL3, TL4, and TL7 best fit our field data so we used all three for simulations to bracket potential fire behavior. Canopy fuels were estimated by FMA from diameters and crown ratios of living trees (Van Wagner 1977, 1993; Reinhardt et al. 2003) (Table 3.2). Standard fuel models were used to estimate potential fire behavior instead of the field estimates since standard fuel models have been calibrated with fire behavior under conditions similar to those used in our study.

Table 3.2. Surface fuel models and canopy fuel estimates derived by FMAPlus that were used to model potential fire behavior in the Beaver Creek Pinery.

Plot	Canopy Fuel Estimates				
	Canopy Base Height (m)	Canopy Ceiling Height (m)	Basal Area (m ²)	Canopy Fuel Loading for Crowning (kg/ha)	Canopy Bulk Density (kg/m ³)
1	0.61	20.12	5.63	4416.2	0.032
2	0.61	32.61	12.05	4416.2	0.037
3	8.75	34.44	14.86	5783.6	0.026
4	7.01	32.00	13.23	8249.4	0.048
5	7.31	30.18	13.98	9616.9	0.067
6	0.91	22.25	7.41	4348.9	0.021
	Surface Fuel Models				
	Fuel Depth (cm)	1-hour (kgs/ha)	10-hour (kgs/ha)	100-hour (kgs/ha)	Total Fuel Load (kgs/ha)
TL03	9.1	1,120.9	4,931.8	6,276.8	12,329.5
TL04	12.2	1,120.9	3,362.6	9,415.2	13,898.7
TL07	12.2	672.5	3,138.3	18,157.8	21,968.6

Chapter 4 – Results

Demography

I. Overstory Trees

Changes in tree density and basal area (m^2ha^{-1}) varied by species and plot. Living *P. ponderosa* density increased in five of the six plots, with the greatest increase observed in plots 1 and 6 (Table 4.1). Basal area of *P. ponderosa* increased in four of the six plots. On the other hand, *Q. kelloggii* density increased in two plots, decreased in three plots, and remained the same in one plot (Table 4.1). Basal area of *Q. kelloggii* decreased in four of the six plots. In 2000, trees that didn't survive the census period experienced greater competition than those who survived to 2016 ($H= 3.06$ vs 2.01 , $p<0.05$) and surviving trees experienced similar levels of competition in 2000 and 2016 ($H=2.01$ vs 1.97 , $p>0.05$).

Table 4.1. Characteristics of live and standing dead trees (>5cm dbh), density of seedlings (0.2-1.4m tall), and saplings (>1.4m tall, <5cm dbh) for six ~1ha plots in the Beaver Creek Pinery.

			<i>Plot</i>											
			1		2		3		4		5		6	
			2000	2016	2000	2016	2000	2016	2000	2016	2000	2016	2000	2016
Pinus ponderosa	Basal area (m ² ha ⁻¹)	Live	13.57	12.64	28.20	27.47	27.80	29.45	26.91	30.76	28.56	33.89	16.04	16.14
		Snags	1.43	2.93	1.88	5.06	0.08	1.40	1.95	0.91	2.69	1.45	5.05	6.22
	Tree Density (ha ⁻¹)	Live	82	410	103	106	65	90	139	163	184	176	64	281
		Snags	17	13	16	30	1	2	13	15	34	14	17	22
	Seedlings (ha ⁻¹)		675	3231	691	9151	41	804	121	1553	1760	3019	730	1872
	Saplings (ha ⁻¹)		-	1556	-	1563	-	75	3	239	-	104	-	640
Quercus kelloggii	Basal area (m ² ha ⁻¹)	Live	0.91	0.97	1.78	2.05	7.62	7.21	2.88	1.86	1.26	0.64	2.05	1.91
		Dead	-	-	0.84	0.21	0.52	1.51	0.37	0.32	-	0.65	0.59	0.55
	Tree Density (ha ⁻¹)	Live	1	1	26	44	63	59	19	14	3	2	7	10
		Snags	-	-	17	3	8	11	4	2	-	1	3	2
	Seedlings (ha ⁻¹)		60	50	342	50	252	14	61	4	41	26	73	63
	Saplings (ha ⁻¹)		1	2	70	46	27	23	4	-	-	1	3	13

Pinus ponderosa experienced higher recruitment and lower mortality than *Q. kelloggii* over the study period. On average, the change in number of living stems (λ_{stems}) was 3.7% per year for *P. ponderosa* while it was -1.3% for *Q. kelloggii* (Table 4.2). *Quercus kelloggii* declined in half the plots while only one plot experienced a decline in *P. ponderosa* (Table 4.2). Mortality was also size-dependent, with the highest rates of *P. ponderosa* mortality in small (5-15cm) and large (100-120cm) trees and large (65-75cm) trees for *Q. kelloggii* (Figure 4.1).

Table 4.2. 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).

		Plot					
		1	2	3	4	5	6
<i>Pinus ponderosa</i>	Living Stems ₂₀₀₀ (N_b)	83	103	59	139	148	64
	Living Stems ₂₀₁₆ (N_e)	411	106	83	163	141	281
	Mortality ($N_b - N_s$)	12	12	2	8	13	7
	Recruitment ($N_e - N_s$)	340	15	26	32	6	224
	Mortality rate (% year ⁻¹)	0.98	0.77	0.22	0.37	0.57	0.72
	Recruitment rate (% year ⁻¹)	10.9	0.95	2.35	1.37	0.27	9.97
	λ_{stems} (% year ⁻¹)	10.0	0.18	2.13	1.00	-0.30	9.24
<i>Quercus kelloggii</i>	Living Stems ₂₀₀₀ (N_b)	1	26	57	19	3	8
	Living Stems ₂₀₁₆ (N_e)	1	44	54	14	2	10
	Mortality ($N_b - N_s$)	0	3	7	6	1	3
	Recruitment ($N_e - N_s$)	0	21	4	1	0	5
	Mortality rate (% year ⁻¹)	0	0.76	0.82	2.37	2.53	2.94
	Recruitment rate (% year ⁻¹)	0	4.05	0.48	0.46	0	4.33
	λ_{stems} (% year ⁻¹)	0	3.29	-0.34	-1.91	-2.53	1.39

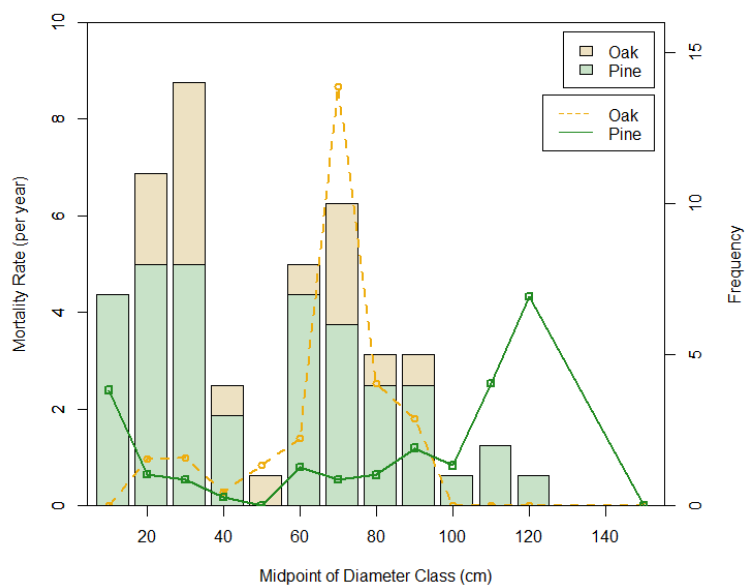


Figure 4.1. Diameter class distribution (bars) and size-specific mortality rates for *P. ponderosa* (green) and *Q. kelloggii* (yellow) that died during the study period (2000 – 2016).

For both species, drivers of basal area change were loss from mortality and gain from growth (Table 4.3). On average, the change in basal area per year was 0.29% for *P. ponderosa* and -0.79% for *Q. kelloggii*; plots with the greatest loss of *Q. kelloggii* basal area experienced the highest gains in *P. ponderosa* basal area (Table 4.3).

Table 4.3. Basal area (m^2ha^{-1}) of living trees (stems $\geq 5\text{cm}$) on each census date and the rate of basal area loss (from mortality) and gain (from growth and recruitment) over the study period.

		<i>Plot</i>					
		1	2	3	4	5	6
<i>Pinus ponderosa</i>	Living BA ₂₀₀₀ (BA _b)	13.7	28.2	25.7	26.9	23.0	16.0
	Living BA ₂₀₁₆ (BA _e)	12.7	27.5	26.8	30.8	27.1	16.1
	Loss of BA (BA _l)	4.98	2.09	1.41	0.66	0.53	3.26
	BA recruitment (BA _r)	1.26	0.05	0.09	0.08	0.05	1.01
	BA growth (BA _g)	2.72	1.34	2.42	4.48	4.58	2.35
	BA loss rate (% year ⁻¹)	2.27	0.46	0.34	0.15	0.14	1.27
	BA gain rate (% year ⁻¹)	1.82	0.31	0.61	1.06	1.26	1.31
	λ_{BA} (% year ⁻¹)	-0.46	-0.16	0.27	0.91	1.11	0.04
<i>Quercus kelloggii</i>	Living BA ₂₀₀₀ (BA _b)	0.91	1.78	7.01	2.88	1.00	2.05
	Living BA ₂₀₁₆ (BA _e)	0.97	2.05	6.56	1.86	0.51	1.91
	Loss of BA (BA _l)	0	0.20	1.21	1.18	0.52	0.62
	BA recruitment (BA _r)	0	0.07	0.11	0.003	0	0.01
	BA growth (BA _g)	0.06	0.4	0.65	0.16	0.03	0.47
	BA loss rate (% year ⁻¹)	0	0.7	1.08	2.56	3.25	1.89
	BA gain rate (% year ⁻¹)	0.41	1.65	0.68	0.35	0.19	1.46
	λ_{BA} (% year ⁻¹)	0.41	0.95	-0.4	-2.21	-3.06	-0.43

II. Seedlings & Saplings

Regeneration patterns for *P. ponderosa* and *Q. kelloggii* between 2000 and 2016 were nearly opposite. In all plots, the density of *P. ponderosa* seedlings increased while *Q. kelloggii* seedlings decreased (Table 4.1). *Pinus ponderosa* sapling density increased in all plots, while *Q. kelloggii* sapling density increased in half of the plots; however, in two of these three plots, *Q. kelloggii* sapling density only increased by one sapling per hectare (Table 4.1).

Spatial Patterns

I. Group Characteristics

A greater proportion of trees were classified into larger group sizes as intertree distances increased and the proportion of trees in a functional clump type varied between 2000 and 2016.

On average, the proportion of trees classified in individual to small clumps declined while the proportion of medium clumps increased at 1-3m intertree distances and extra-large clumps increased at intertree distances of 1-7m (Figure 4.2).

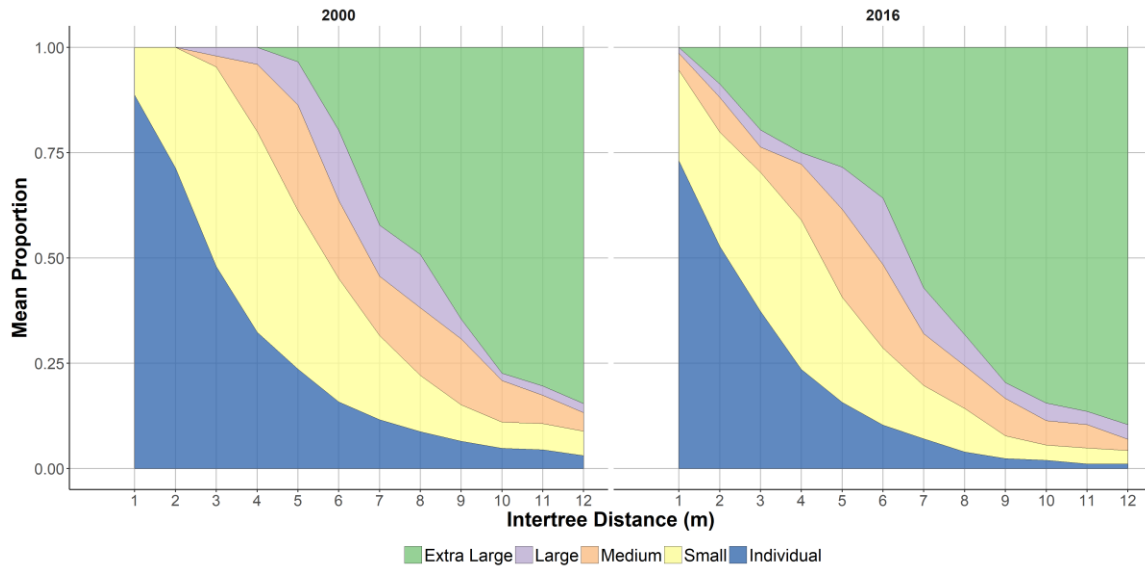


Figure 4.2. Mean proportion of trees in different tree group sizes at 1-12m intertree distances for six ~1ha plots. The data shown in this figure are fully reported in Appendix.

At the 6m intertree distance, the frequency of different group sizes was similar in 2000 and 2016 ($p > 0.05$, Figure 4.3). The results were similar for clump type frequency when trees were clustered by crown diameter rather than a fixed 6m intertree distance (Figure 4.2, Appendix Figures 2, 3; Appendix Table 2) and the average distance to the nearest tree was similar in 2000 to 2016 for all clump sizes (Figure 4.4).

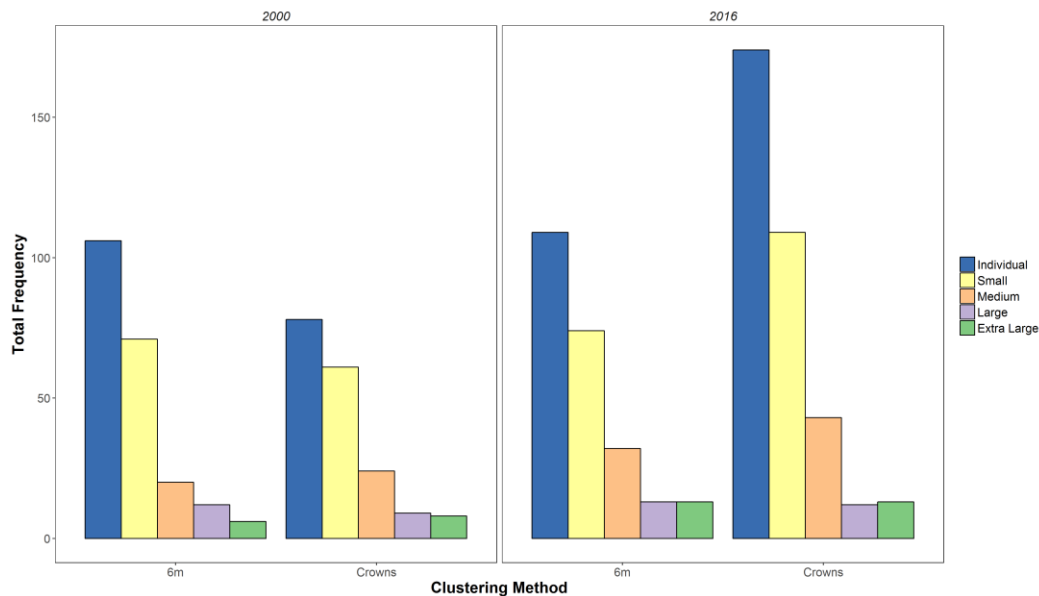


Figure 4.3. Pooled frequency of individual trees, small, medium, large, and extra-large clumps in 2000 (left) and 2016 (right) using two different clustering methods – 6m intertree distance and crown diameters.

