Use of a forest reconstruction model to assess changes to Sierra Nevada mixed-conifer forest conditions during the fire suppression era

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USE OF A FOREST RECONSTRUCTION MODEL TO ASSESS CHANGES TO SIERRA NEVADA MIXED-CONIFER FOREST CONDITIONS DURING THE FIRE SUPPRESSION ERA

By

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Fire suppression has resulted in dramatic changes to species composition and structural diversity in the Sierra Nevada mixed-conifer forests of California. Advancing the ecological understanding and management of these forests requires a better understanding of changes that occurred during the fire suppression era, but empirical historical datasets are rare and methodologies for developing new historical reference information are subject to many limitations. I sought to develop historical reference information for the Yosemite Forest Dynamics Plot (YFDP), a research plot located in an old-growth mixed-conifer stand in Yosemite National Park. I performed a dendrochronological fire history analysis to characterize the historical fire regime of the YFDP (pre-1900 fire return interval: 29.5 years). I then developed two different forest reconstruction models to estimate pre-suppression forest conditions. Two alternative tree growth models, one regionally-parameterized and one locally-parameterized, and a decay model based on published estimates of tree decay rates were evaluated. Limited tree decay data available in the literature is a source of uncertainty in forest reconstructions, both for this study and other studies in the Sierra Nevada. Model analysis demonstrated that the regionally-parameterized growth model resulted in unreasonably fast tree growth rates. The site-specific growth model produced results similar to empirical historical datasets (84.5 trees ha⁻¹ and 25.7 m² ha⁻¹ in 1900) – I utilized these results to investigate patterns of tree establishment during the fire suppression era. I found evidence for spatial attraction between early ingrowth (trees that established between 1930 and 1970) sugar pine and legacy trees (trees established before 1930) and spatial repulsion between late ingrowth (trees that established after 1970) sugar pine and legacy trees. This indicates that fire suppression is driving changes to intertree relationships, causing current tree spatial patterns to be outside of their historical range and variability. These results highlight the need for a substantial increase in research efforts regarding tree decay data for Sierra Nevada mixed-conifer forests. When developing restoration targets, managers should avoid a “one size fits all” approach and consider site-specific factors, such as parent material and the historical fire regime, which have influenced changes to forest conditions during the fire suppression era.
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CHAPTER 1
INTRODUCTION

Fire suppression has resulted in dramatic changes to species composition and structural diversity in dry coniferous forests across the western United States (Abella et al. 2007). The mixed-conifer forests of the Sierra Nevada in California, including those in Yosemite National Park (Yosemite), are no exception (Scholl and Taylor 2010). For decades, scientists have been documenting the ecological changes associated with fire suppression across the Sierra Nevada mixed-conifer forests, ranging from increased tree densities and a greater abundance of shade-tolerant species (Parsons and DeBenedetti 1979, Bonnicksen and Stone 1982), increases in fire size and severity (Miller et al. 2009), a decline of large-diameter trees (Lutz et al. 2009), and the spread of invasive pathogens (van Mantgem et al. 2004). Climate change will likely confound these ecological problems, bringing a continued increase in fire frequency and severity (Miller and Urban 1999), tree species range shifts (Lutz et al. 2010), declines in forest productivity (Battles et al. 2008), drought-triggered tree mortality (Guarín and Taylor 2005), and a loss of biological diversity (Stephenson and Parsons 1993). Given the significant alteration of these forests and the uncertain ecological impacts of future climate change, it is imperative that we exercise timely, adaptive management and restoration based on the best available science if we hope to sustain western dry forests and the ecological services they provide in the future.

Evaluating the historical range of variability (HRV) of the compositional, structural, and functional attributes of a forested ecosystem (known as “reference conditions”) is a benchmark for assessing forest change over time and provides us with an improved understanding of the natural dynamics of these systems (Landres et al. 1999). Restoration strategies that consider a forest’s HRV to both assess degradation and guide restoration targets are more likely to improve
ecological adaptive capacity towards future disturbances and climate change (Keane et al. 2009). Unfortunately, historical datasets for the Sierran mixed-conifer forests are rare, especially for Yosemite, and use of limited historical data to guide range-wide restoration may result in unintended ecological consequences. Forest reconstructions, which use contemporary inventories of live and dead trees to estimate forest structure and composition at some point in the past, are a technique to expand the availability of reference information, especially when historical datasets are lacking (Fulé et al. 1997).

The Yosemite Forest Dynamics Plot (YFDP) is a long-term research installation located in Yosemite National Park, California, USA (Figure 1). The YFDP is situated in the Rockefeller Grove, an old-growth white fir—sugar pine (Abies concolor—Pinus lambertiana) forest (Lutz et al. 2012, Gabrielson et al. 2012) (Figure 2). The goals of the YFDP project include detecting and attributing change in mixed-conifer forest ecosystems and providing scientific data to inform future forest management in Yosemite and the greater Sierra Nevada (Lutz et al. 2012). The YFDP is the largest contiguous study plot in the western dry forests (25.6 ha in size and roughly 40,000 mapped live and dead trees) (Figure 3) and provides scientists with the opportunity to investigate aspects of mixed-conifer forests not previously attainable with smaller, non-contiguous study plots.

The YFDP was established in 2009 and we therefore lack historical reference data with which to assess the degree to which the plot has changed during the fire suppression era and to frame interpretation of contemporary data and analyses. A forest reconstruction of the YFDP to the onset of fire suppression can expand the breadth of knowledge attainable from this research installation. A historical reconstruction of the YFDP would allow new inferences about the
HRV of mixed-conifer systems and to better understand how these forests have changed over the past century, all at a high spatial resolution.

Forest reconstructions are an invaluable research tool and are worth improving, despite some inherent limitations to the method. For example, most reconstructions use estimates of tree decay rates to assess each dead tree’s presence and size during the reference year, however our understanding of tree decay in western coniferous forests, especially Sierra Nevada mixed-conifer forests, is very limited (Harmon et al. 1987, Morrison and Raphael 1993). Uncertainties in methodologies can have the potential to introduce biases and inaccuracies into reconstructed results; however no previous study has ever systematically investigated the impact of methodological uncertainties on reconstruction estimates of forest attributes. If we use reference information developed from forest reconstructions to assess ecological change or guide management, it is essential that we have a nuanced understanding about the accuracy and limitations of reconstruction models.

The overall goals of this study are to expand the availability of information needed for scientists to better detect and attribute ecological changes that have occurred in Sierra Nevada mixed-conifer forests during the fire suppression era as well as to provide forest managers with reference information to help guide restoration goals in these forests. Specifically, our objectives are to:

1) Use dendrochronological records to characterize the historical fire regime of the YFDP;
2) Develop a new forest reconstruction model for Sierra Nevada mixed-conifer forests;
3) Reconstruct historical forest structure, composition, and tree spatial patterns on the YFDP at the time of the last widespread fire;
4) Systematically investigate the influence of uncertainty with respect to tree growth and decay rates on reconstruction model results;

5) Use the validated forest reconstruction model to investigate the spatio-temporal patterns of tree establishment during the fire suppression era.