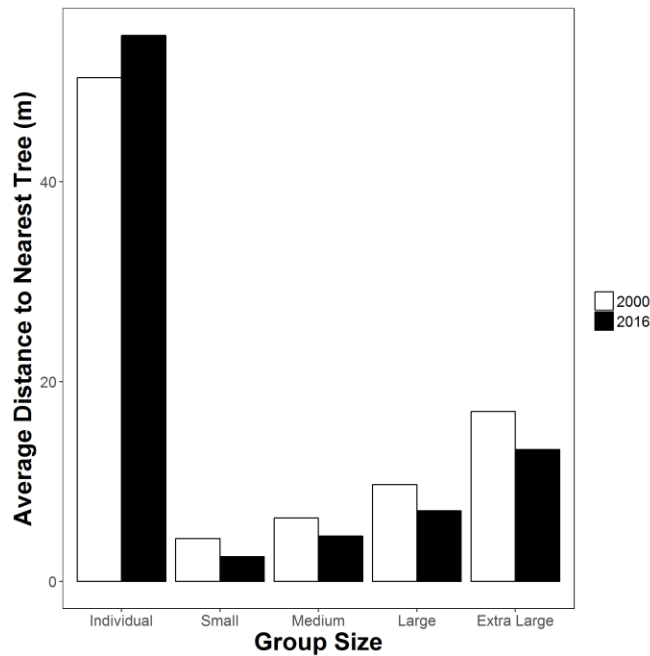


Figure 4.4. Average distance to nearest tree for trees in different clump sizes in 2000 (white) and 2016 (black) using crown diameters to cluster trees.

Variation in tree age (range of age ranges) within tree groups differed in plots and by group size (Figure 4.5). Assuming that a group is comprised of similar aged trees (difference of ≤ 20 years), ~70% of small clusters are even-aged but fewer medium (30%), and no large (0%) or extra-large clusters (0%) are even-aged (Table 4.4).

Table 4.4. Proportion of clumps that consist of trees with similar (even) ages (<20 years) or different (uneven) ages (>20 year range in ages) within different group sizes in 2000.

Clustering Method	Group Size	Even Aged	Uneven Aged
6m Intertree Distance	Small (2-4 trees)	0.69	0.31
	Medium (5-9 trees)	0.15	0.85
	Large (10-15 trees)	0	1.0
	Extra Large (16+ Trees)	0	1.0
Crown Diameters	Small (2-4 trees)	0.70	0.30
	Medium (5-9 trees)	0.25	0.75
	Large (10-15 trees)	0	1.0
	Extra Large (16+ Trees)	0	1.0

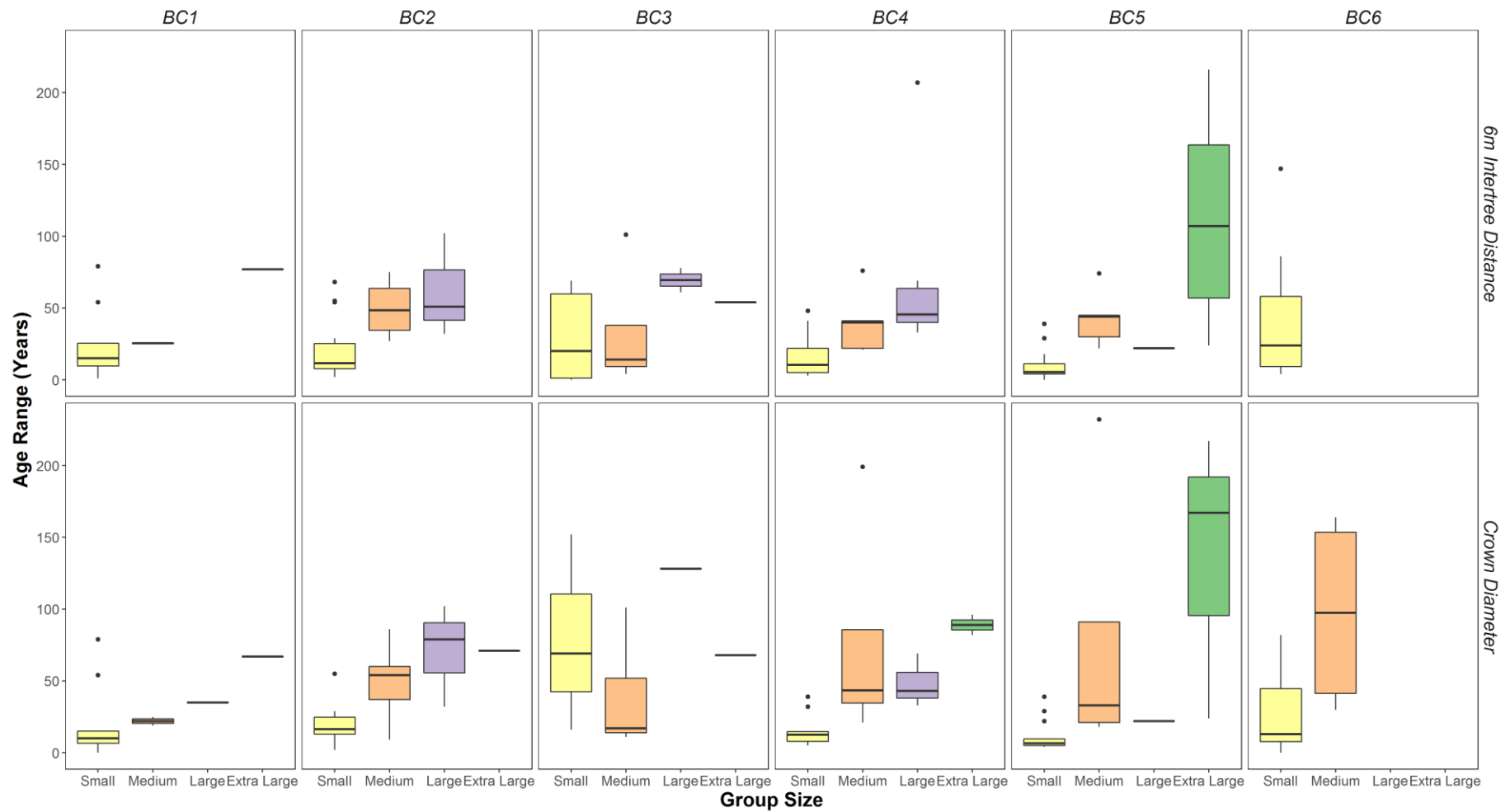


Figure 4.5. Box plots of age ranges for different group sizes using the 6m intertree distance (top) and crown diameter (bottom) clustering methods in each ~1 ha stem map plot in the Beaver Creek Pinery

The global spatial statistic, Ripley's $L(r)$ reveals a significant clustering pattern for all plots in 2000 and 2016; however, the scale and intensity of tree clustering differed among plot, by species, and by year. For plots 1, 2, and 6 the intensity of clustering of all trees and *P. ponderosa* trees increased from 2000 to 2016 (Figure 4.6). For plots 3, 4, and 5 the intensity of clustering of living trees did not change, but the scale over which clustering was observed shifted. For example, in 2000, trees in plot 4 were clustered at distances 20-50m; in 2016, significant clustering was observed at distances 1-30m. In plots with both codominants, *Q. kelloggii* was more intensely clustered than *P. ponderosa*, with the exception of plot 4.

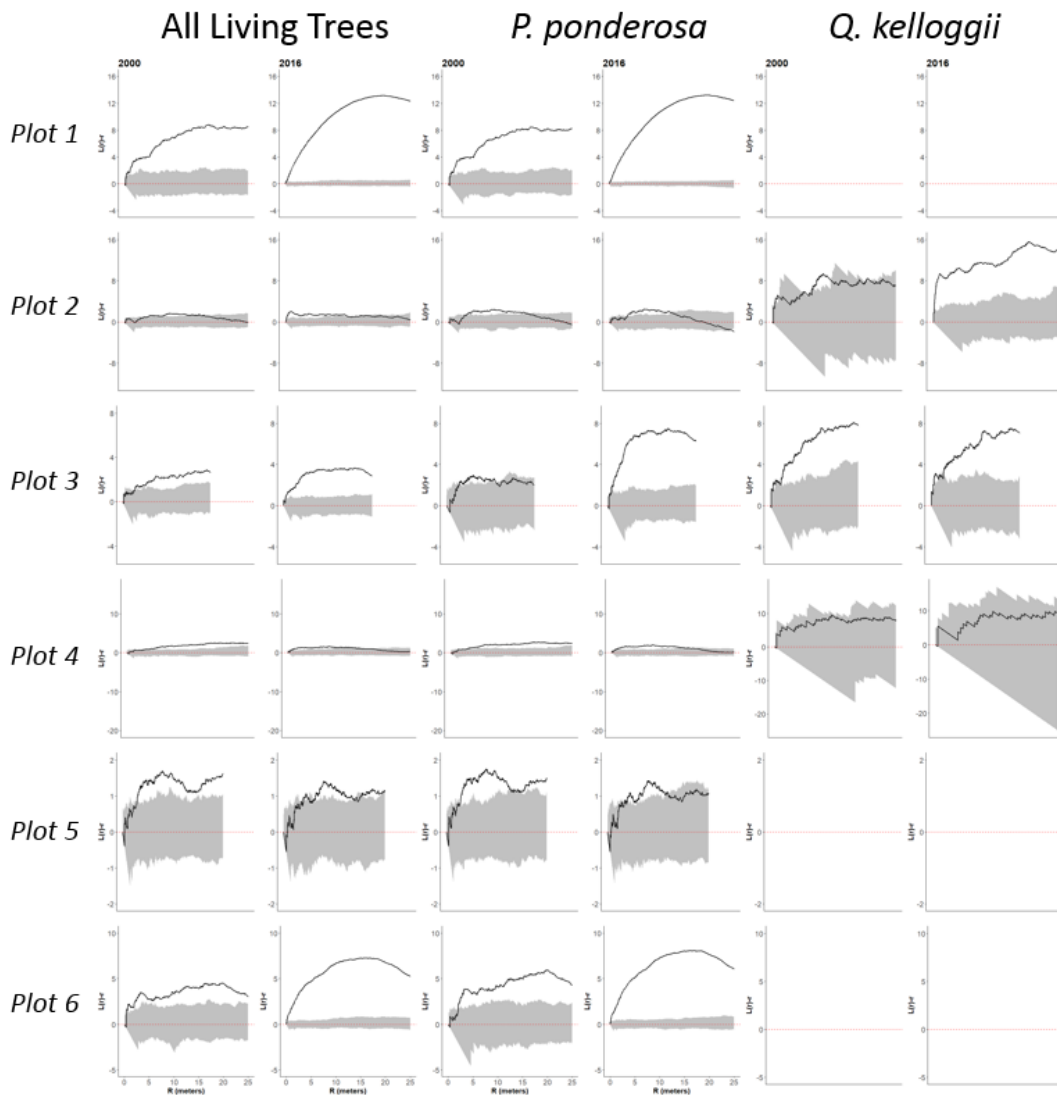


Figure 4.6. Global spatial patterns identified by Ripley's $L(r)$ for 1) all living trees in 2000 and 2016, 2) all living *P. ponderosa* trees in 2000 and 2016, 3) all living *Q. kelloggii* in 2000 and 2016 for each stem map plot, at inter-tree distances of r . Pattern is clumped when values exceed the envelope of complete spatial randomness (CSR) and uniformly spaced when values are below the CSR envelope.

II. Gap Characteristics

The frequency distribution and sizes of gaps did not significantly change between 2000 and 2016 (Figure 4.7, 4.8, Appendix Figure 4, $p > 0.05$). However, total gap area ($>9\text{m}$ from tree) in 2016 was marginally smaller ($p = 0.07$) than in 2000. On average, the rate of gap infilling from tree regeneration was 1.44% per year, the rate of crown extension into gaps was 1.05%, and the rate of new gap creation was 0.58% per year (Table 4.5).

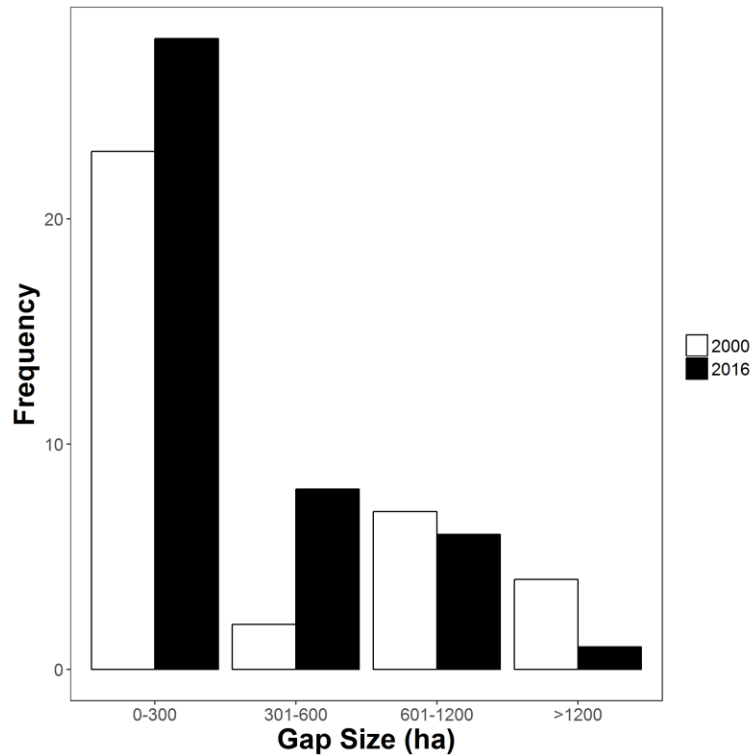
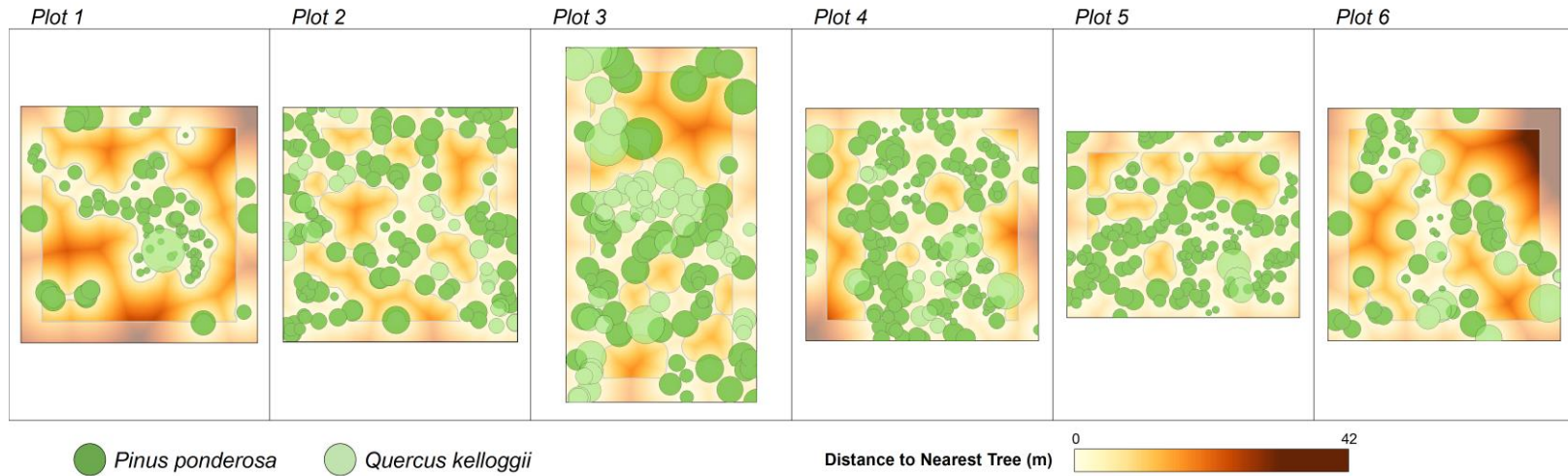


Figure 4.7. Pooled frequency of different gap sizes in 2000 (white) and 2016 (black) for six ~1ha stem map plots in the Beaver Creek Pinery.

2000



2016

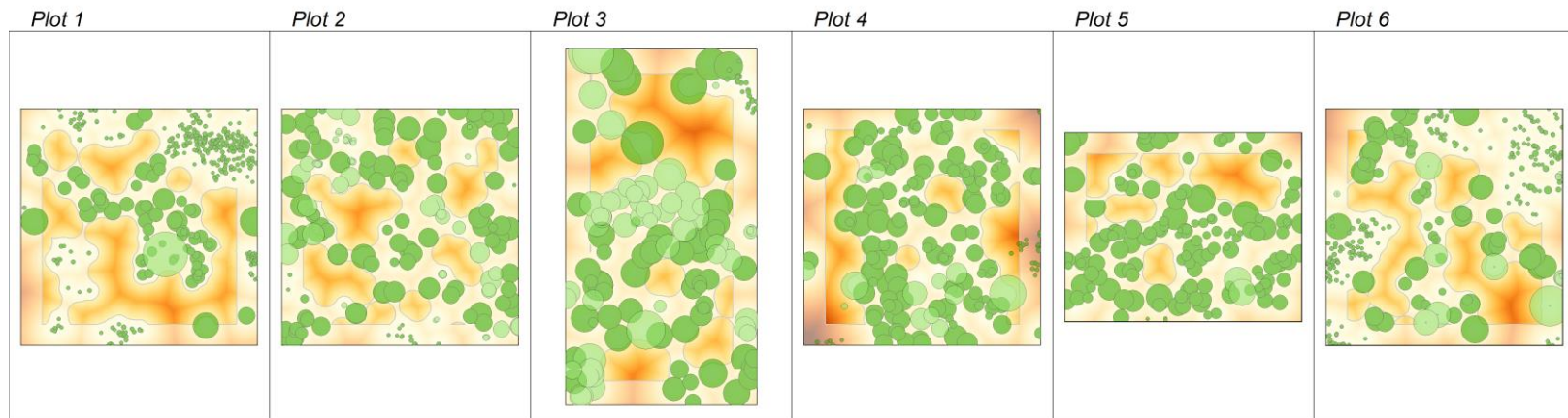


Figure 4.8. Maps of tree groups and canopy gaps for each of the six stem map plots in 2000 (top row) and 2016 (bottom row). Background shading indicates the distance to near tree (empty space function) and regions >9m away from any tree are outlined and bolded. Darker green circles represent *P. ponderosa* and light green circles indicate *Q. kelloggii*.

Table 4.5. Area occupied by gaps and rates of crown extension, gap infilling from tree recruitment, and gap creation from tree mortality over the study period (2000 to 2016).

	<i>Plots</i>					
	1	2	3	4	5	6
Crown Diameters ₂₀₀₀ (m ²)	34.8	27.7	232.5	54.7	35.0	61.8
Crown Diameters ₂₀₁₆ (m ²)	41.2	32.2	256.1	65.1	41.8	72.6
Gap ₂₀₀₀ (m ²)	4626	2929	2402	1938	1586	4178
Gap ₂₀₁₆ (m ²)	3330	2377	2276	1692	1658	2853
Gap _{both} (m ²)	3164	2075	2102	1551	1526	2448
Area infilled	1462	854	300	387	61	1730
New Gap Area	166	302	174	141	132	405
Gap Extension Rate (% year ⁻¹)	1.15	1.02	0.63	1.19	1.21	1.09
Infilling Rate (% year ⁻¹)	1.98	1.82	0.78	1.25	0.24	2.59
Creation Rate (% year ⁻¹)	0.31	0.49	0.48	0.52	0.50	0.89
λ Gap Area (% year ⁻¹)	-2.82	-2.35	-0.93	-1.92	-0.95	-2.79

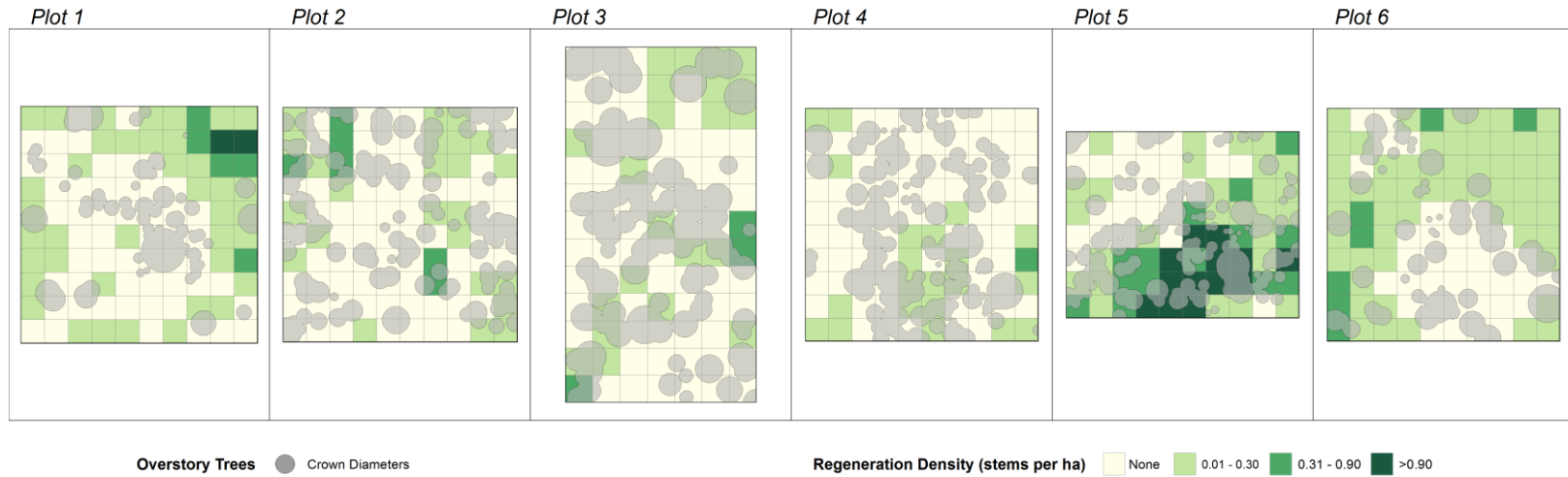
III. Regeneration and Gap Characteristics

Areas of regeneration increased significantly between 2000 and 2016 (Figure 4.9) but this was mainly due to an increase of *P. ponderosa* (Figure 1.d.11), particularly for the 0.01-0.30 and 0.30-0.90 stems ha⁻¹ density classes. In contrast, there was a significant decrease in areas occupied by *Q. kelloggii* seedlings (Figure 1.d.12, $p < 0.05$, paired t-test). In 2016, both *P. ponderosa* and *Q. kelloggii* seedlings were more abundant in canopy gaps (<33% cover) than in either intermediate or closed canopy conditions (Table 4.6, Kruskal Wallance $p < 0.05$). The same pattern was observed for *P. ponderosa* saplings; however, *Q. kelloggii* sapling abundance was not related to canopy openness.

Table 4.6. Density of regeneration in 2016 beneath three canopy cover conditions – open, intermediate, and closed. Regeneration was pooled for six ~1 ha plots in the Beaver Creek Pinery.

		<i>Canopy Cover</i>		
		Open (0-33%)	Intermediate (33-66%)	Closed (>66%)
<i>Quercus kelloggii</i>	Seedlings	26.0	6.0	1.5
	Saplings	9.5	3.3	1.0
<i>Pinus ponderosa</i>	Seedlings	2,015.3	733.5	408.7
	Saplings	662.2	25.8	3.5

2000



2016

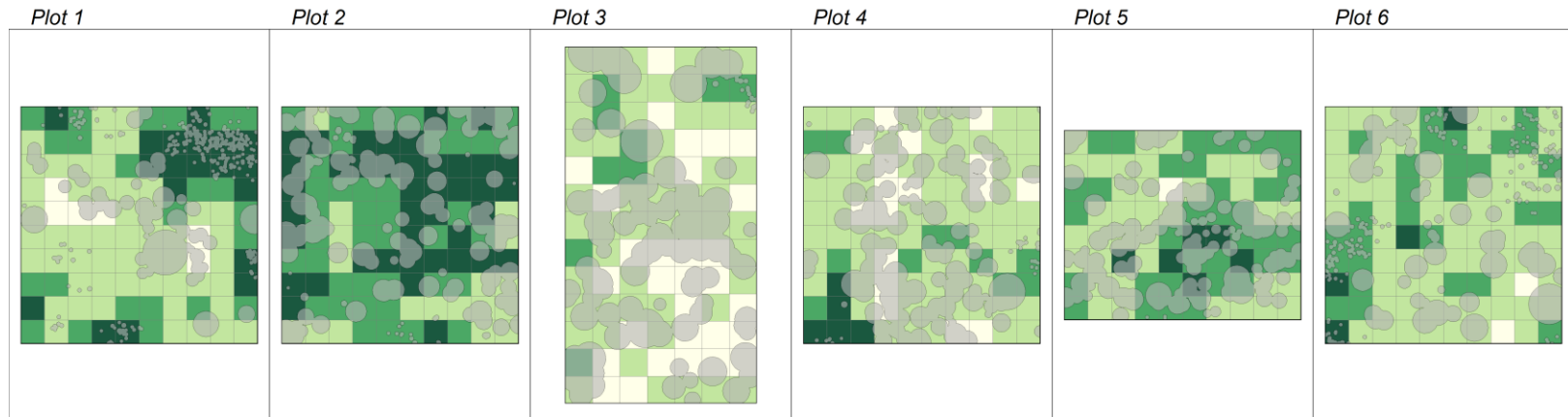


Figure 4.9. Maps of regeneration density (*P. ponderosa* and *Q. kelloggii* seedlings and saplings) in 2000 (top row) and 2016 (bottom row). Darker shading represents higher density of regeneration and overstory tree groups gray and partially transparent.

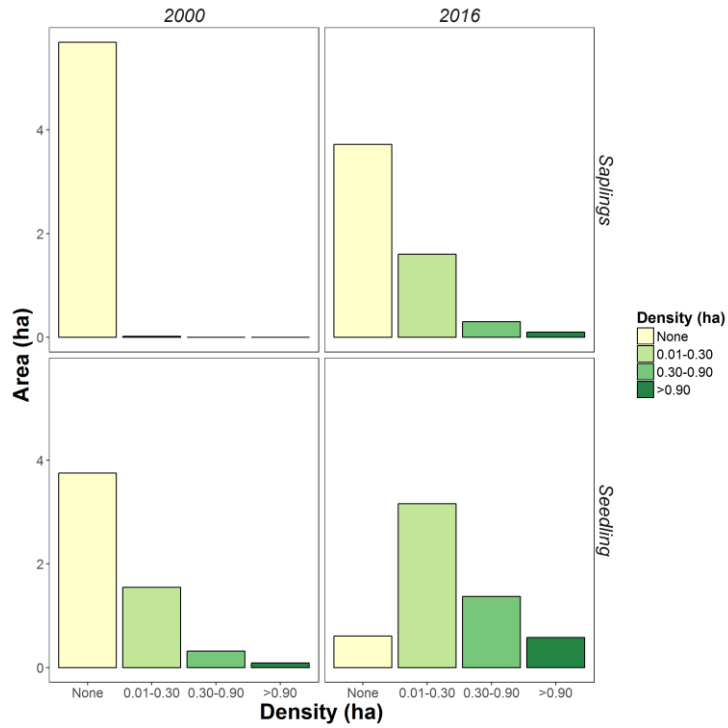


Figure 4.10. Pooled area of *P. ponderosa* regeneration in 2000 (left) and 2016 (right) by density class. Saplings are shown on the top row and seedlings are shown on the bottom row.

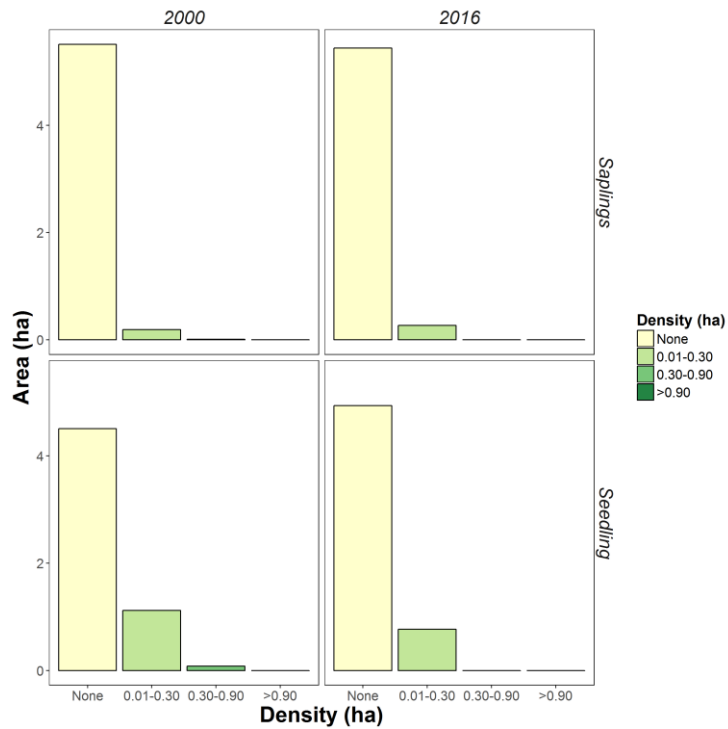


Figure 4.11. Pooled area of *Q. kelloggii* regeneration in 2000 (left) and 2016 (right) by density class. Saplings are shown on the top row and seedlings are shown on the bottom row.

Fire Behavior

Potential fire behavior and fire effects suggest BCP is still resilient to wildfire. Under all weather conditions and fuel loads, four of the six plots experience only potential surface fires. With the most abundant fuel scenario (TL07), two plots were predicted to experience potential passive crown fire under extreme weather conditions (Table 4.7). These two plots also had the highest density of *P. ponderosa* saplings. Flame lengths and rate of spread increased with fuel loads (TL03→ TL04→ TL07) and as weather became more extreme (80-98th percentile). Average probability of mortality was greatest for saplings (<5cm, <1.4m tall) and lowest for large trees (>30cm) (Table 4.7). Even under the most extreme weather conditions, the mean of the average probability of mortality for all large trees (>30cm) within plots was only for 8.9%.

Table 4.7. Potential fire behavior and fire effects for saplings (<5cm dbh, >1.4m tall), small trees (5-30cm dbh), and large trees (>30cm dbh) in six ~1ha plots in the Beaver Creek Pinery. Models were run in FMAPlus using three different fuel models across four weather percentiles – 80th, 90th, 95th, 98th.