Sierra Nevada mixed-conifer forests present an opportunity for forest scientists to investigate how the removal of a keystone process—fire—can influence forest dynamics, self-organization, and ecological functions and services. This study will expand the availability of scientific evidence needed to both improve our ecological understanding of these systems as well as address specific research needs identified in contemporary Sierra Nevada mixed-conifer management frameworks (North et al. 2009, North 2012). Through our quantification of uncertainties in reference conditions and our investigation of forest change over the past century at a large spatial scale, scientists and managers in YNP and other Sierra Nevada mixed-conifer forest will be better informed in their decisions to prepare these forests for potential future environmental changes.
Figure 1. The location of the Yosemite Forest Dynamics Plot (YFDP) within Yosemite National Park (purple boundary) in the Sierra Nevada mountains of California (inset), USA.
Figure 2. Characteristic flora and forest structure of the Yosemite Forest Dynamics Plot. Major tree species present include sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and Pacific dogwood (*Cornus nuttallii*). Emergent canopy trees, mostly sugar pine and white fir, are typically $\geq 100$ cm in diameter at breast height (dbh) and as large as 200 cm dbh.
Figure 3. Stem map of the contemporary YFDP, showing the rooting locations of all 35,498 live trees, 2,734 snags, and 696 logs that comprise the dataset.
CHAPTER 1 REFERENCES


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CHAPTER 2
HISTORICAL FIRE REGIME HETERogeneity IN A SIERRA NEvADA MIXED-CONIFER FOREST

1. INTRODUCTION

Fire is an integral ecosystem process in Sierra Nevada mixed-conifer forests (van Wagendonk and Fites-Kaufman 2006) and fire suppression has significantly altered forest structure, composition, and function across the region (Ansley and Battles 1998), including in Yosemite National Park (Yosemite). Therefore, to understand and interpret contemporary Sierra Nevada mixed-conifer forest structure and dynamics, we need to understand the natural disturbance regime prior to fire suppression. This knowledge provides insight into the degree of departure these forests have experienced as compared to historical conditions and allows us to better predict future changes to ecological functions as a result of management efforts and climate change (Scholl and Taylor 2010, Collins et al. 2011). Estimates of historical fire regime attributes at regional scales are useful for understanding fire as a landscape-level process, but site-specific information provides a detailed perspective, which is especially useful when assumptions regarding the historical role of fire may lead to incorrect ecological interpretations and management recommendations (Reinhardt et al. 2008). For example, were the fire return interval to vary considerably in a single forest type, it would have implications for the calculation of fire return interval departure – a metric commonly used to assess the fire risk implied by the period of fire suppression (van Wagendonk et al. 2002).

Historical fires in Sierra Nevada mixed-conifer forests were heterogeneous in size, severity and frequency and similar sites had the potential to experience quite different natural fire regimes (Van de Water and North 2010, Perry et al. 2011). Small-scale topographic variables have been found to affect fire characteristics in some Sierra Nevada mixed-conifer stands...
(Taylor and Skinner 2003, Lydersen and North 2012), but not at others (Phillips and Verner 2002, Scholl and Taylor 2010). Based on studies from across the region, we would expect that a given mixed-conifer stand in Yosemite would have experienced fires every 5-50 years (mean: 11 years) (Van de Water and Safford 2011) with most fires confined to a single slope or drainage (Kilgore and Taylor 1979). While there have been a number of fire history studies throughout the Sierra Nevada, studies in Yosemite that can validate the applicability of these predictions in regards to local fire activity are relatively rare (but see Swetnam et al. 2009, Scholl and Taylor 2010, Collins et al. 2011). Dendrochronological records of past fire events inferred from legacy old-growth trees can provide insight into a stand’s historical fire regime (Agee 1998, Baker 2009). Increasing the availability of site-specific historical fire data improves understanding about the variability natural fire regimes across the mixed-conifer landscape, informs fire management planning, and aids in interpretation of contemporary ecological data.

We conducted a dendrochronological investigation of the natural fire regime of the Yosemite Forest Dynamics Plot (YFDP), a long-term forest dynamics research site in Yosemite. We sought to broaden understanding of natural fire regimes in Sierra Nevada mixed-conifer forests and to determine whether the historical fire regime of the YFDP is consistent with the regional historical fire regime of frequent, non-stand-replacement fires inferred from other sites in this forest type (Beaty and Taylor 2007, Collins and Stephens 2007, Scholl and Taylor 2010). Our specific objectives were to characterize the historical fire regime of the YFDP in terms of point fire return interval (PFRI), fire seasonality, and fire size.
2. METHODS

2.1 Study site

The YFDP is a 25.6 ha permanent plot near Crane Flat in Yosemite, California (37.77ºN, 119.82ºW) (Lutz et al. 2012). Major tree species include sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and California black oak (*Quercus kelloggii*). The YFDP experiences a Mediterranean climate, with hot, dry summers and cool, moist winters, and is situated on a generally north-facing slope at an elevation ranging between 1774 m and 1911 m. Additional information about the physical, biological, and climatological attributes of the YFDP is provided by Lutz et al. (2012) and Gabrielson et al. (2012).

2.2 Field sampling

In 2011 and 2012, we censused the entire plot and immediate area outside the plot boundary for logs and snags with intact, visible fire scars that lacked substantial decay and removed cross-sections from ten sugar pines and two incense cedars (Figure 4). We were not permitted to collect fire scar samples from live trees. We collected increment cores from living trees near the perimeter of the YFDP (coring trees within the YFDP was not permitted). We collected two cores from opposite radii of 35 live incense cedars to develop a site master chronology to facilitate cross-dating of fire scars.

2.3 Lab Work

Cross-sections and increment cores were prepared using standard dendrochronological techniques (Stokes and Smiley 1968). Samples were scanned at a resolution of 1200 dots per inch and growth rings were measured using CooRecorder version 7.5 (Cybis Elektronik & Data AB, Sweden).
We first developed an incense cedar master chronology from 1583–2012 for the Crane Flat area of Yosemite using Cdendro version 7.5 (Cybis Elektronik & Data AB, Sweden). The chronology is cross-dated with other local published chronologies for the area (King and Graumlich 1990), but extends the length of available chronologies by nearly 300 years. The chronology is archived in the NOAA National Climatic Data Center (Barth et al. 2014).

Cross-sections were cross-dated in Cdendro using the site master chronology as well as published chronologies (King and Graumlich 1990) to establish dates for individual tree rings and fire scars. For those samples that could not be cross-dated due to ring complacency (a common challenge in mixed-conifer sites; e.g. Taylor and Skinner 2003, Guarín and Taylor 2005), we established fire years by counting forwards or backwards from the known dates of outer rings or known marker years. Fire scars were assigned to calendar years by identifying characteristic ring disruption and growth and matched to individual ring formation years (McBride 1983). Fire seasonality was inferred from the position of scars within a ring and recorded as occurring in the earlywood, latewood, or dormancy. Scars that fell between two years were said to occur in the dormant season of the earlier year, as fires in this area occur most frequently the dormant season (Caprio and Swetnam 1995). Due to a combination of decay and complacency, we were unable to cross-date five samples.

2.4 Analysis

We calculated point fire return intervals (PFRI) for single trees (Baker 2009) and investigated PFRI at 100 year intervals to assess changes in fire frequency over time. Undated samples were considered separately in interval analysis. We chose not to investigate composite fire return intervals because of our small sample size. We assessed fire size by looking for scars occurring during the same year both across samples. Fire interval statistics were calculated using
the FHX2 software package (Grissino-Mayer 2001) and graphics were made using FHAES (Grissino-Mayer 2001).