Weather Percentile		80 th			90 th			95 th			98 th		
Fuel Model		TL03	TL04	TL07	TL03	TL04	TL07	TL03	TL04	TL07	TL03	TL04	TL07
Fire Type	1	Surface	Surface	Surface	Surface	Surface	Passive Crown	Surface	Surface	Passive Crown	Surface	Surface	Passive Crown
	2	Surface	Surface	Surface	Surface	Surface	Passive Crown	Surface	Surface	Passive Crown	Surface	Surface	Passive Crown
	3	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface
	4	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface
	5	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface
	6	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface	Surface
Surface Rate of Spread (km/hr)		0.02	0.03	0.04	0.03	0.04	0.05	0.03	0.05	0.06	0.04	0.06	0.09
Surface Flame Length (cm)		27.4	36.6	51.8	30.5	39.6	54.9	33.5	45.7	70.1	45.7	48.8	70.1
Average Probability of Mortality													
Saplings (<9cm, >1.4m)	1	83.0 (32.0)	85.6 (39.4)	99.3 (12.0)	83.1 (31.6)	91.4 (59.0)	99.8 (3.5)	83.1 (31.4)	93.8 (67.3)	99.9 (1.0)	83.1 (31.2)	95.5 (72.7)	100 (0.3)
	2	84.9 (9.6)	88.2 (29.6)	99.7 (21.8)	85.1 (14.5)	94.9 (17.3)	99.8 (16.9)	85.2 (28.0)	97.7 (21.9)	99.8 (13.5)	85.3 (36.5)	99.7 (26.4)	99.8 (7.8)
	3	82.7 (16.6)	87.5 (26.6)	95.6 (31.5)	83.9 (17.5)	91.5 (30.2)	97.7 (17.6)	85.0 (23.1)	93.2 (35.0)	99.0 (8.8)	85.6 (27.6)	94.4 (38.1)	99.5 (5.8)
	4	83.8 (23.5)	86.8 (25.1)	97.6 (46.5)	84.0 (21.2)	92.9 (41.8)	98.7 (26.0)	84.1 (19.8)	95.6 (48.1)	99.5 (12.1)	84.2 (19.2)	97.4 (51.8)	99.8 (4.6)
	5	84.7 (5.2)	88.2 (9.5)	99.4 (9.3)	85.1 (6.2)	94.4 (6.5)	100 (7.2)	85.3 (8.5)	97.1 (11.4)	100 (0)	85.5 (10.2)	99.0 (11.6)	100 (0)
	6	82.4 (22.8)	85.0 (27.3)	98.2 (16.6)	82.5 (22.2)	89.5 (19.3)	99.8 (3.5)	82.6 (21.8)	92.6 (47.4)	99.8 (3.5)	82.7 (21.7)	94.1 (51.3)	99.9 (2.0)
Small Trees (9-30cm)	1	51.9 (7.2)	51.9 (7.2)	60.1 (7.8)	51.9 (7.2)	51.9 (7.2)	65.6 (8.1)	51.9 (7.2)	51.9 (7.2)	69.9 (8.4)	51.9 (7.2)	51.9 (7.2)	73.3 (8.6)
	2	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.1 (6.7)	45.7 (6.8)	45.1 (6.7)	45.1 (6.7)	46.8 (6.8)
	3	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	45.8 (6.8)	46.0 (6.8)	45.8 (6.8)	45.8 (6.8)	47.0 (6.9)
	4	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	37.8 (6.1)	38.2 (6.2)
	5	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)	30.6 (5.5)
	6	52.8 (7.3)	52.8 (7.3)	56.0 (7.5)	52.8 (7.3)	52.8 (7.3)	61.7 (7.9)	52.8 (7.3)	52.8 (7.3)	67.2 (8.2)	52.8 (7.3)	52.8 (7.3)	73.4 (8.6)
Large Trees (>30cm)	1	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)	9.7 (4.7)
	2	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)	8.4 (7.2)
	3	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)	11.7 (11.2)
	4	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)	7.9 (5.4)
	5	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)	8.3 (5.6)
	6	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)	7.6 (5.3)

(Table 4.7 continues on page 31)

<i>Weather Percentile</i>		80 th			90 th			95 th			98 th		
Fuel Model		TL03	TL04	TL07	TL03	TL04	TL07	TL03	TL04	TL07	TL03	TL04	TL07
Average Crown Scorch (%)													
Saplings	1	0.1 (5.3)	17.8 (53.8)	94.2 (93.6)	0.2 (7.4)	39.3 (14.8)	97.5 (41.8)	0.3 (9.8)	55.0 (77.7)	99.1 (15.8)	0.4 (12.6)	70.8 (23.0)	99.7 (5.0)
	2	0.2 (20.8)	22.9 (18.1)	98.7 (98.3)	1.1 (39.4)	47.9 (13.8)	99.0 (78.5)	1.7 (54.5)	66.0 (83.0)	99.2 (78.5)	2.3 (22.5)	84.2 (80.1)	99.3 (23.3)
	3	1.8 (19.5)	32.1 (14.0)	83.5 (51.3)	7.7 (40.8)	48.3 (15.5)	90.1 (72.7)	11.7 (95.2)	59.1 (99.8)	94.5 (44.5)	16.1 (12.5)	70.4 (11.6)	97.3 (29.7)
	4	0.5 (17.9)	21.1 (41.7)	91.7 (64.2)	1.2 (31.6)	44.0 (18.5)	94.7 (10.5)	1.7 (43.3)	60.6 (91.2)	97.3 (56.4)	2.3 (56.9)	77.3 (15.5)	98.9 (27.2)
	5	1.2 (19.7)	24.7 (50.4)	97.6 (31.8)	2.7 (30.4)	48.0 (41.0)	99.3 (42.8)	3.8 (41.0)	64.8 (39.1)	99.9 (1.0)	5.0 (53.8)	82.3 (40.4)	100 (0)
	6	0.2 (7.0)	17.9 (42.1)	90.1 (87.4)	0.8 (15.7)	36.3 (81.7)	95.1 (45.3)	1.2 (23.2)	52.2 (87.2)	97.5 (25.8)	1.6 (31.8)	66.7 (16.0)	99.1 (12.4)
Small Trees	1	0 (0)	0 (0)	21.4 (4.6)	0 (0)	0 (0)	30.7 (5.5)	0 (0)	0 (0)	40.1 (6.3)	0 (0)	0 (0)	49.9 (7.1)
	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.7 (3.3)	0 (0)	0 (0)	3.5 (1.9)
	3	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.8 (0.9)	0 (0)	0 (0)	3.2 (1.8)
	4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.3 (1.1)
	5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	6	0 (0)	0 (0)	11.6 (3.4)	0 (0)	0 (0)	22.8 (4.8)	0 (0)	0 (0)	32.9 (5.7)	0 (0)	0 (0)	45.2 (6.7)
Large Trees	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (1.1)	0 (0)	0 (0)	0.2 (1.5)	0 (0)	0 (0)	0.3 (1.9)
	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	3	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	4	0 (0)	0 (0)	0.1 (0.7)	0 (0)	0 (0)	0.1 (0.8)	0 (0)	0 (0)	0.1 (1.1)	0 (0)	0 (0)	0.1 (1.4)
	5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	6	0 (0)	0 (0)	0.8 (2.4)	0 (0)	0 (0)	1.2 (3.3)	0 (0)	0 (0)	1.5 (4.2)	0 (0)	0.06 (1.9)	2.0 (5.3)

Chapter 5. Discussion

Forest conditions in BCP resemble estimates of live tree density and basal area from forest inventories and tree ring reconstructions of pre-fire exclusion forests. In BCP, mean live tree density and basal area was 126 tree ha⁻¹ and 26.3m²ha⁻¹ in 2000 and 226 trees ha⁻¹ and 27.5 m²ha⁻¹ in 2016 with standards deviations of 44 trees ha⁻¹ and 8.1m²ha² in 2000 and 105 trees ha⁻¹ and 9.4 m²ha⁻¹ in 2016, respectively (Table 4.1). Reported live tree densities and basal area averaged from 67-315 trees ha⁻¹ and 21.4-53.9 m²ha⁻¹ for mixed conifer and Jeffrey pine forests in the Sierra Nevada (Taylor 2004, North et al 2007, Collins et al. 2011, Scholl & Taylor 2010 Van de Water & North 2011, Knapp et al. 2013), 40-80 trees ha⁻¹ and 8-12 m²ha⁻¹ for *P. ponderosa* forests (Hagmann et al. 2013) and 16-94 trees ha⁻¹ and 16-30.9 m²ha⁻¹ for mixed conifer forests in the eastern Cascades in Oregon (Youngblood et al. 2004, Hagmann et al. 2013), 52-203 trees ha⁻¹ and 9.1-59.1m²ha⁻¹ in *P. ponderosa* forests in the southwest (Fulé et al. 2000; Heinlein et al. 2005; Moore et al. 2004, Vankat et al. 2011). By contrast, the mean density of living trees in contemporary, fire-excluded forests is between 250-1200 trees ha⁻¹ (Stephens et al. 2008, Scholl & Taylor 2010, Nacify et al. 2010, Collins et al. 2011, Knapp et al. 2013). Whenever making comparisons to forest estimates from historical inventories and tree ring reconstructions, it is important to recognize these estimates have limitations. In tree ring reconstructions, death and complete decomposition of trees, especially in small diameter classes, can underestimate tree density and slower decay rates can lead to an overrepresentation of certain species (Fulé et al. 1997, North et al. 2007). Many historical datasets (e.g. from the US Forest Service Forest Inventory Analysis – FIA – and General Land Office – GLO data), were initially collected for economic rather scientific purposes; consequently, non-random site selection, bias tree selection and under-reporting of non-timber (hardwood) species is likely (Steward 1935, Bourdo 1957). Consequently, density estimates from these datasets can be lacking in precision and accuracy (Anderson et al. 2006) and variables in these datasets can be mis-interpreted. For example, the “stand age” variable from US Forest Service Forest Inventory Analysis program doesn’t represent the multi-aged structure found in plots yet continues to be incorrectly used to determine timing of high severity, stand replacing, fires in the western dry forests (Stevens et al. 2016). These limitations in historical inventories and reconstructions do not always invalidate findings; however, they do reinforce the value of studying contemporary examples of resilient forest structure since contemporary reference forests provide opportunities to measure a greater depth of data on forest structure and composition which can be used to better quantify post-fire forest development and population dynamics (Stephen & Fulé 2005, Larson & Churchill 2012).

Demography

Forest development in the time since the 1990 Campbell and 1994 Barkley wildfires reveals contrasting effects on the demography of *P. ponderosa* and *Q. kelloggii* in BCP. These two, low-mid severity wildfires initially promoted *Q. kelloggii* regeneration; in 2000, *Q. kelloggii* seedling density ranged from 61-342 ha⁻¹ and most of these seedlings (77%) and saplings (92%) were sprouts from top-killed trees. In 2016, many of these post-fire sprouts had grown large enough to become trees. However, by 2016, the density of *Q. kelloggii* seedlings decreased by ~75%, most regeneration (85%) was from seed, and only 11% of the total area in our plots had *Q. kelloggii* seedlings or saplings (Table 4.1, Figure 4.11). On the other hand, in 2016, *P. ponderosa* seedling density ranged from 1553-1951 seedlings ha⁻¹ and 90% of the total area in our plots had *P. ponderosa* regeneration (Table 4.1, Figure 4.10). From 2000 to 2016, similar demographic patterns were observed in the overstory as the understory. *Pinus ponderosa* experienced higher rates of tree recruitment and lower rates of tree mortality than *Q. kelloggii* and plots with the greatest loss of *Q. kelloggii* experienced the highest gains in *P. ponderosa* basal area (Table 4.3, Table 1.d.5). These results suggest that in mixed *P. ponderosa* and *Q. kelloggii* forests adapted to frequent (~10 year), low-moderate severity fire regimes, a longer, ~20-year, fire free interval allows *P. ponderosa* to outcompete *Q. kelloggii*. Though little research exists for mixed *P. ponderosa* – *Q. kelloggii* forests, recent studies examining conifer encroachment into *Q. kelloggii* woodlands in the southern Cascades found frequent fire intervals can be used to ensure *Q. kelloggii* persists at a site; however, a high severity fire might be needed initially to kill off fire-intolerant conifer species (Cocking et al. 2012, 2014, Hammitt et al. 2017). As *P. ponderosa* and *Q. kelloggii* are both tolerant of low to moderate fire intensity but have different strategies for post-fire survival (i.e. resistance vs resilient, Barton 1999, 2008), a high severity wildfire could remove *P. ponderosa* and favor *Q. kelloggii*, leading to a potential shift in vegetation type from mixed species forest to an oak woodlands or shrubland, as observed in other mixed *Pinus-Quercus* forests in the southwestern United States and northern Mexico (Fulé et al. 2000, Barton 2002). As such, restoring a frequent, low-moderate fire severity fire regime is recommended to maintain mixed *Pinus-Quercus* forests (Fulé et al. 2000).

Spatial Patterns

Spatial patterns consisting of individual trees, tree groups, and canopy gaps are conspicuous structural features of forests on BCP and this group-gap structure in 2000 is

consistent with data and descriptions of other contemporary reference and old growth forests adapted to frequent low-moderate severity wildfire (Taylor 2004, Scholl & Taylor 2010, Larson & Churchill 2012). Consistent with the majority of studies, the average (global) spatial pattern in BCP was spatial aggregation of trees at spatial scales <0.4 ha (Cooper 1960, White 1985, Larson & Churchill 2012, Fry et al. 2014) with considerable local variation in spatial patterns (Getis and Franklin 1987, Churchill & Larson 2012, Churchill et al. 2017). In 2000, irrespective of clustering method, average tree group size was 4 trees group⁻¹ and group sizes ranged from 2-70 trees clump⁻¹. Other studies report similar average group size, but smaller maximum group sizes with values up to 40 trees clump⁻¹ in the eastern Cascades (Churchill et al. 2013, 2017), 25 trees clump⁻¹ for *P. ponderosa* forests in the southwest (Abella & Denton 2009; Sánchez Meador et al. 2011), and 26 trees clump⁻¹ in the Rocky Mountains (Brown et al. 2015). Consequently, many of these studies also report lower proportions of trees within large (10-15) and extra-large (≥ 16 trees) clusters at a 6m intertree distance (Figure 4.2, Harrod et al. 1999, Abella & Denton 2009, Sánchez Meador et al. 2011, Larson and Churchill 2012, Churchill et al. 2017). One likely explanation for higher within group tree density is high site productivity (Larson and Churchill 2012, Lyderson et al. 2013, Clyatt et al. 2016; Churchill et al. 2017). In particular, highly productive forests that experience a more variable fire regime might exhibit a wider range of structure and composition and be able to support denser tree groups (Everett et al. 2000, Heyerdahl et al. 2001, Churchill et al. 2017). Growth rate from 2000 and 2016 suggest BCP is highly productive (Table 4.3) and the contemporary fires return intervals have been more variable than historically experienced. The historic median fire return interval in BCP was 12 years (Taylor 2010). Following fire exclusion in 1905, the BCP experienced an extended (66 year) fire interval before the 1990 Campbell fire followed by a four year fire-free interval before the Barkley fire in 1994 (Taylor 2010). During this extended interval, seedling and saplings could have grown large enough to survive the 1990 and 1994 wildfires which resulted in denser tree groups following reintroduction of fire. Yet, despite slight discrepancies on the maximum number of trees per group, average clump densities from contemporary *P. ponderosa* reference forests are remarkably similar to the 18 groups ha⁻¹ found in BCP (Figure 4.3), with ~19 groups ha⁻¹ found in the eastern Cascades (Churchill et al. 2013, 2017), ~15 groups ha⁻¹ in the southwest (Abella & Denton 2009), and ~18 groups ha⁻¹ in the Rocky Mountains (Brown et al. 2015, Clyatt et al. 2016). Canopy gap size in BCP ranged from 0.01 to 0.42 ha, which, again, is similar to reports from old growth *P. ponderosa* forests (0.02 – 0.64 ha, Cooper 1961, White 1985, Taylor

2004, Larson et al. 2012, Larson & Churchill 2012, Clyatt et al. 2016, Churchill et al. 2017). Fewer studies have used the empty space function (Diggle 2003) to quantify gap area within *P. ponderosa* stands; of those, Churchill et al. 2017, found ~13-30% of their plots consists of area >9m from any tree and Clyatt et al. 2016 found 5-25%, which is comparable, if not slightly less, than what was found in the BCP (9-42% of area >9m from any tree in 2000, Figure 4.8, Appendix Figure 4); there is also general agreement between findings in these studies and BCP on the density (groups ha⁻¹) of different gap sizes (Clyatt et al. 2016, Churchill et al. 2017, Figure 4.7). Cumulatively, these results suggest the 1990 and 1994 wildfires restored a group-gap spatial structure to BCP.