We recognized that our fire years may be slightly inaccurate due to our inability to statistically cross-date some samples and the potential for missing and false rings, especially near the scarred portion of the boles (McBride 1983). To quantify the potential effects of dating errors on our fire history parameters, we compared YFDP fire years to years in which large fires occurred at a nearby site in the same watershed, Scholl and Taylor’s (2010) Big Oak Flat (BOF) study area (Figure 5). For this analysis, we assumed that the widespread fires in BOF also burned the YFDP. Eight fires in the YFDP were within three years of widespread fires that occurred in BOF (Scholl and Taylor 2010), and we adjusted the dates of those YFDP fires to match BOF fire years (Arno and Sneck 1977, Means 1989). We explored other dating thresholds, but the three year window yielded the highest increase in matches across sites. We made all calculations with both original and adjusted data.

3. RESULTS

Historical fires on the YFDP occurred with intermediate frequency (Figure 6). Mean PFRI during the pre-suppression period (before 1900) was 29.5 years. Fires were most frequent during the 1600s and decreased in frequency during the 1700s and 1800s (Table 1). Fire frequency was lowest during the 1900s (mean PFRI = 65.4 years), as would be expected with fire suppression, although changes in PRFI were not significant ($P > 0.05$). Using adjusted dates to calculate interval statistics did not produce any material changes (Table 1). On average, the YFDP has not experienced a fire in at least 65 years, with the most recent widespread fire occurring in 1900 (BOF adjusted date: 1899) and most recent smaller fire occurring in 1947. The fire return interval departure for this site is therefore 2.2.
Eight fires (1684, 1712, 1730, 1763, 1818, 1841, 1861, and 1900) were extensive enough to scar two samples located at least 200 m apart (Figure 7). After adjusting fire dates to match widespread BOF fires, we found evidence for six fires (1686, 1706, 1818, 1829, 1841, and 1899) that scarred at least two samples on the YFDP as well as samples in the BOF, indicating larger landscape fires that burned at less than high severity. We found evidence for small, localized fires occurring well into the fire suppression era (i.e. in 1916, 1926, and 1947).

Fires occurred most often late in the growing season and after dormancy (earlywood: 31.8%, latewood: 12.7%, after dormancy: 33.3%), although due to decay and burning of scars we were unable to determine seasonality of 22.2% of scars.

4. DISCUSSION

Fires on the YFDP were consistent with a regime of frequent, non-stand-replacement fires characteristic of other Sierra Nevada mixed-conifer forests. In Sierra Nevada mixed-conifer forests, fires were generally small and burned on only one slope or drainage (Kilgore and Taylor 1979) and most frequently occurred late in the growing season or during dormancy, when lightning ignitions are at their peak (Caprio and Swetnam 1995, Stephens and Collins 2004, Beaty and Taylor 2007, Swetnam et al. 2009). Most fires on the YFDP were small, as evidenced by few samples experiencing scars during the same years, but larger fires were not uncommon (Figure 7), and our samples demonstrate a similar seasonality to regional fires, with most occurring during the late season after dormancy. Similar to other sites in the Sierra Nevada, fire frequency dropped after the late 1800s, when fire suppression began to take effect, yet small, localized fires continued to burn (Swetnam et al. 2009, Scholl and Taylor 2010). Thus, we conclude that historical fire regime of the YFDP is broadly characteristic of other higher productivity sugar pine/white fir forests in the Sierra Nevada.
Mean PRFIs on the YFDP of 30 years (1531–1899) and 39 years (1531–2011) are on the upper end of PRFIs for Sierra Nevada mixed-conifer forests. When compared to the larger landscape, the YFDP experienced fires at roughly the same frequency as similar forest types – the mean PRFI was 10–20 years in northern Sierra Nevada mixed-conifer forests (1649–1921) (Stephens and Collins 2004) and 11–39 years (1700–1975) in Sequoia mixed-conifer stands (Kilgore and Taylor 1979). However, the differences in fire frequency between the YFDP and nearby BOF, located downslope and north of the YFDP on a generally south-facing aspect, highlight the fine-scale heterogeneity of historical mixed-severity fire regimes. A PFRI of 12 years (1575–2002) in BOF was surprisingly shorter than that of the YFDP (Scholl and Taylor, 2010). This difference in PRFI could be attributed to the generally northerly aspect and higher elevation of the YFDP, which likely harbors moister conditions (Stephenson 1998) and is consequently less conducive to fire than BOF (Miller and Urban 1999b).

Historical frequent fires and suppression of widespread fires since the late 1800s have contributed to contemporary tree spatial patterns of the YFDP. Although fires were relatively frequent at some point on the landscape (Figure 7), fire may have been absent for extended periods of time at isolated fire refugia on the plot, as evidenced by high variability in PRFI across samples (Table 1). Heterogeneous fire spread and patchy fire effects have likely contributed to the contemporary spatial patterns of large-diameter white fir trees, which exhibit an aggregated pattern, likely due to clustered establishment in fire refugia and patchy survival after fire (Lutz et al. 2012, 2013, Kolden et al. 2012). Historical fires would have maintained widely-spaced individual trees and smaller tree clumps (Lydersen et al. 2013), removing fire-intolerant ingrowth surrounding more fire-tolerant trees. PFRI reflects the time it takes fuels to accumulate sufficiently to support a fire at a given point (Taylor 2001). Contemporary PRFI (65
years) is well outside of historical PFRI (30 years), suggesting that an accumulation of fuels outside of historical levels are likely contributing to altered forest dynamics during the fire suppression era (Ansley and Battles 1998, Scholl and Taylor 2010). It is likely that, due to a lack of fire, there has been a recent decrease in the number of individual trees, small tree clumps, and forest canopy openings, and a concurrent increase in large tree clumps (Lydersen et al. 2013). Evidence of spatial repulsion between large and small-diameter trees (Lutz et al. 2012) could be a result of a lack of fire over the past century to maintain openings and suitable microsites for seedling establishment near large-diameter trees.

Our objective was to quantify the fire history of a localized area, not the larger landscape, and we consider our methodology appropriate given our objective. Targeting large trees with visible fire scars for sampling can potentially bias estimates of fire frequency to areas more conducive to high-frequency surface fires (Baker and Ehle 2001). However, live large-diameter trees with visible fire scars are common throughout the plot (Figure 8), consistent with our interpretation of a historical fire regime of primarily non-stand-replacement fires. The scars present on a given sample are only a minimum estimate of historical fires, due to the potential for either a fire burning an area, but not scarring a given tree, or the possibility of subsequent fires burning away scars (Dieterich and Swetnam 1984, Agee 1998). Therefore, we may have underestimated PFRI, and fires may have occurred more frequently than expressed in our samples.

While we did not find that fire frequency varied significantly between centuries ($P > 0.05$), as found in other Sierra Nevada mixed conifer stands (Beaty and Taylor 2007, Scholl and Taylor 2010), earlier centuries are not as well represented as more contemporary centuries in our samples. This lack of evidence is due to relatively fast tree decay rates (Harmon et al. 1987),
making it difficult to discern temporal changes in fire frequency. PFRI for undated samples was small (19 years), potentially because these samples were removed from very decayed, older snags and logs, whose fire record extended longer into the past when fires have been found to be more frequent (Caprio and Swetnam 1995, Taylor 2010).

Our study demonstrates that while an understanding of regional pre-suppression fire regimes in Sierra Nevada mixed-conifer forests can be used to inform general trends in past fire frequency, seasonality, and size, site-specific metrics may differ, even between two adjacent areas. Managers seeking to reestablish the natural fire regime, or the vegetation structure and composition that would have been maintained under a natural fire regime, should avoid applying a “one size fits all” approach, and should recognize the potential for local variability in historical fire frequency, which would have resulted from, and contributed to, highly heterogeneous forest structure and composition. We do not suggest that a fire history analysis is required at any given site prior to restoration; rather, we highlight the important contribution of historical fire regime heterogeneity to contemporary forest conditions and encourage managers to incorporate this heterogeneity at multiple spatial scales in the design and implementation of restoration treatments.

ACKNOWLEDGEMENTS

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CHAPTER 2 TABLES

Table 1. Mean point fire return intervals (PFRI) in years as determined from samples collected from dead trees on the Yosemite Forest Dynamics Plot, Yosemite National Park, California, USA. Adjusted dates reflect adjusting eight fire years (≤3 year shift) to match widespread fires documented at the nearby Big Oak Flat study site of Scholl and Taylor (2010).

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<td>1700s</td>
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<td>30.2 (25.3)</td>
</tr>
<tr>
<td>1800s</td>
<td>29.0 (15.5)</td>
<td>28.8 (15.2)</td>
</tr>
<tr>
<td>1900s</td>
<td>65.4 (36.8)</td>
<td>52.3 (38.4)</td>
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<tr>
<td>Pre-1900</td>
<td>29.5 (24.6)</td>
<td>29.6 (24.7)</td>
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<td>All years</td>
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Undated samples Mean PFRI: 18.7 (13.5)
CHAPTER 2 FIGURES

**Figure 4.** Locations of fire-scarred samples collected within and adjacent to the Yosemite Forest Dynamics Plot, Yosemite National Park, California, USA. Diamonds represent samples that we able to cross-date; circles represent samples that we were unable to cross-date.

**Figure 5.** Location of Scholl and Taylor’s (2010) -Big Oak Flat study area in comparison to the YFDP, Yosemite National Park, California, USA. The two sites are located approximately 6 km apart.
Figure 6. Composite fire history diagram of individual scars from the Yosemite Forest Dynamics Plot, Yosemite National Park, California, USA (A). Adjusted dates (B) reflect adjusting eight fire years (≤3 year shift) to match widespread fires documented at the nearby Big Oak Flat study site of Scholl and Taylor (2010).
Figure 7. Distance between samples recording fire events from 1531-2011 on the Yosemite Forest Dynamics Plot, Yosemite National Park, California, USA. Adjusted dates reflect adjusting eight fire years (≤3 year shift) to match widespread fires documented at the nearby Big Oak Flat study site of Scholl and Taylor (2010).

Figure 8. Removing a cross-section from a “catface” fire scar on a standing dead sugar pine tree in on the Yosemite Forest Dynamics Plot, Yosemite National Park, California, USA. Photo: M.A.F. Barth
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CHAPTER 3
QUANTIFYING THE INFLUENCE OF UNCERTAINTY IN FOREST RECONSTRUCTIONS

1. INTRODUCTION

Fire suppression has caused dramatic changes to species composition and structural diversity in historically fire-frequent forests across western North America (Arno et al. 1995, Everett et al. 2000), including the Sierra Nevada mixed-conifer forests of California (Ansley and Battles 1998, Scholl and Taylor 2010). Regionally, Sierra Nevada mixed-conifer forests have missed approximately five fire-return cycles (Caprio and Graber 2000), and the concomitant degree of forest change in the absence of this influential disturbance agent is unprecedented for as long as human records have documented. Fire suppression in the Sierra Nevada has resulted in numerous ecological problems: increasing tree densities have been related to higher mortality rates and increased pathogen and insect activity (Smith et al. 2005, Guarín and Taylor 2005); accumulated fuels have increased the risk of uncharacteristically high-severity fires (Miller et al. 2009); and changes in forest structure and composition impact populations of at-risk wildlife that evolved in fire-dependent habitats (van Wagtendonk and Fites-Kaufman 2006). Studying Sierra Nevada mixed-conifer forests both prior to and during the absence of fire can advance our understanding of fire’s role in shaping complex ecological interactions as well as how these interactions have shifted in a fire-free system.

Recent widespread high-severity fires in mixed-conifer forests demonstrate the need for timely, effective management intervention to reduce the likelihood of future uncharacteristic fires and resultant loss of biological diversity, especially given predicted changes in climate (Stephens et al. 2013). Traditional guidelines for fuel reduction treatments have focused on
establishing tree spacing, basal area targets, and species composition that promote manageable fire severity, rather than restoration of natural forest conditions that would have been maintained by active fire (North 2012). Recently developed range-wide restoration strategies for Sierra Nevada mixed-conifer forests (North et al. 2009, North 2012) encourage restoration practices that create or maintain forest conditions as they would have been prior to human alternation of the natural disturbance regime, in order to increase likelihood of conserving ecosystems services derived from active fire regime forests, including habitat for biological diversity.

1.1 Historical ecology and reference information

Knowledge of historical forest conditions facilitates comparative investigation of forest conditions during an active fire regime and during the present day absence of fire. Such historical reference information may include, but is not limited to, species composition, tree age and size class distributions, tree spatial patterns, and the frequency, timing, and patterns of disturbance events (Foster et al. 1996). Investigation of historical forest conditions provides insight into forest developmental processes and forest responses to environmental perturbations on time scales much longer than our observations of contemporary forests allow (Covington and Moore 1994, Fulé et al. 1997, Swetnam et al. 1999).

Historical reference information is also useful in an applied context, because it can directly inform contemporary forest restoration planning (Swetnam et al. 1999, Churchill et al. 2013). One strategy to restore fire-suppressed forests is to develop target stand-level conditions for restoration projects based on a suite of historical structural and compositional attributes (Landres et al. 1999, Hessburg et al. 1999). The purpose of such restoration approaches is not to replicate historical conditions exactly, but to create or maintain forest conditions associated with
natural disturbance regimes that contributed to forest resilience and adaptability in the past (Hobbs and Norton 1996). Development of restoration targets in line with the historical characteristics of these forests represents our best option for increasing a forest’s ability to adapt in the future (Swetnam et al. 1999, Keane et al. 2009), especially given unknown consequences of management practices and uncertainties in future climate (Hobbs and Norton 1996).

1.2 Forest reconstructions

A forest reconstruction is a research method to estimate stand structure and composition at some point in the past and is especially useful for developing reference conditions where empirical historical data are lacking (Harrod et al. 1999, Everett et al. 2007). While there are a number of potential sources for reference information, such datasets collected during early-settlement timber and land surveys, historical accounts, historical photographs and pollen records (Bonnicksen and Stone 1982), details of stand conditions, which are useful for studying fine-scale forest dynamics, are extremely rare. Forest reconstructions therefore represent our best available option for obtaining new reference information.

Forest reconstructions generally involve incorporating dendrochronological techniques, estimates of tree growth and decay rates, and inventories of live trees, snags, and logs to “grow trees backwards” (Fulé et al. 1997, Bakker et al. 2008). The specific methodology employed varies depending on site characteristics and data collection feasibility. Presence or absence and size of all contemporary live trees at some point in the past can be estimated by analyzing cores extracted from trees or by estimating tree age from age-size regressions or growth rates (Bakker et al. 2008). Estimates of tree decay rates presented in published literature can be used to predict the presence or absence of trees that are currently dead and decaying. In some studies,
researchers extract and analyze cores from dead trees when possible, but often have to revert to using published decay rates to estimate the ages of dead trees because deterioration of tree rings makes dating cores impossible (e.g. Scholl and Taylor 2010, Van de Water and North 2010).