Examining the age structure in 2000, 6-years post-fire, offers insights into how this group-gap spatial structure developed. Stem map plots in BCP contained an average of 10.3 (+/- 2.2) 20-year age classes with tree establishment years ranging from 1525 to 1969. This wide range in ages is often observed in old-growth forests adapted to frequent, low to moderate severity fire (White 1985, Agee 1993, Taylor & Skinner 2003, Beaty & Taylor 2007, Scholl & Taylor 2010). This pattern can result from small similar-aged groups establishing in burned patches following the death of overstory tree(s) (Cooper 1960, 1961) and partial mortality of seedling and overstory groups following surface fires, creating uneven aged groups (White 1985, Stephens & Fry 2005) which ultimately creates a single, uneven aged tree cluster consisting of small, even-aged groups (Beaty & Taylor 2007, Scholl & Taylor 2010). However, few studies have been able to quantify tree ages within particular tree groups to better understand the how this pattern evolves. One other study which quantified within group age structure was White 1985's study of pre-settlement structure in *P. ponderosa* forests in Gus Pearson Natural Area, Arizona; this study found the average age within a group ranged from 141 to 382 years, the range of ages within a groups varied from 33 to 282 years, and groups with at least 10 aged trees had a minimum of three and as maximum of twelve, 10-year, age classes represented (White 1985). By comparison, our study found evidence that groups consist of multiple age classes, in particular, groups with ≥ 5 trees were mostly un-even aged or contained multiple 20-year age classes while small groups (2-4 trees) were more likely to be even-aged (Table 4.4). This supports findings in White 1985 and previous work using Moran's I showing that large uneven age clusters consist of overlapping even aged groups (Beaty & Taylor 2007; Scholl & Taylor 2010). Interestingly however, 50% of extra-large groups (≥ 16 trees) had the majority of their trees (≥ 8 individuals) in a single 20-year size class which established during the 20th w century. This, as with the

relatively high proportion of large tree groups, could be a consequence of fire exclusion in BCP. Without frequent fire, large groups of trees were able to establish near pre-existing, small even-aged groups or individual trees, resulting in large uneven aged groups with the majority of trees in a single 20-year age class. At the same time, frequent fires prior to fire exclusion and the short, 4-year, interval between the Campbell and Barkley fires could have promoted small even aged groups as well as larger uneven aged groups which consist of even-aged groups of 2-4 trees. Ultimately, more research on within-group age structure, in conjunction with site-specific information on site conditions and fire regimes, could reveal similar or a diversity of mechanisms shaping group-gap structure in frequent-fire adapted forests.

After 22-years of post-fire succession, the scale and intensity of tree clustering increased, and canopy gaps created by the 1990 and 1994 wildfires are now being infilled with tree regeneration. At the smallest intertree distance (1m), only individual and small tree groups were observed in 2000 while individual, small, medium, large and even extra-large groups were identified in 2016 (Figure 4.2). At a 6m intertree distance, the proportion of trees in extra-large groups increased by ~60% and the proportion of individual trees decreased by ~70% in plots with high post-fire tree recruitment (Appendix Table 1, Appendix Figure 2,3). Alternatively, plot 5 was the only plot where the rate of *P. ponderosa* mortality exceeded that of tree recruitment (Table 4.2). Plot 5 was also the only plot in which the proportion of trees in extra-large groups decreased and the proportion of individuals increased, at a 6m intertree distance (Appendix Table 1). Importantly however, in 2016, a diversity of group sizes were still observed in all plots (Figure 4.2, Appendix Figure 2,3,4). Though gap area was similar in 2000 and 2016, there was some evidence that tree infilling was breaking large gaps (>600m²) into smaller gaps (<600m²) (Figure 4.7 and panels for plots 1 and 6 in Figure 4.8); however, in 2016, each plot still contained gaps that were at least 90m² in size and ≥9m away from trees. The presence of these large gaps is indicative of a resilient forest structure since they create fuel mosaics (Stephens & Fry 2005), reduce the likelihood of crown fires (Beatty and Taylor 2007; Stephens et al. 2010), and can slow the spread of insects (Fettig et al. 2007). In contrast, fire-excluded forest structure lacks canopy gaps and consists of contiguous forest (i.e. lack distinct groups of overstory tree) (Lydersen et al. 2013; Fry et al. 2014). This fire-excluded forest structure is a result of regeneration establishing and filling canopy openings which were historically maintained by frequent fire (Lydersen et al. 2013) and regeneration in *P. ponderosa* forests is often aggregated in canopy gaps (Gray & Spies 1996; Beatty & Taylor 2007; Larson & Churchill 2012); however, the process of gap creation and

infilling has been understudied in frequent fire-adapted, western dry forests compared to eastern temperate forest (Runkle 1981; 1990), the tropical rainforest (Denslow 1987; Brokaw 1985), and boreal forests (McCarthy 2001). Spies et al. 1990 found an annual increase in canopy gap area of 0.5% in an old growth *Pseudotsuga mensiesii* (Douglas fir) forests in the western Cascades, which is comparable to gap creation rates in BCP (Table 4.5). Yet, while gaps are still being created from tree mortality, a negative percent change in gap area (as a result of from tree infilling from 2000 to 2016, and to a lesser degree, canopy extension into gaps), shows without another disturbance, gap area will decrease in BCP (Tables 4.5; Figure 4.9). Given there was a significant increase in regeneration from 2000 to 2016 (Table 4.1, Figures 4.9, 4.10, 4.11) and that high densities of *P. ponderosa* regeneration are aggregated in canopy gaps (Table 4.6), the rates of tree infilling and the predicted rate of gap infilling in BCP will increase into the future. However, results also suggest that spatial heterogeneity (in the form of groups and gaps of trees) is likely to persist for at least 20 years after last wildfire. Therefore, use of wildland fire at slightly longer fire-return intervals might be an effective management strategy for restoring and maintaining structural heterogeneity in fire-adapted forests (North et al. 2012).

It is also important to briefly discuss the two clustering methods – 6m intertree distance (fixed radius) and crown diameters (variable radius) – used in this study. For the 2000 dataset, 50% of trees were classified as the same type and most misclassification was when trees classified using the 6m intertree distance method were classified into the next largest or smallest size category when using the variable radius method (Appendix Table 2); this is unsurprisingly since crown radii didn't significantly differ from the 3m radii which corresponds to a 6m intertree distance (Appendix Figure 5). In 2016, the percentage of trees classified in the same group size between both methodologies decreased to 36% (Appendix Table 2) and the discrepancy was largest for small diameter trees (<15cm dbh). With the 6m intertree distance methodology, the majority of these small trees were aggregated into extra-large clumps yet when using a variable radius, crown diameters of small trees were less likely to overlap, resulting in a greater frequency of small, medium, and large groups (Figure 4.3). Benefits of using a fixed radius to groups trees is that results are directly comparable to many other studies (Abella & Denton 2009, Larson et al. 2012, Churchill et al. 2013, 2017, Clyatt et al. 2016) and it easy for forest managers to implement when designing prescriptions (Churchill et al. 2013). On the other hand, clustering trees using overlap in crown diameters might produce more ecologically

appropriate groupings, especially when crown diameters at a site are highly variable (Lydersen et al. 2013).

Potential Fire Behavior

Post-fire stand development as of 2016 still has not created conditions that are likely to lead to a severe wildfire. One well-documented consequence of fire exclusion is increased density of small-diameter trees that in turn, act as ladder fuels since they lower the average canopy base height within a stand to allow surface fires to travel into tree crowns (Agee & Skinner 2005, Hessburg et al. 2005). In BCP, plots with higher densities of saplings and small trees (i.e. ladder fuels) were more likely to exhibit passive crown fire under extreme weather conditions and high fuel loads (Tables 4.1, 4.7); however, the average probability of mortality and percent crown scorch for large overstory (> 25 cm) trees in those plots was still low – 8.6 and 0.4%, respectively (Table 4.7). This low probability of mortality and percent of crown scorch in the overstory reflects low crown bulk densities (0.03-0.04 km m³, Table 3.2) in these plots. Further, all six plots were predicted to experience surface fires, with flame lengths ranging from 0.3 to 0.5 meters, when fire behavior was modelled using low-moderate fuel loads (TL03 and TL04 fuel models) (Table 4.7). Predictably, within plots, the largest trees had the lowest probability of mortality and no crown scorch; this reiterates the importance of having large fire-resistant trees within a stand – they have the tallest crowns, which raises the stand’s canopy base heights and reduces potential for crown fires, and the thickest bark, increasing the likelihood of post-fire survival and ensuring a potential seed source following fire (Peterson & Ryan 1986, Agee & Skinner 2005). The relatively low severity fire and moderate fire effects predicted for BCP are similar to potential fire behavior observed in pre-fire exclusion forests (Fulé et al. 2004; Hessburg et al. 2005; Van de Water & North 2011; Taylor et al. 2014) and suggests restoring a heterogeneous forest structure has long-lasting effects on stand resiliency to wildfire.

Conclusions

Forest structure in BCP is within the historical range of variability of pre-fire exclusion structure for fire-adapted dry forests, was resilient to previous wildfires, and modelling suggests it remains resilient to future fire. This research provides additional empirical evidence that unlogged, fire-excluded *P. ponderosa* forests maintain a latent resiliency to wildfire (Larson et al. 2013) and once restored, suggests that group-gap forest structure will likely persist for an

extended period following the last wildfire. However, maintaining a relatively frequent fire interval will be necessary to promote *Quercus kelloggii* and maintain canopy openings into the future. Cumulatively, this research provides empirical evidence that supports recent policy pushes for increase use and management of wildland fire, burning under appropriate conditions in unlogged and fire-excluded areas, to restore and maintain heterogeneous and resilient group gap structure to large tracts of western conifer forests and reduce the financial costs and negative ecological consequences associated with current fire suppression policies (North et al. 2009, 2012, Franklin & Johnson 2012, Nacify et al. 2016, Taylor et al. 2016). Managing wildland fire can be an especially important tool for wilderness areas, where climate change and current fire exclusion policies are creating high density and physiologically stressed conditions outside the range of historical variability that warrant management interventions; however, policy prohibits or severely restricts other common fire-management practices, such as mechanical thinning or prescribed burning in these wilderness areas (Hobbs et al. 2011; Stephenson and Millar 2011 Nacify et al. 2016).

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(12), 2391–2403.
- Agee, J. K., & Skinner, C. N. (2005). Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*, 211(1–2), 83–96.
- Allen, C. D., Savage, M., Falk, D. A., Suckling, K. F., Swetnam, T. W., Schulke, T., ... Klingel, J. T. (2002). Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications*, 12(5), 1418–1433.
- Anderson, H. E. (1982). Aids to Determining Fuel Models for Estimating Fire Behavior. USDA Forest Service General Technical Report.
- Anderson, M. K. (1996). The ethnobotany of deergrass, *Muhlenbergia rigens* (Poaceae): Its uses and fire management by California Indian tribes. *Economic Botany*, 50(4), 409–422.
- Anderson, M. K. (2005). *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources*. University of California Press.
- Anderson, R. C., Jones, S. L., & Swigart, R. (2009). Modifying Distance Methods to Improve Estimates of Historical Tree Density from General Land Office Survey Records. *Journal of the Torrey Botanical Society*, 133(3):449-459.
- Baddeley, A., & Turner, R. (2005). Spatstat: An R Package for Analyzing Spatial Point Patterns. *Journal of Statistical Software*, 12(6), 1–42.
- Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E., & Fites-Kaufmann, J. (2009). Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. *Journal of Vegetation Science*, 13(4): 461-472.
- Barton, A. (2008). Madrean pine-oak forest in Arizona: past dynamics, present problems. In: Narog, Marcia G., Tech. Coord. 2008. *Proceedings of the 2002 Fire Conference: Managing Fire and Fuels in the Remaining Wildlands and Open Spaces of the Southwestern United States*. Gen. Tech. Rep. PSW-GTR-189. Albany, CA: U.S. Department of Agriculture, 189, 185–192.
- Barton, A. M. (2002). Intense wildfire in southeastern Arizona: transformation of a Madrean oak–pine forest to oak woodland. *Forest Ecology and Management*, 165(1–3), 205–212.
- Barton, A. M. (1999). Pines versus oaks: effects of fire on the composition of Madrean forests in Arizona. *Forest Ecology and Management*, 120(1–3), 143–156.
- Beaty, R. M., & Taylor, A. H. (2007). Fire disturbance and forest structure in old-growth mixed conifer forests in the northern Sierra Nevada, California. *Journal of Vegetation Science*, 18(6), 879–890.
- Binkley, D., Sisk, T., Chambers, C., Springer, J., & Block, W. (2007). The Role of Old-growth Forests in Frequent-fire Landscapes. *Ecology and Society*, 12(2), 18.
- Blonski, K. S., & Schramel, J. L. (1981). Photo series for quantifying natural forest residues: southern Cascades, northern Sierra Nevada. Gen. Tech. Rep. PSW-56. Berkeley, Calif.: U.S.DA, Forest Service, Pacific Southwest Forest and Range Exp. Stn.
- Bonan, G. B., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., ... Veblen, T. T. (2008). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320(5882), 1444–9.
- Bonnet, V. H., Schoettle, A. W., & Shepperd, W. D. (2005). Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research*, 35(1), 37–47.
- Bourdo, E. A. (1956). A Review of the General Land Office Survey and of Its Use in Quantitative Studies of Former Forests. *Ecology*, 37(4), 754–768.
- Brokaw, N. V. L. (1985). Gap-Phase Regeneration in a Tropical Forest. *Ecology*, 66(3), 682–687.
- Brown, P. M., Battaglia, M. A., Fornwalt, P. J., Gannon, B., Huckaby, L. S., Julian, C., & Cheng, A. S. (2015). Historical (1860) forest structure in ponderosa pine forests of the northern Front Range, Colorado. *Canadian Journal of Forest Research*, 45(11), 1462–1473.