Forest reconstructions are inherently limited in their accuracy because they generally rely on several assumptions, including: 1) all evidence of historical forest structures is detectable during contemporary inventories; 2) the ages of snags and logs can be predicted based on a field classification of tree decay; and 3) tree growth and decay rates are consistent across space and time. While there have been a number of reconstruction studies in Sierra Nevada mixed-conifer forests (Beaty and Taylor 2007, North et al. 2007, Scholl and Taylor 2010, Van de Water and North 2011), given the above limitations, commonly used reconstruction methodologies are likely more appropriate for use in the arid ponderosa pine forests (Moore et al. 2004) where the dendrochronological record is better preserved (Mast et al. 1999), local tree species decay data are available (Bull 1983, Rogers 1984), and tree decay rates are relatively slow (Harmon et al. 1986).

1.3 Forest reconstructions in the Sierra Nevada

Tree decay in Sierra Nevada mixed-conifer forests is relatively rapid (Harmon et al. 1987) and decay rate data are limited, which has the potential to confound uncertainties and introduce errors into reconstructed results. We have a limited understanding of the decay rates of the dominant Sierra Nevada mixed-conifer tree species and how different structures of the same species (i.e., logs versus snags) and trees of different diameter may vary in their rate of decay (Harmon et al. 1986). There is also the potential that evidence of trees that were alive in the reference year may have already decayed beyond the threshold for detection in contemporary
field surveys, which would lead to underestimates of historical tree density. For example, white fir (*Abies concolor*), a ubiquitously abundant species in these forests (Fites-Kaufman et al. 2007), once dead, can have a half-life as brief as 14 years (Harmon et al. 1987). In addition, evidence of small diameter trees of all species may have also disappeared, as small-diameter trees tend to decay more rapidly than larger trees (Harmon et al. 1986). While many reconstruction studies acknowledge that evidence of historical trees, especially small diameter trees, may have disappeared from the contemporary forest, thereby introducing biases into reconstructed estimates, this “missing tree” component has never been investigated.

Quantifying historical reference conditions in the Sierra Nevada mixed-conifer forests with a forest reconstruction is further complicated by the complexity of the natural disturbance regime. Historically, fire was the dominant disturbance agent in mixed-conifer forests, but fires were extremely variable in size, intensity, and severity across time and space (van Wagtendonk and Fites-Kaufman 2006). Mixed-severity fires shaped forest spatial patterns by differentially thinning tree populations, leaving some areas more or less severely burned and produced scattered openings within a matrix of surviving trees (Stephenson et al. 1991, van Wagtendonk and Fites-Kaufman 2006). Large, contiguous data sets are therefore required to capture the high variability inherent to stand structure and composition in this forest type (Lydersen and North 2012), yet reconstructions across large spatial scales are very difficult and seldom attempted. For example, Scholl and Taylor (2010) and Van de Water and North (2011) sampled nested plots at varying resolutions, but even their largest plots were at most 1 ha in size. An increase in study area size, therefore, if often coupled with a decrease in spatial resolution due to data collection feasibility.
Most reconstruction studies, especially those encompassing large areas, exclude small-diameter trees from data collection and analysis. This is generally not problematic in arid systems with a limited understory. The Sierra Nevada mixed-conifer forests, however, are composed of many shade-tolerant tree species, which can grow very slowly in the understory, rendering tree diameter a poor predictor of tree age (Van Pelt 2008). When small-diameter trees are excluded or assumed to be of young age in reconstruction studies, the result could be a potential underestimation of the historical small tree component. Investigations of forest change during the fire-suppression era that do not account for small trees may neglect to identify relationships between small and larger diameter trees, which could be important drivers of forest self-organization and dynamics.

1.4 Study goals

The purpose of this study is to develop a new reconstruction methodology and to rigorously investigate the consequences of uncertainty in tree growth rates, tree decay rates, and contemporary data resolution on reconstructed estimates of historical forest structure and composition. We then use this methodology to estimate historical conditions for a large, spatially explicit forest plot in Yosemite National Park (Yosemite). In doing so, we seek to increase the availability of defensible sources of reference conditions for Sierra Nevada mixed-conifer forests. Our specific objectives are to:

1) Develop a forest reconstruction model for use in Sierra Nevada mixed-conifer forests and evaluate the use of two alternative tree growth models;
2) Systematically investigate how uncertainties in tree growth and decay rates incorporated into these models have the potential to introduce biases into reconstructed results;

3) Use the models to estimate historical stand structure and composition for a Sierra Nevada mixed-conifer forest prior to the onset of fire suppression, and investigate the temporal sequence of successional change during the fire suppression era.

2. METHODS

2.1 Study site

This study was conducted at the Yosemite Forest Dynamics Plot (YFDP), a 25.6 ha (320 m by 800 m) permanent plot established in an old-growth mixed-conifer forest near Crane Flat in Yosemite National Park (Yosemite), California (Lutz et al. 2012) (see Chapter 1). The YFDP is centered at 37.77°N, 119.82°W, with an elevation of 1774.1 m to 1911.3 m. The climate is Mediterranean, with warm dry summers and cool, wet winters. Soils are from metamorphic parent material. Major tree species on the plot include sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*) and, to a smaller extent, Pacific dogwood (*Cornus nuttallii*), with canopy emergent trees, primarily sugar pines and white fir, reaching 60–67 m in height and over 200 cm in diameter at breast height. Shrub cover is dominated by California hazelnut (*Corylus cornuta* var. *californica*), Sierra Chinquapin (*Chrysolepis sempervirens*), and northern bilberry (*Vaccinium uliginosum*) (Lutz et al. 2012) (Figure 2). the forest within the YFDP has never been subject to timber harvest. Prior to the onset of fire suppression, the YFDP experienced a point fire return
interval (PFRI) of 29.5 years (Chapter 2). Fire suppression, which began in the region as early as 1891 (Rothman 2007), significantly reduced fire frequency and the YFDP has not experienced a significant fire since 1900. We therefore chose 1900 as the reference year for this reconstruction.

2.2 Data collection

All live trees on the YFDP ≥1 cm in diameter at breast height (dbh; 1.37 m above ground level) and all snags ≥ 10 cm dbh and ≥ 1.8 m in height were inventoried and mapped (Figure 3). To avoid over-sampling downed logs, we used estimates of species-specific tree growth rates developed from local Forest Inventory Analysis data [USFS], species-specific log decay rates (Harmon et al. 1986), as well as allometric equations relating dbh to diameter at stump height (dsh) (Walters and Hann 1986, Weigel and Johnson 1997) to estimate the minimum dsh that downed trees would have to be in the present to have been alive in 1900. We recorded the species and decay class (Figure 9) (Thomas et al. 1979) of each downed tree that met minimum dsh requirements and mapped their original rooting locations. To account for losses in bole volume due to decay from 1900-present, we estimated the dsh or dbh (if discernible) prior to decay for each tree, using structural clues such as remaining bark around the root collar or protruding branches (Figure 10) (Van de Water and North 2011). The total contemporary tree inventory includes 35,498 live trees, 2,734 snags, and 696 logs. In addition, we collected tree cores around the perimeter of the YFDP to provide us with estimates of species-specific growth rates to aid in model development and validation. We sampled from all size classes and major species present on the plot (white fir: n = 27, sugar pine: n = 34, incense cedar: n = 35, black oak: n = 11), although we could not core trees > 130 cm dbh, because our largest increment borer was 70 cm in length. We did not collect cores from Pacific dogwood.
2.3 Objective 1: Develop a forest reconstruction model

We used a data-driven reconstruction approach (Figure 11) to derive historical estimates of stand structure and composition, given the large size of the YFDP dataset, the infeasibility of coring all trees to determine their presence or absence in the reference year, and the prohibition against coring live trees within the plot boundary. We developed two different tree growth models and combined these with a decay model, which is based on published tree decay estimates. Our goals in developing the reconstruction models were to minimize potential biases associated with our dataset and to create a methodology feasible for use at high-spatial resolution across large, contiguous study areas (i.e., stem map plots).

2.3.1 Regionally-calibrated tree growth model. First, we chose to use a regionally-calibrated, competition-dependent tree growth model developed for the Sierra Nevada mixed-conifer forests to predict radial growth increment at five year intervals (Das 2012). The Das growth model is parameterized for the major conifer tree species found on the YFDP, including sugar pine, incense cedar, and white fir. Radial growth for a given focal tree is in part predicted by the neighborhood crowding index (NCI) surrounding the focal tree (trees that are within \(\leq 18.5\) m radius are considered neighbors, with the radius dependent on focal species). NCI characterizes the interspecific and size-dependent interactions between a focal tree and all of its neighbors (Das 2012). To account for edge effects while calculating crowding indices, we established an 18.5 m buffer (the maximum potential radius of neighborhood influence) around all plot edges. Trees inside this buffer zone (\(n = 6,141\)) were not considered in subsequent analysis because they could have neighbors outside plot boundaries.
The Das growth model was originally developed to predict future five year radial growth increment. To instead predict past growth, we needed to “jump start” the model to grow a focal tree’s neighbors backwards. To do so, we calculated the mean NCI values for each 10 cm diameter size class of each species, across all live trees present at the beginning of each five year timestep. These mean values were then used to predict past growth of neighborhood trees surrounding the focal tree to start the model running. After cycling through all trees during one timestep, the model was then run again for the same timestep and the growth of any trees that was predicted based on mean NCI values was updated to reflect a more precise NCI.

The Das growth model is not parameterized for California black oak or Pacific dogwood. For black oak, we instead developed five year diameter growth increment estimates from black oak cores along the perimeter of the plot (mean: 1.04 cm⁻⁵yr). We estimated Pacific dogwood growth using published five year diameter growth rates of Pacific dogwood trees in Oregon (mean: 1.02 cm⁻⁵yr) (Hann and Hanus 2002). Oaks were considered competitors to coniferous trees and included in the calculation of NCI; dogwoods were not, due to lack of data on dogwood competitive effects.

2.3.2 Site-specific tree growth model. We were curious how the use of a more parsimonious growth model in which tree growth rates were based on locally-derived tree growth estimates might affect reconstructed results. We used tree cores collected around the YFDP to develop estimates of five year diameter growth rates for sugar pine, white fir, incense cedar, and black oak. In this site-specific growth model, we set all tree growth rates based on the growth rates derived from YFDP tree cores. At each time step, each individual tree was assigned a diameter change by generating random normal deviates using the R function “rnorm” (see below). Black oak and Pacific dogwood growth were left unchanged. We did not employ any
edge adjustments for the site-specific model because tree growth was not based on spatial relationships to other trees.

2.3.3 Tree decay. To “undecay” trees, we followed a similar methodology to other nearby reconstruction studies (North et al. 2007, Scholl and Taylor 2010, Van de Water and North 2011), which involved piecing together the best available decay data for each species (Appendix A, Table A.1). We estimated the time for sugar pine and white fir snags to transition between decay classes (Figure 9) from transition matrices developed by Morrison and Raphael (1993) which predict genus-specific snag decay class transitions over time (Pinus rates developed from sugar pine, Jeffery pine (Pinus jeffreyi) and lodgepole pine (Pinus contorta); Abies developed from white fir and red fir (Abies magnifica)). We predicted the age of incense cedar snags using estimates for western redcedar (Thuja plicata) presented in Daniels (1997). Oak snags transitioned to lesser stages of decay based on a randomized probabilistic transition matrix, due to lack of available decay information. Log decay for sugar pine, white fir, and oak was modeled based on log-bole mineralization rates presented in the literature (MacMillan 1981, Harmon et al. 1987, Dunn 2011), estimates of wood density by decay class (Harmon et al. 2008), and the exponential decay function (Harmon et al. 1986):

\[ D_t = D_o e^{-kt} \]

where \( D_t \) is the density (g cm\(^{-3}\)) at time \( t \) (years), \( D_o \) is the initial density, and \( k \) is the species-specific decay rate constant for density. We substituted ponderosa pine (Pinus ponderosa) decay rates for sugar pine and eastern oak decay rates for black oak. Incense cedar log time since death for was estimated based on data for western redcedar presented in Daniels (1997).
2.3.4 Incorporating variability. We used a simulation approach in which we ran the Das model 100 times and the site-specific model 30 times, as one way to assess the effects of uncertainties in growth and decay rate parameter estimates (Figure 11). We were limited to 30 simulations of the site-specific model due to time constraints (each simulation takes many hours of computation time). During each run of the Das model, tree growth and competition parameters (12 total) were allowed to vary based on the 2-unit support intervals presented for each parameter in Das (2012). These 2-unit support intervals, defined in a maximum likelihood framework, are roughly equivalent to 95% confidence intervals of a parametric framework (Das 2012) and were treated as such in our model. We determined the standard deviation of each parameter for each species using the mean values and pseudo-95% confidence intervals presented in Das (2012). We used the R “rnorm” function to generate random normal deviates for each parameter, setting the mean value to the published mean and standard deviation to the standard deviation we calculated (Appendix B: lines 381-444). Tree growth rates were also allowed to vary each timestep for the site-specific model. Similar to the Das model, for each live tree at the start of each timestep, we generated random normal deviates for tree growth rates using the R function “rnorm,” with the mean and standard deviation in the function set to the mean and standard deviation of the species-specific growth rates calculated from the measured tree cores. In each model version, transition times between decay classes and log-bole mineralization rates for each dead tree also varied. We also generated random normal deviates for decay rates for each dead tree, using the mean and standard deviation for decay rates as presented in the literature. Allowing growth and decay rates to stochastically vary resulted in a unique historical forest for each simulation.
2.3.5 Model implementation. The models were written and implemented in R version 3.0.2 (R Development Core Team 2014). Model code is presented in Appendix B. After a series of test runs, we error checked the models by tracking each individual tree backwards in time to ensure each tree was growing and undecaying in a plausible trajectory. Implementing the models in R on our lab computers (16 GB RAM, Intel Core i7 processor) limited the input datasets to about 15,000 trees (depending on size and proximity of trees). To overcome this, we also developed the models in Python version 2.7.3, using a high performance computing cluster to run parallelized code. Initial runs of the Python code demonstrate its ability to handle large datasets (40,000+ trees) efficiently; more time is needed to finalize and debug this version.

2.4 Objective 2: Systematically investigate uncertainties

2.4.1 Quantifying the effects of uncertainties. We sought to understand which types of trees (including different species, size classes, and tree statuses) were most sensitive to model uncertainties. To gain insight into components of each model version, we calculated, for each tree in the dataset, the probability of being alive in 1900, based on results from all simulations. We also investigated how predicted 1900 dbh of each individual tree varied across simulations of both models. Additionally, we sought to understand how overall stand metrics (such as density, total basal area, ect.) changed across simulations to see if incorporating stochasticity in the individual tree growth and decay rates at each time step introduced variation into the stand level metrics.

2.4.2 Growth sensitivity analysis. Given that we had to remove trees <10 cm dbh from our dataset due to computational constraints prior to running the Das model, we were particularly interested in how exclusion of these small diameter trees might impact reconstructed results. To
investigate this, we ran 30 simulations of the R version of the Das model on a 2 ha subset of the plot, but included trees <10 cm dbh (the “high resolution subset” version) – that is to say that we included all trees in the 2010 dataset. Given the reduced number of trees in the 2 ha subset (n = 1,263 ≥ 10 cm dbh; n = 1,161 < 10 cm dbh), this was computationally feasible. To account for changes in edge effects resulting from changing the plot borders, we also ran 30 simulations of the model on the same 2 ha subset with trees <10 cm dbh excluded.