- Buchanan, J. B., Rogers, R. E., Pierce, D. J., & Jacobson, J. E. (2003). Nest-Site Habitat Use by White-Headed Woodpeckers in the Eastern Cascade Mountains, Washington. *Northwestern Naturalist*, 84(3), 119.
- Carton, D. (2004). *Fuels Management Analyst Plus Software, Version 3.02*. Estacada, Oregon: LLC.
- 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.
- Churchill, D. J., Carnwath, G. C., Larson, A. J., & Jeronimo, S. A. (2017). *Historical Forest Structure , Composition , and Spatial Pattern in Dry Conifer Forests of the Western Blue Mountains , Oregon*. General Technical Report, USDA Forest Service.
- Clyatt, K. A., Crotteau, J. S., Schaedel, M. S., Wiggins, H. L., Kelley, H., Churchill, D. J., & Larson, A. J. (2016). Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. *Forest Ecology and Management*, 361, 23–37.
- Cocking, M. I., Varner, J. M., & Knapp, E. E. (2014). Long-term effects of fire severity on oak–conifer dynamics in the southern Cascades. *Ecological Applications*, 24(1), 94–107.
- Cocking, M. I., Varner, J. M., & Sherriff, R. L. (2012). California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. *Forest Ecology and Management*, 270, 25–34.
- 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*, 2(4):51.
- Collins, B. M., Miller, J. D., Thode, A. E., Kelly, M., van Wagtenonk, J. W., & Stephens, S. L. (2009). Interactions Among Wildland Fires in a Long-Established Sierra Nevada Natural Fire Area. *Ecosystems*, 12(1), 114–128.
- Condit, R., Ashton, P. S., Manokaran, N., Lafrankie, J. V., Hubbell, S. P., & Foster, R. B. (1999). Dynamics of the forest communities at Pasoh and Barro Colorado : comparing two 50-ha plots. *Philosophical Transactions of the Royal Society B*, (354), 1739–1748.
- Condit, R., Hubbell, S. P., & Foster, R. B. (1995). Mortality Rates of 205 Neotropical Tree and Shrub Species and the Impact of a Severe Drought. *Ecological Monographs*, 65(4), 419–439.
- Cooper, C. F. (1960). Changes in Vegetation, Structure, and Growth of Southwestern Pine Forests since White Settlement. *Ecological Monographs*, 30(2), 129–164.
- Cooper, C. F. (1961). Pattern in Ponderosa Pine Forests. *Ecology*, 42(3), 493–499.
- Coppoletta, M., Merriam, K. E., & Collins, B. M. (2016). Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications*, 26(3), 686–699.
- Covington, W. W., & Moore, M. M. (1994). Postsettlement Changes in Natural Fire Regimes and Forest Structure. *Journal of Sustainable Forestry*, 2(1–2), 153–181.
- Covington, W. W., & Moore, M. M. (1994). Southwestern Ponderosa Forest Structure: Changes Since Euro-American Settlement. *Journal of Forestry*, 92(1), 39–47.
- Crotteau, J. S., Morgan Varner, J., & Ritchie, M. W. (2013). Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management*, 287, 103–112.
- Denslow, J. S. (1987). Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics*, 18(1), 431–451.
- Devine, W. D., & Harrington, C. A. (2013). Restoration release of overtopped Oregon white oak increases 10-year growth and acorn production. *Forest Ecology and Management*, 291, 87–95.
- Diggle, P. J. (2013). *Statistical Analysis of Spatial and Spatio-Temporal Point Patterns*, 3rd Ed Boca Raton, Florida: CRC Press.
- Dodson, E. K., Peterson, D. W., & Harrod, R. J. (2008). Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. *Forest Ecology and Management*, 255(8–9), 3130–3140.
- Elsasser, A. B. (1981). Notes on Yana Ethnobotany. *Journal of California and Great Basin Anthropology*. Malki Museum, Inc.
- Engber, E. A., & Varner, J. M. (2012). Predicting Douglas-fir Sapling Mortality Following Prescribed Fire in an Encroached Grassland. *Restoration Ecology*, 20(6), 665–668.

- Estes, B. L., Knapp, E. E., Skinner, C. N., Miller, J. D., & Preisler, H. K. (2017). Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA. *Ecosphere*, 8(5).
- Fettig, C. J., Klepzig, K. D., Billings, R. F., Munson, A. S., Nebeker, T. E., Negrón, J. F., & Nowak, J. T. (2007). The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*, 238(1–3), 24–53.
- Frankin, J.F. & Agee J. K. (2003). Forging a Science-Based National Forest Fire Policy. Issues in Science and Technology. University of Texas at Dallas.
- Franklin, J. F., & Johnson, K. N. (2012). A restoration framework for federal forests in the Pacific Northwest. *Journal of Forestry*, 110, 429–439.
- Fry, D. L., & Stephens, S. L. (2010). Stand-level spatial dependence in an old-growth Jeffrey pine – mixed conifer forest, Sierra San Pedro Mártir, Mexico. *Canadian Journal of Forest Research*, 40(9), 1803–1814.
- Fry, D. L., Stephens, S. L., Collins, B. M., North, M. P., Franco-Vizcaíno, E., & Gill, S. J. (2014). Contrasting Spatial Patterns in Active-Fire and Fire-Suppressed Mediterranean Climate Old-Growth Mixed Conifer Forests. *PLoS ONE*, 9(2), e88985.
- Fulé, P. Z., Covington, W. W., & Moore, M. M. (1997). Determining Reference Conditions for Ecosystem Management of Southwestern Ponderosa Pine Forests. *Ecological Applications*, 7(3), 895–908.
- Fulé, P. Z., Crouse, J. E., Cocke, A. E., Moore, M. M., & Covington, W. W. (2004). Changes in canopy fuels and potential fire behavior 1880–2040: Grand Canyon, Arizona. *Ecological Modelling*, 175(3), 231–248.
- Fulé, P. Z., García-Arévalo, A., & Covington, W. W. (2000). Effects of an Intense Wildfire in a Mexican Oak-Pine Forest. *Forest Science*, 46(1), 52–61.
- Getis, A., & Franklin, J. (1987). Second-Order Neighborhood Analysis of Mapped Point Patterns. *Ecology*, 68(3), 473–477.
- Hagmann, R. K., Franklin, J. F., & Johnson, K. N. (2013). Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. *Forest Ecology and Management*, 304, 492–504.
- Hammett, E. J., Ritchie, M. W., & Berrill, J.-P. (2017). Resilience of California Black Oak Experiencing Frequent Fire: Regeneration Following Two Large Wildfires 12 Years Apart. *Fire Ecology*, 13(1), 91–103.
- Harris, L., & Taylor, A. H. (2015). Topography, Fuels, and Fire Exclusion Drive Fire Severity of the Rim Fire in an Old-Growth Mixed-Conifer Forest, Yosemite National Park, USA. *Ecosystems*, 18(7), 1192–1208.
- Hegyí, F. (1974). A simulation model for managing jack-pine stand. In *Growth Models for Tree and Stand Simulation* (pp. 74–90). Stockholm, Sweden: Royal College of Forestry.
- Heinlein, T. A., Moore, M. M., Fule, P. Z., & Covington, W. W. (2005). Fire history and stand structure of two ponderosa pine – mixed conifer sites: San Francisco Peaks, Arizona, USA. *International Journal of Wildland Fire*, 14, 307–320.
- 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(1–2), 117–139.
- Jackson, J. F., Adams, D. C., & Jackson, U. B. (1999). Allometry of Constitutive Defense: A Model and a Comparative Test with Tree Bark and Fire Regime. *The American Naturalist*, 153(6), 614–632.
- Keane, R. E., Gray, K., & Bacciu, V. (2012). Spatial Variability of Wildland Fuel Characteristics in Northern Rocky Mountain Ecosystems. General Technical Report, USDA Forest Service.
- Keyser, C. E. (2008). Inland California and Southern Cascades (CA) Variant Overview - Forest Vegetation Simulator. Fort Collins, CO.

- Knapp, E. E., Skinner, C. N., North, M. P., & Estes, B. L. (2013). Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management*, 310: 903–914, 310, 903–914.
- Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Report. PSW-GTR-224. Albany, CA: USDA Forest Service, Pacific Southwest Research Station, 80p.
- Larson, A. J., Belote, R. T., Cansler, C. A., Parks, S. A., & Dietz, M. S. (2013). Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecological Applications*, 23(6), 1243–1249.
- 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.
- Latif, Q. S., Saab, V. A., Mellen-Mclean, K., & Dudley, J. G. (2015). Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forest. *The Journal of Wildlife Management*, 79(2), 263–273.
- Long, J. W., Anderson, M. K., Quinn-davidson, L. N., Goode, R. W., Lake, F. K., & Skinner, C. N. (2016). Restoring California black oak ecosystems to promote tribal values and wildlife. In *Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world*. Gen. Tech. Rep. PSW-GTR-251. Redding, California: USDA Forest Service, Pacific Southwest Research Station.
- Long, J. W., Goode, R. W., Gutteriez, R. J., Lackey, J., & Anderson, M. K. (2016). Managing California Black Oak for Tribal Ecocultural Restoration. *Journal of Forestry*, 115, 426–434.
- Lydersen, J. M., North, M. P., Knapp, E. E., & Collins, B. M. (2013). Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. *Forest Ecology and Management*, 304, 370–382.
- Lydersen, J., & North, M. (2012). Topographic Variation in Structure of Mixed-Conifer Forests Under an Active-Fire Regime. *Ecosystems*, 15(7), 1134–1146.
- Main, W., Pananen, D., & Burgan, R. (1999). *FireFamily 1988*. USDA Forest Service General Technical Report NC-138.
- Martinez-Ramos, M., Alvarez-Buylla, E., & Sarukhan, J. (1989). Tree Demography and Gap Dynamics in a Tropical Rain Forest. *Ecology*, 70(3), 555–558.
- Mast, J. N., Fulé, P. Z., Moore, M. M., Covington, W. W., & Waltz, A. E. M. (1999). Restoration of Presettlement Age Structure of an Arizona Ponderosa Pine Forest. *Ecological Applications*, 9(1), 228–239.
- McCarthy, J. (2001). Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Reviews*, 9(1), 1–59.
- McDonald, P. M. (1969). Silvical characteristics of California black oak (*Quercus kelloggii* Newb.). Res. Paper PSW-RP-53. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.
- McDonald, P. M., & Huber, D. W. (1994). California's hardwood resource: status of the industry and an ecosystem management perspective. Gen. Tech. Rep. PSW-GTR-153. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 24 p. (Vol. 153).
- McDonald, P. M., & Tappeiner, J. C. (2002). California's Hardwood Resource: Seeds, Seedlings, and Sprouts of Three Important Forest-Zone Species. Gen. Tech. Rep. PSW-GTR-185. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 39 p. (Vol. 185).
- McIntyre, P. J., Thorne, J. H., Dolanc, C. R., Flint, A. L., Flint, L. E., Kelly, M., & Ackerly, D. D. (2015). Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences of the United States of America*, 112(5), 1458–63.
- Mckenzie, D., Miller, C., & Falk, D. A. (2011). Toward a Theory of Landscape Fire. In *The Landscape Ecology of Fire*. Springer

- 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(7), 1851–1864.
- North, M. P., Stephens, S. L., Collins, B. M., Agee, J. K., Aplet, G., Franklin, J. F., & Fulé, P. Z. (2015). Reform forest fire management: Agency incentives undermine policy effectiveness. *Science (New York, N.Y.)*, 349(6254), 1280–1.
- North, M., Collins, B. M., & Stephens, S. (2012). Using Fire to Increase the Scale, Benefits, and Future Maintenance of Fuels Treatments. *Journal of Forestry*, 392–401.
- 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(2), 331–342.
- North, M., Oakley, B., Fiegner, R., Gray, A., & Barbour, M. (2005). Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecology*, 177(1), 13–24.
- North, M., Stine, P., O'hara, K., Zielinski, W., & Stephens, S. (2009). An Ecosystem Management Strategy for Sierran Mixed- Conifer Forests.
- Parks, S. A., Miller, C., Nelson, C. R., & Holden, Z. A. (2014). Previous Fires Moderate Burn Severity of Subsequent Wildland Fires in Two Large Western US Wilderness Areas. *Ecosystems*, 17(1), 29–42.
- Peterson, D. L., & Ryan, K. C. (1986). Modeling postfire conifer mortality for long-range planning. *Environmental Management*, 10(6), 797–808.
- Pimont, F., Dupuy, J.-L., Linn, R. R., & Dupont, S. (2011). Impacts of tree canopy structure on wind flows and fire propagation simulated with FIRETEC. *Annals of Forest Science*, 68(3), 523–530.
- Plotkin, J. B., Chave, J., & Ashton, P. S. (2002). Cluster Analysis of Spatial Patterns in Malaysian Tree Species. *The American Naturalist*, 160(5), 629–644.
- Purcell, K. L., Mazzoni, A. K., Mori, S. R., & Boroski, B. B. (2009). Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. *Forest Ecology and Management*, 258(12), 2696–2706.
- Purcell, K., & Drynan, D. (2008). Use of Hardwood Tree Species by Birds Nesting in Ponderosa Pine Forests. In: Merenlender, Adina; McCreary, Douglas; Purcell, Kathryn L., Tech. Eds. 2008. *Proceedings of the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities*. Gen. Tech. Rep. PSW-GTR-217. Albany, CA: U.S. Department of Agriculture, Fore, 217, 417–431.
- Quigley, T. M., Haynes, R. W., & Graham, R. T. (1996). Integrated scientific assessment for ecosystem management in the interior Columbia Basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-382. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- R Core Team. (2013). *A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing. Vienna Austria.
- Reinhardt, E. D., & Crookston, N. L. (2003). *The Fire and Fuels Extension to the Forest Vegetation Simulator*. General Technical Report, USDA Forest Service.
- Ritchie, M. W., Skinner, C. N., & Hamilton, T. A. (2007). Probability of tree survival after wildfire in an interior pine forest of northern California: Effects of thinning and prescribed fire. *Forest Ecology and Management*, 247(1–3), 200–208.
- Runkle, J. R. (1990). Gap dynamics in an Ohio Acer – Fagus forest and speculations on the geography of disturbance. *Canadian Journal of Forest Research*, 20(5), 632–641.
- Runkle, J. R. (1981). Gap Regeneration in Some Old-growth Forests of the Eastern United States. *Ecology*, 62(4), 1041–1051.
- Ryan, K. C., Knapp, E. E., & Varner, J. M. (2013). Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the Environment*, 11(s1), e15–e24.
- 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(4), 490–499.

- Schneider, E. E., Sánchez Meador, A. J., & Covington, W. W. (2016). Reference conditions and historical changes in an unharvested ponderosa pine stand on sedimentary soil. *Restoration Ecology*, 24(2), 212–221.
- 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(2), 362–380.
- 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 : A Publication of the Ecological Society of America*, 20(2), 362–80.
- Schulz, P. E. (1988). *Indians of Lassen: Volcanic National Park and Vicinity*. Loomis Museum Association.
- Scott, J. H., & Burgan, R. E. (2005). *Standard Fire Behavior Fuel Models : A Comprehensive Set for Use with Rothermel's Surface Fire Spread Model of Agriculture Standard Fire Behavior Fuel Models : A Comprehensive Set for Use with Rothermel' s Surface Fire Spread Model*. General Technical Report, USDA Forest Service.
- Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., & Teste, F. P. (2012). Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews*, 26(1), 39–60.
- Skinner, C. N. (1995). Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. *Landscape Ecology*, 10(4), 219–228.
- Skinner, C. N., Taylor, A. H., & Agee, J. K. (2006). Klamath Mountains bioregion. In: N. G. Sugihara, J. W. van Wagtenonk, J. Fites-Kaufmann, K. E. Shaffer, and A. E. Thode, Editors. 2006. *Fire in California's Ecosystems*. University of California Press, Berkeley. Pp. 170-194, 170–194.
- Spies, T. A., & Franklin, J. F. (1989). Gap Characteristics and Vegetation Response in Coniferous Forests of the Pacific Northwest. *Ecology*, 70(3), 543–545.
- 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(6), 693–702.
- Stephens, S. L., Fry, D. L., & Franco-Vizcaíno, E. (2008). Wildfire and spatial patterns in forests in northwestern Mexico: the United State wishes it had similiar fire problems. *Ecology and Society*, 13(2).
- Stephens, S. L., & Gill, S. J. (2005). Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in north-western Mexico. *Forest Ecology and Management*, 205(1–3), 15–28.
- Stephens, S. L., Lydersen, J. M., Collins, B. M., Fry, D. L., & Meyer, M. D. (2015). Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere*, 6(5).
- Stephens, S. L., Finney, M. A., & Schantz, H. (2004). Bulk Density and Fuel Loads of Ponderosa Pine and White Fir Forest. *Northwest Sceince*, 78(2), 93–100.
- Stephens, S. L., & Fulé, P. Z. (2005). Western Pine Forests with Continuing Frequent Fire Regimes: Possible Reference Sites for Management. *Journal of Forestry*, 358–362.
- Stephens, S. L., Millar, C. I., & Collins, B. M. (2010). Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. *Environmental Research Letters*, 5(2), 24003.
- Stevens, J. T., Safford, H. D., North, M. P., Fried, J. S., Gray, A. N., Brown, P. M., ... Taylor, A. H. (2016). Average Stand Age from Forest Inventory Plots Does Not Describe Historical Fire Regimes in Ponderosa Pine and Mixed-Conifer Forests of Western North America. *PLOS ONE*, 11(5).
- Steward, L. O. (1935). *Public Land Surveys: History, Instructions, Methods*. Collegiate Press Incorporated, 1935.
- Taylor, A. H. (2000). Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. *Journal of Biogeography*, 27(1), 87–104.

- Taylor, A. H. (2010). Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *Journal of Vegetation Science*, 21(3), 561–572.
- Taylor, A. H. (2004). Identifying Forest Reference Conditions on Early Cut-Over Lands, Lake Tahoe Basin, USA. *Ecological Applications*, 14(6), 1903–1920.
- Taylor, A. H., Jinyan, H., & ShiQiang, Z. (2004). Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies*–*Betula* forests in southwestern China: a 12-year study. *Forest Ecology and Management*, 200(1–3), 347–360.
- Taylor, A. H., & Skinner, C. N. (2003). Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, 13(3), 704–719.
- Taylor, A. H., Vandervlugt, A. M., Maxwell, R. S., Beaty, R. M., Airey, C., & Skinner, C. N. (2014). Changes in forest structure, fuels and potential fire behaviour since 1873 in the Lake Tahoe Basin, USA. *Applied Vegetation Science*, 17(1), 17–31.
- Taylor, A. H., Vandervlugt, A. M., Maxwell, R. S., Beaty, R. M., Airey, C., & Skinner, C. N. (2014). Changes in forest structure, fuels and potential fire behaviour since 1873 in the Lake Tahoe Basin, USA. *Applied Vegetation Science*, 17(1), 17–31.
- Thompson, J. R., & Spies, T. A. (2010). Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. *Landscape Ecology*, 25(5), 775–789. <https://doi.org/10.1007/s10980-010-9456-3>
- 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. *Forest Ecology and Management*, 262(2), 215–228.
- Wagner, C. E. Van. (1977). Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research*, 7(1), 23–34.
- Wagner, C. E. Van. (1993). Prediction of crown fire behavior in two stands of jack pine. *Canadian Journal of Forest Research*, 23(3), 442–449.
- Webster, K. M., & Halpern, C. B. (2010). Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere*, 1(5), art9.
- WF, L., Darr, H., & Smith, S. (1989). Historical effects of forest management practices on eastside pine communities in northeastern California. USDA Forest Service General Technical Report RM-267, 37–387.
- White, A. S. (1985). Presettlement Regeneration Patterns in a Southwestern Ponderosa Pine Stand. *Ecology*, 66(2), 589–594.
- Yamada, I., & Rogerson, P. A. (2003). An Empirical Comparison of Edge Effect Correction Methods Applied to K-function Analysis. *Geographical Analysis*, 35(2), 97–109.
- York, R. A., Heald, R. C., Battles, J. J., & York, J. D. (2004). Group selection management in conifer forests: relationships between opening size and tree growth. *Canadian Journal of Forest Research*, 34(3), 630–641.

APPENDIX – SUPPLEMENTAL INFORMATION

Table A1. Proportion of trees clustered in different cluster sizes at different intertree distances for each of the six plots in 2000 and 2016

Year	Plot	Intertree Distance (m)	Individual (1 tree)	Small (2-4 trees)	Medium (5-9 trees)	Large (10-15 trees)	Extra Large (16+ trees)
2000	1	1	0.819	0.181	0	0	0
2000	1	2	0.53	0.47	0	0	0
2000	1	3	0.434	0.446	0	0.12	0
2000	1	4	0.253	0.506	0.096	0.145	0
2000	1	5	0.169	0.47	0.217	0.145	0
2000	1	6	0.12	0.277	0.145	0	0.458
2000	1	7	0.108	0.169	0.06	0	0.663
2000	1	8	0.072	0.145	0.12	0	0.663
2000	1	9	0.072	0.145	0.06	0	0.723
2000	1	10	0.072	0.145	0.06	0	0.723
2000	1	11	0.072	0.145	0.06	0	0.723
2000	1	12	0.072	0.12	0.06	0	0.747
2000	2	1	0.907	0.093	0	0	0
2000	2	2	0.86	0.14	0	0	0
2000	2	3	0.636	0.318	0.047	0	0
2000	2	4	0.45	0.372	0.178	0	0
2000	2	5	0.349	0.326	0.248	0.078	0
2000	2	6	0.24	0.341	0.178	0.24	0
2000	2	7	0.178	0.295	0.202	0.326	0
2000	2	8	0.085	0.217	0.07	0.496	0.132
2000	2	9	0.039	0.054	0.054	0.178	0.674
2000	2	10	0.023	0.062	0	0	0.915
2000	2	11	0.023	0.062	0	0	0.915
2000	2	12	0.016	0.031	0	0	0.953
2000	3	1	0.888	0.112	0	0	0
2000	3	2	0.784	0.216	0	0	0
2000	3	3	0.483	0.517	0	0	0
2000	3	4	0.379	0.379	0.147	0.095	0
2000	3	5	0.31	0.207	0.276	0	0.207
2000	3	6	0.233	0.138	0.207	0.198	0.224
2000	3	7	0.147	0.129	0.19	0.103	0.431
2000	3	8	0.129	0.138	0.19	0.103	0.44
2000	3	9	0.086	0.052	0.31	0.103	0.448
2000	3	10	0.06	0.043	0.241	0.103	0.552
2000	3	11	0.052	0.043	0.121	0.129	0.655
2000	3	12	0.017	0.06	0.129	0.129	0.664
2000	4	1	0.918	0.082	0	0	0
2000	4	2	0.734	0.266	0	0	0

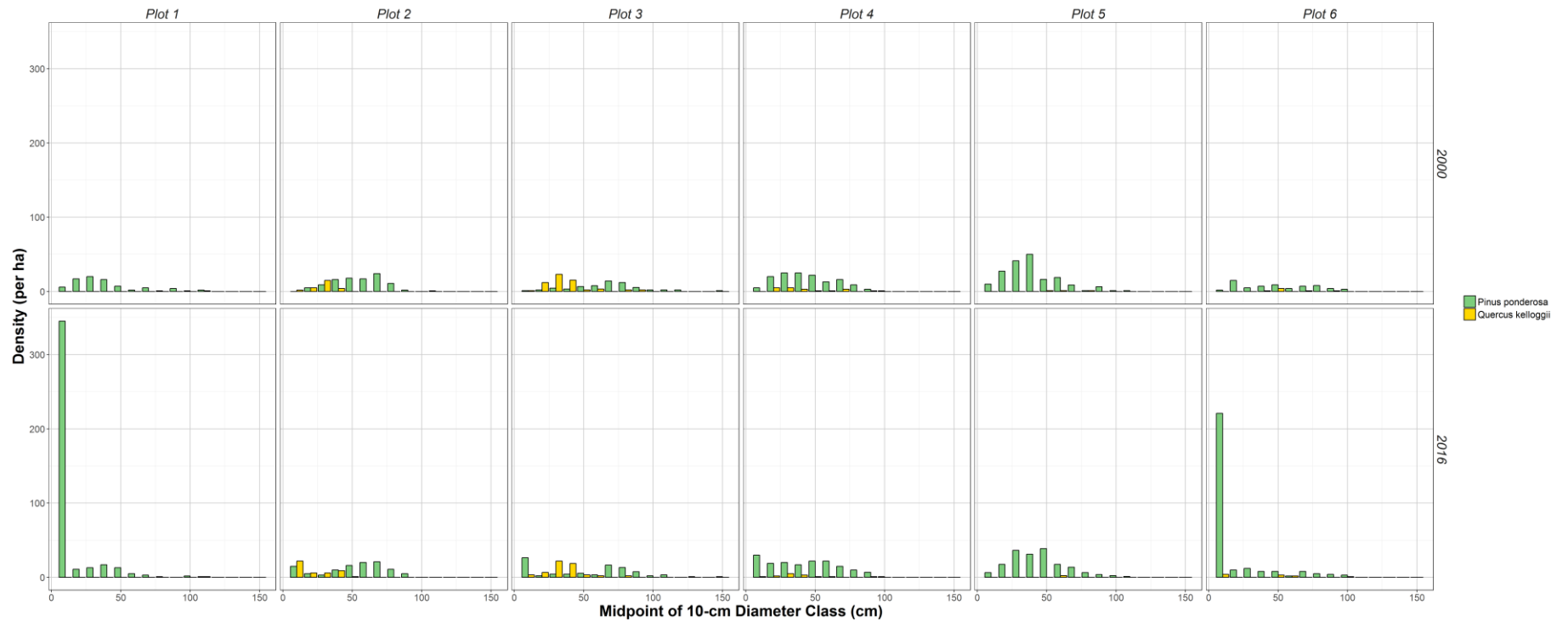
Year	Plot	Intertree Distance (m)	Individual (1 tree)	Small (2-4 trees)	Medium (5-9 trees)	Large (10-15 trees)	Extra Large (16+ trees)
2000	4	3	0.506	0.449	0.044	0	0
2000	4	4	0.291	0.532	0.177	0	0
2000	4	5	0.165	0.361	0.335	0.139	0
2000	4	6	0.051	0.253	0.234	0.462	0
2000	4	7	0.032	0.082	0.032	0.07	0.785
2000	4	8	0.025	0.032	0	0	0.943
2000	4	9	0.019	0.032	0	0	0.949
2000	4	10	0.019	0.032	0	0	0.949
2000	4	11	0.019	0.032	0	0	0.949
2000	4	12	0.006	0.044	0	0	0.949
2000	5	1	0.894	0.106	0	0	0
2000	5	2	0.636	0.364	0	0	0
2000	5	3	0.397	0.536	0.066	0	0
2000	5	4	0.238	0.464	0.298	0	0
2000	5	5	0.146	0.278	0.325	0.252	0
2000	5	6	0.093	0.212	0.099	0.099	0.497
2000	5	7	0.046	0.113	0.113	0.073	0.656
2000	5	8	0.04	0.073	0.113	0	0.775
2000	5	9	0.026	0.04	0.119	0	0.815
2000	5	10	0.02	0.013	0.119	0	0.848
2000	5	11	0.02	0.013	0.119	0	0.848
2000	5	12	0.02	0.013	0.073	0	0.894
2000	6	1	0.895	0.105	0	0	0
2000	6	2	0.737	0.263	0	0	0
2000	6	3	0.421	0.579	0	0	0
2000	6	4	0.329	0.605	0.066	0	0
2000	6	5	0.276	0.618	0.105	0	0
2000	6	6	0.211	0.539	0.25	0	0
2000	6	7	0.184	0.408	0.25	0.158	0
2000	6	8	0.171	0.197	0.474	0.158	0
2000	6	9	0.145	0.197	0.395	0	0.263
2000	6	10	0.092	0.079	0.171	0	0.658
2000	6	11	0.079	0.079	0.105	0	0.737
2000	6	12	0.053	0.079	0	0	0.868
2016	1	1	0.447	0.369	0.133	0.051	0
2016	1	2	0.175	0.201	0.114	0.117	0.393
2016	1	3	0.121	0.136	0.032	0.024	0.687
2016	1	4	0.083	0.112	0.051	0.027	0.728
2016	1	5	0.051	0.078	0.068	0.053	0.75
2016	1	6	0.032	0.024	0.073	0.024	0.847
2016	1	7	0.027	0.024	0.061	0.024	0.864
2016	1	8	0.012	0.019	0.029	0.027	0.913

Year	Plot	Intertree Distance (m)	Individual (1 tree)	Small (2-4 trees)	Medium (5-9 trees)	Large (10-15 trees)	Extra Large (16+ trees)
2016	1	10	0.007	0.012	0.029	0.027	0.925
2016	1	11	0.007	0.012	0.017	0.027	0.937
2016	1	12	0.007	0.005	0.017	0.034	0.937
2016	2	1	0.759	0.203	0.038	0	0
2016	2	2	0.658	0.304	0.038	0	0
2016	2	3	0.557	0.361	0.082	0	0
2016	2	4	0.354	0.449	0.133	0.063	0
2016	2	5	0.266	0.373	0.234	0.127	0
2016	2	6	0.196	0.329	0.278	0.196	0
2016	2	7	0.12	0.19	0.247	0.323	0.12
2016	2	8	0.057	0.19	0.158	0.342	0.253
2016	2	9	0.025	0.095	0.108	0.127	0.646
2016	2	10	0.019	0.057	0.032	0.152	0.741
2016	2	11	0	0.063	0.032	0.089	0.816
2016	2	12	0	0.038	0	0	0.962
2016	3	1	0.81	0.19	0	0	0
2016	3	2	0.635	0.248	0.117	0	0
2016	3	3	0.467	0.387	0	0	0.146
2016	3	4	0.321	0.277	0.161	0.073	0.168
2016	3	5	0.226	0.226	0.27	0.095	0.182
2016	3	6	0.153	0.139	0.27	0.255	0.182
2016	3	7	0.109	0.146	0.182	0.073	0.489
2016	3	8	0.08	0.131	0.175	0.073	0.54
2016	3	9	0.058	0.088	0.146	0.073	0.635
2016	3	10	0.044	0.051	0.102	0.073	0.73
2016	3	11	0.022	0.066	0.102	0.073	0.737
2016	3	12	0.022	0.066	0	0.175	0.737
2016	4	1	0.87	0.13	0	0	0
2016	4	2	0.65	0.311	0.04	0	0
2016	4	3	0.418	0.475	0.107	0	0
2016	4	4	0.277	0.497	0.226	0	0
2016	4	5	0.147	0.345	0.311	0.198	0
2016	4	6	0.056	0.26	0.294	0.282	0.107
2016	4	7	0.034	0.153	0.113	0.056	0.644
2016	4	8	0.028	0.085	0.113	0	0.774
2016	4	9	0.017	0.056	0.034	0	0.893
2016	4	10	0.011	0.056	0.034	0	0.898
2016	4	11	0.011	0.056	0.034	0	0.898
2016	4	12	0.011	0.056	0.034	0	0.898
2016	5	1	0.916	0.084	0	0	0
2016	5	2	0.741	0.259	0	0	0
2016	5	3	0.517	0.378	0.105	0	0