2.4.3 Decay sensitivity analysis. Presence or absence in 1900 for dead trees was dependent on both decay rates and growth rates, and as such, it was difficult to separate out the effect of decay and growth on model output. To overcome these confounding effects, we investigated the decay model independently and tested the effects of slowing down log decay rates (k) on estimated log ages and snag transition rates on estimated snag ages. These variations, however, we not based on empirical data as there were none available. Additionally, we investigated an extreme decay scenario in which all contemporary snags (n = 2,734) and logs (n = 696) were assumed to have been alive in 1900.

2.4.4 Quantifying missing evidence. We used the decay model to investigate the potential for missing evidence of white fir and sugar pine, the two most prevalent species on the plot. Starting in the year 1900, hypothetical white fir and sugar pine logs and snags of decay class 0 (representing a recent death) were decayed using the same model as employed in the reconstruction, except run forward in time. We set the initial start year at 1900, then moved the start year five years later for each subsequent run of simulations, until a start year of 2010 was reached. We decayed each hypothetical tree from the start year until 2010 and then calculated its predicted wood density (g/cm\(^3\)). Snags could transition to logs along the decay pathway. We deemed a tree “undetectable” if its density in 2010 was more than one standard error away the
mean decay class 5 density for its species (Harmon et al. 2008). We simulated decay after each start year 100 times, allowing the decay rates and snag transition times to vary stochastically as in the reconstruction model. We then quantified the probability of not detecting each tree in 2010, depending on the year of its death.

2.5 Objective 3: Reconstruct historical stand structure and composition.

We used R to analyze stand structure and composition of the resultant reference forests for both the Das and site-specific model versions. For each simulated reconstruction, we calculated total number of stems, trees per hectare (tph), and basal area (m²/hectare) for each 10 cm size class of each species, as well as all species pooled. For each model, we then calculated the mean, standard deviation, standard error, range, and 95% confidence intervals of these metrics across simulations to gain insight into the variability of stand structure and composition.

3. Results

3.1 Objective 1: Develop a forest reconstruction model

3.1.1 Growth model comparison. Analysis of tree growth rates across simulations of the Das reconstruction model and comparison to growth rates derived from tree cores collected around YFDP demonstrates that the use of the Das (2012) growth model did not produce growth rates consistent with local empirical data (Figure 12). The Das model resulted in unreasonably fast tree growth rates for sugar pine (mean 5 year diameter change: 3.10 cm). While white fir growth rates were plausible, they were generally faster than our cores would suggest (mean 5 year diameter change: 2.89 cm). Incense cedar rates were reasonable (mean 5 year diameter change: 2.32 cm). The site-specific model resulted in more biologically reasonable growth rates,
as would be expected given that in this model version tree growth rates were based on growth rates derived from the tree cores (Figure 12).

3.1.1 Tree decay. The decay model predicts that, on average, 334 (of 2,734) snags and 185 (of 696) logs were alive in 1900. Investigation of tree decay across simulations revealed that, in general, the decay model is biologically appropriate in a relative sense, with trees in higher decay classes older than trees in lower decay classes (Table 2). The temporal aspect of decay, however, appears to be entirely too fast. White fir decay was fastest as would be expected (avg. age of DC 5 snag: 23 years), with slower rates for sugar pine (avg. age of DC 5 snag: 26 years) and the slowest rates for incense cedar (avg. age of DC 5 snag: 160 years). In general, snags decayed more slowly than logs.

3.2 Objective 2: Systematically investigate uncertainties

3.2.1 Presence/absence. In each version of the reconstruction model, incense cedar trees experienced high variability in probability of presence in 1900, both within and across size classes, with probability not increasing linearly with dbh as might be expected. In both models, trees in larger size classes experienced higher variability of probability of presence in 1900 than trees in smaller size classes, likely due to the lower number of large-diameter trees (Figure 14). In the site-specific model, probabilities of presence in 1900 for middle size classes were higher than the Das model. No Pacific dogwood trees were estimated to be alive in 1900 in either model.

3.2.2 Diameter. In the Das model, white fir and incense cedar exhibited high variability in projected historical dbh, evidenced by the large vertical spread of points for a given 2010 size class (Figure 16). The estimated 1900 dbh of sugar pines and black oaks were more confined. In
the site-specific model, variability in tree growth was much lower in general and more consistent between species (Figure 16).

3.2.3 Das model growth sensitivity. Running the Das model on a 2 ha subset of the contemporary data and including trees <10 cm dbh (the high resolution subset) did not substantially alter the results (Table 3). There was a slightly higher, but negligible, 1900 tree density and basal area with the high-resolution subset simulations than in the original subset simulations (Figure 13 B).

3.2.4 Decay. The stochastic elements of the decay model introduced variability in decay rates across species and tree status (logs vs. snags), although variability was fairly low for white fir, sugar pine, and black oak snags and logs (max. SD of age: 8.8 years) (Table 2). In general, variability increased with increasing snag and log decay class. Incense cedar logs and snags, however, exhibited high variability in age (max. SD of age: 104.8 years). In our sensitivity analysis, we found that changing the decay rates ($k$) for logs did not introduce any material changes to log ages, because the majority of logs transition (“undecay”) to the snag decay model after a few timesteps. Only when we changed the parameters in the snag model, coercing snags to remain in higher stages of decay for longer did tree ages change substantially, although these changes were not based on empirical data.

3.2.5 Quantifying missing evidence. Based on decay rates and parameters present in our model, there would be a high likelihood of not detecting trees that were alive in the reference year due to lack of evidence (Figure 17). The probability of not detecting sugar pines is not linearly related to year of death and there is generally a lower probability of not detecting sugar pines compared to white firs.
3.3 Objective 3: Reconstruct historical stand structure and composition.

Analysis of stand structure and composition in the 1900 reference plots revealed that both the Das and site-specific models predict significant reductions in live tree density for all species, from 539 tph ≥10 cm dbh in 2010 to only 27.1 tph (Das) and 84.5 tph (site-specific) in 1900 (Table 4, Figure 13 A). For the Das model, reductions in live tree density were relatively consistent across size classes, as illustrated by a reverse-J shaped diameter distribution in both 2010 and 1900 (Figure 15). The site-specific model resulted in a more even distribution of tree size classes in 1900 (Figure 15). For both models, total live tree basal area also decreased substantially, from 62.6 m²/ha in 2010 to only 3.59 m²/ha (Das) and 25.7 m²/ha (site-specific) in 1900 (Figure 13 A). For each model, there were considerable reductions in the number of stems for each species, although density reductions were not proportionate across species (Table 4). The models both predict species composition shifting from co-dominance by white fir and sugar pine in 2010 (45.0 and 45.8% of basal area, respectively) to being dominated primarily by sugar pine (62.7% (Das) and 75% (site-specific) of basal area), with a substantial loss of white fir (Table 4). The Das model predicted a considerable decrease in the abundance of large diameter trees (dbh ≥ 100 cm), from 410 trees on the plot in 2010 to only 16 trees (range: 10-23) in 1900. In contrast, the site-specific model predicted 171 (range: 165-179) large-diameter trees in 1900.