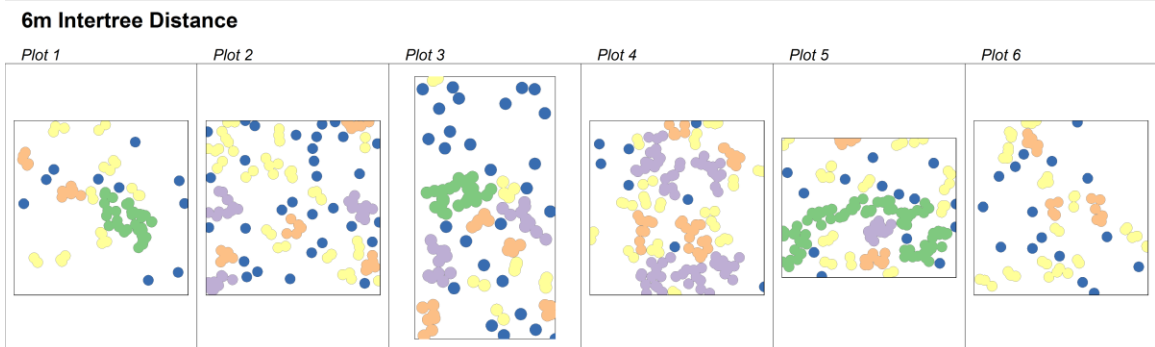
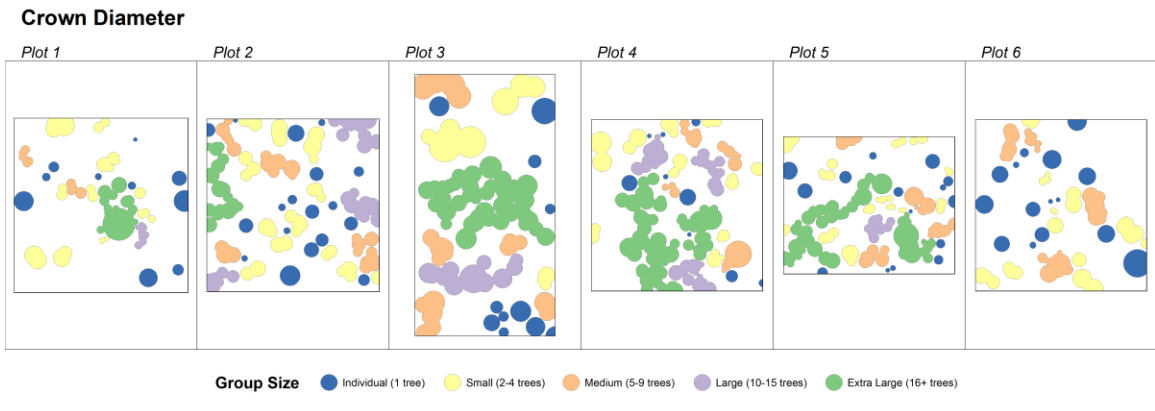
Year	Plot	Intertree Distance (m)	Individual (1 tree)	Small (2-4 trees)	Medium (5-9 trees)	Large (10-15 trees)	Extra Large (16+ trees)
2016	5	4	0.287	0.58	0.133	0	0
2016	5	5	0.182	0.308	0.287	0.091	0.133
2016	5	6	0.126	0.231	0.189	0.189	0.266
2016	5	7	0.084	0.175	0.077	0.175	0.49
2016	5	8	0.028	0.112	0.077	0	0.783
2016	5	9	0.021	0.014	0.119	0	0.846
2016	5	10	0.021	0.014	0.119	0	0.846
2016	5	11	0.021	0.014	0.119	0	0.846
2016	5	12	0.021	0.014	0.077	0	0.888
2016	6	1	0.581	0.314	0.071	0.034	0
2016	6	2	0.304	0.307	0.186	0.074	0.128
2016	6	3	0.155	0.247	0.034	0.22	0.345
2016	6	4	0.091	0.209	0.095	0	0.605
2016	6	5	0.071	0.166	0.084	0.037	0.642
2016	6	6	0.054	0.115	0.084	0	0.747
2016	6	7	0.047	0.074	0.057	0	0.821
2016	6	8	0.03	0.081	0.057	0	0.831
2016	6	9	0.014	0.051	0.098	0	0.838
2016	6	10	0.014	0.027	0.03	0	0.929
2016	6	11	0.003	0.014	0.03	0	0.953
2016	6	12	0.003	0.014	0.03	0	0.953

Table 2A. Matrices comparing proportion of trees classified into cluster types for 2000 and 2016 between two clustering methods – fixed radius 6m intertree distances (columns) and variable radius, crown diameters (rows). Proportions are pooled for all six ~1ha plots and similar classifications between methods are highlighted in gray.

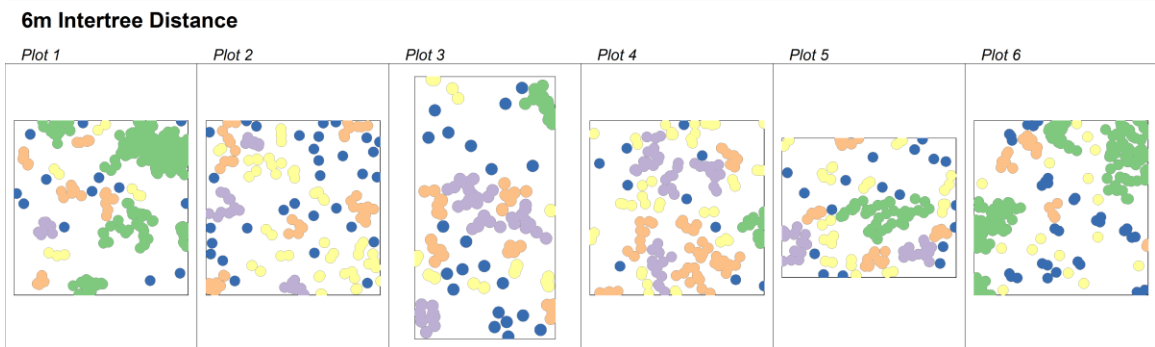
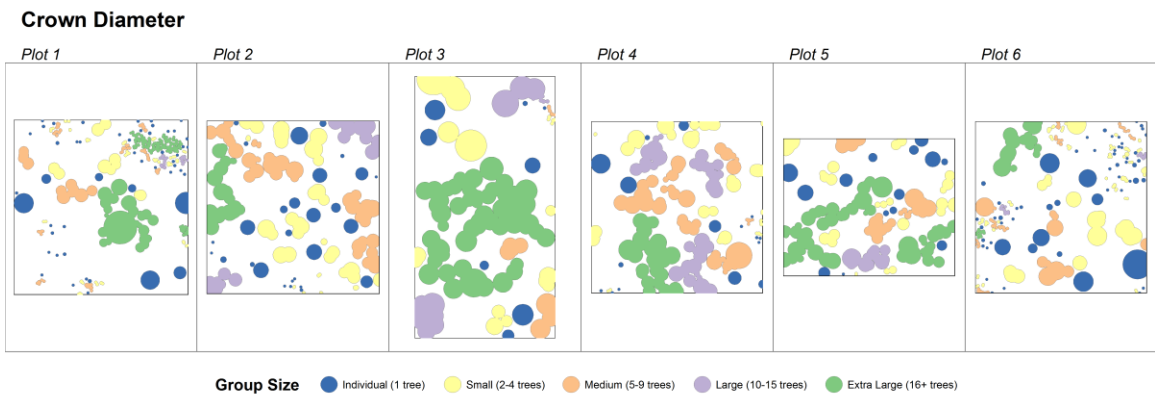
		2000				
		6m Intertree Distance Types				
		Individual	Small	Medium	Large	Extra Large
Crown Diameter Types	Individual	0.77	0.10	0.05	0.05	0.03
	Small	0.12	0.64	0.76	0.05	0.12
	Medium	0.05	0.23	0.53	0.11	0.07
	Large	0.07	0.07	0.06	0.71	0.10
	Extra Large	0.06	0.18	0.13	0.18	0.45
		2016				
		6m Intertree Distance Types				
		Individual	Small	Medium	Large	Extra Large
Crown Diameter Types	Individual	0.36	0.05	0.06	0.06	0.48
	Small	0.05	0.38	0.03	0.03	0.50
	Medium	0.02	0.12	0.26	0.08	0.52
	Large	0.04	0.01	0.22	0.41	0.32
	Extra Large	0.05	0.10	0.27	0.26	0.32



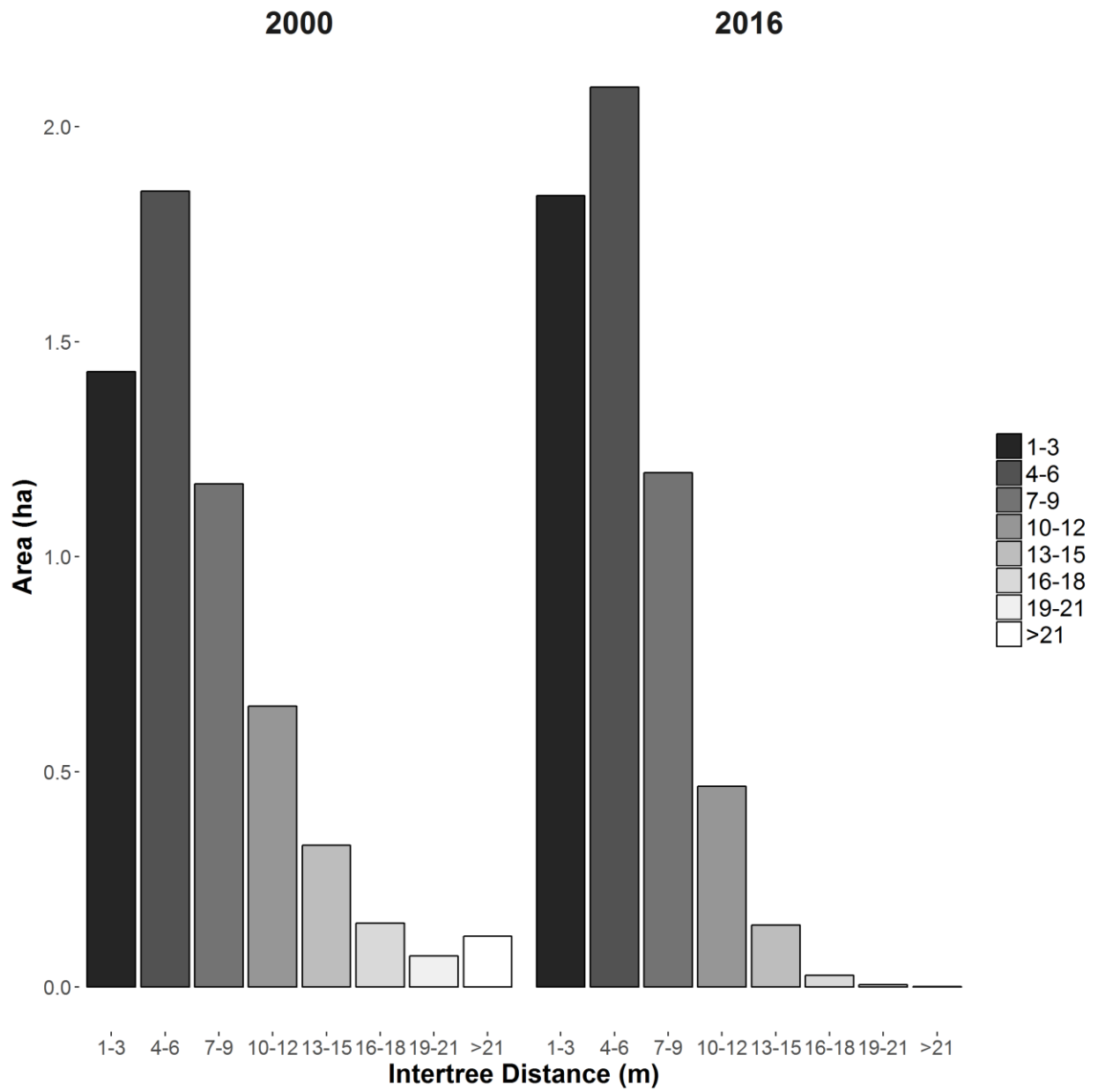
Appendix Figure 1. Diameter distributions of living *P. ponderosa* (green) and *Q. kelloggii* (yellow) trees in 2000 (top) and 2016 (bottom) for each ~1ha plot in the Beaver Creek Pinery.



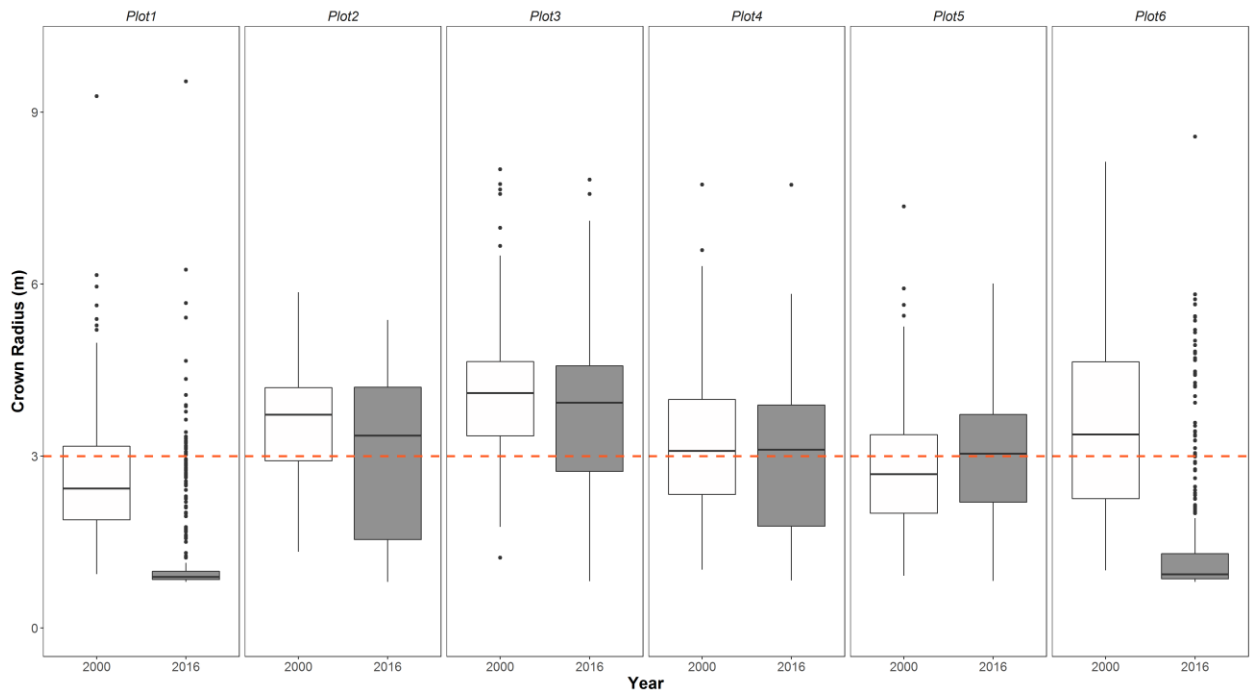
Appendix Figure 2. Maps of tree group sizes using the crown diameter clustering method (top) and 6m intertree distance method (bottom) for all living trees in all six plots in 2000.



Appendix Figure 3. Maps of tree group sizes using the crown diameter clustering method (top) and 6m intertree distance method (bottom) for all living trees in all six plots in 2016.



Appendix Figure 4. Pooled plot area in different distance to nearest tree bins (3m intervals), indicating the availability of open space in 2000 (left) and 2016 (right)



Appendix Figure 5. Estimates of crown radii in 2000 (white) and 2016 (gray) for all six ~1ha plots in the Beaver Creek Pinery. The dotted orange line represents a crown radii of 3m which corresponds to a 6m intertree distance.