4. DISCUSSION

4.1 Comparison of reconstructed 1900 conditions with other reconstruction studies and historical data sets

There have been a number of studies investigating historical forest conditions in Sierra mixed-conifer forests with which to compare and validate the accuracy of our model predictions.
for the YFDP (Table 5). Scholl and Taylor (2010) reconstructed historical forest structure and composition in 1899 at Big Oak Flat (BOF), a site located downslope and north of the YFDP (Figure 5). Scholl and Taylor (2010) estimated higher tree densities and basal area in 1899, with 160 tph ≥10 cm dbh and a basal area of 30 m²/ha. Similarly, Van de Water and North (2011) reconstructed historical forest conditions in a northern Sierra Nevada mixed-conifer forest and estimated a historical density of 201 tph (≥5 cm dbh) and a basal area of 21.4 m²/ha. North et al. (2007) reconstructed forest conditions in 1865 in the Teakettle Experimental Forest, a mixed-conifer stand in the southern Sierra Nevada and estimated only 65 tph ≥5 cm dbh, although their basal area estimate was relatively higher (51.5 m²/ha).

Empirical historical datasets offer another opportunity to validate our results. Collins (2011) investigated a rare historical dataset detailing forest conditions in 1911 in the Gin Flat and Crane Flat areas of Yosemite. Some of these plots overlap BOF and are also nearby the YFDP. They found that there were roughly 60 tph (≥15.2 cm dbh) in 1911. This lower density compared to BOF is likely due to the exclusion of trees <15.2 cm dbh, possibly in conjunction with diminished tree density due to the 1899 fire which may have burned plots prior to data collection (Collins et al. 2011). Knapp et al. (2013), explored a historical dataset collected in 1929 in a mixed-conifer stand the Stanislaus-Tuolumne Experimental Forest (STEF), located approximately 50 km north of the YFDP, where the last widespread fire burned in 1889. They found that there were 315 tph (≥ 10 cm dbh) with a basal area of 53.9 m²/ha.

While there are slight differences in historical conditions between the studies, the general trend shows that there were substantially more, and larger, trees at the onset fire suppression than the Das model predicts (Table 5). Other studies of historical forest conditions and contemporary changes throughout the region confirm our Das growth model results in consistently lower
density estimates compared to other reconstruction studies (Parsons and DeBenedetti 1979, Taylor 2004, North et al. 2007, Beaty and Taylor 2007). Consequently, we conclude that the site-specific model predicts a more reasonable historical tree density and basal area, and although predicted density and basal area are still lower than many other studies, the results are plausible and generally consistent with historical empirical datasets, the best available source of validation data (Table 5).

4.2 Model assessment and model-driven sources of error

Evaluation of each component in our reconstruction model provides insight as to why our estimates of historical forest conditions may be unexpected. Most reconstruction studies utilize tree cores collected from each live and dead (when possible) tree to determine a tree’s presence or absence and size during the reference year (Arno et al. 1995, Fulé et al. 1997). Our approach instead utilizes a computer model (Bakker et al. 2008), and while parameterized for Sierra Nevada mixed-conifer forests, is inherently less accurate than dendrochronological approaches that use empirical measurements for each tree.

4.2.1 Das growth model. Tree growth rates predicted by the Das model are generally too fast, especially for large-diameter trees (Figure 12), which would cause trees that may have actually been alive in the reference year to be unaccounted for. This is likely because the Das model does not capture the complexities inherent to actual tree growth. One major assumption in modeling tree growth is that growth rates are directly linked to competition and modeled rates do not take into account other environmental factors which may affect growth (Das 2012). For example, the Das model does not account for non-competitive density-dependent effects, such as exposure to pathogens, which are difficult not only to quantify, but also to predict in a modeling
framework. The Das model also does not take into account the site characteristics specific to the YFDP, such as soil productivity, which would affect tree growth at the stand scale. Moreover, in this framework, the plot is treated in two-dimensional space with no regard to local environmental heterogeneity, yet trees growing with access to different belowground resources would likely differ in growth (Canham et al. 2006). In short, modeling tree growth is too simplistic at this stage to capture growth variations attributed to complex environmental factors (Astrup et al. 2008).

In general, the tree growth rates predicted by the Das model are too fast, especially for sugar pine (Figure 12). The most probable explanation is that the continual removal of competitors over time combined with the lack of evidence of trees that may have been alive at various points in the past caused tree growth rates to increase unreasonably over time (Figure 12). In reality, tree growth rates in the past were likely more constrained due to the presence of more competitors than we have contemporary evidence for. Furthermore, the Das model was developed to predict future five year radial growth rates; we use it to predict past five year radial growth rates and had to “jump-start” the model using mean NCI values. While this only represents a small temporal window of error at each timestep, it is possible that the effects of this model modification can be amplified over time and result in growth rates that are unreasonable. Additionally, the data Das used to parameterize the model was based on tree growth rates from 2000-2009. It is possible that growth rates during this time period are not representative of growth rates over the past century, especially for long-lived trees such as sugar pine. For example, many of the large-diameter sugar pine on the YFDP likely established during the Little Ice Age (1450-1850), when climate was considerably cooler than the present day (Graumlich
1993) and using growth rates developed in the early 2000s may not be appropriate for sugar pine, as well as other long-lived trees on the plot.

4.2.2 Site-specific growth model. Setting fixed tree growth rates derived from YFDP tree cores resulted in a much higher, and more reasonable 1900 tree density (85 tph vs. 27 tph) and basal area (26 m²/ha vs. 3.6 m²/ha) and produced results more closely in line with historical empirical datasets (Collins et al. 2011, Knapp et al. 2013) (Table 5). The site-specific model predicts on average 73 tph (≥ 15.2 cm dbh) in 1910, which is very close to the tree density in the Crane Flat area in 1911 (60 tph ≥ 15.2 cm dbh) (Collins et al. 2011). The site-specific model predicts only 120 tph (≥10 cm dbh) in 1930 compared to 315 tph in 1929 in the STEF (Knapp et al. 2013), however, this discrepancy could be in part because the last fire in the STEF (1889) was roughly a decade prior to the last fire on the YFDP, and there has been more time without fire for trees to establish on STEF.

Large-diameter tree growth was much slower in the site-specific model (Figure 12) and more of the large trees were predicted to be alive in 1900, contributing to the higher predicted basal area (Table 4). It is likely that using site-specific growth rates is a better way to drive tree growth over time as opposed to using a tree growth model parameterized on a regional scale. Growth rates derived from tree cores collected on site inherently incorporate the many complex, site-specific aspects of tree growth that are difficult to predict in a modeling framework, such as site and substrate characteristics and climate variations. Furthermore, with set growth rates, tree growth is more constant over time as a decreasing number of trees (and therefore decreasing competition) does not cause growth rates to increase as with the Das model. This helps balance model performance further in the past.
4.2.3 Tree decay model. Our decay model predicts that few contemporary snags (mean 334 of 2,734 total) and logs (mean 185 of 696 total) were alive in 1900. We investigated a scenario in which all contemporary snags and logs on the YFDP were alive in 1900. Interestingly, this increased the mean 1900 density to 148 tph (Das model) and 188 tph (site-specific model), directly in line with the 1899 data presented by Taylor and Scholl (2010) from the nearby BOF study area (Table 5). This indicates that the decay model likely represents a large source of error in our 1900 estimates of forest conditions.

Although there is little empirical evidence with which to base our evaluation of tree decay rates, we believe tree decay in our model to be overall too rapid, especially for sugar pine (Table 2). Dendrochronological analysis of cross-sections from large-diameter fire-scarred sugar pine snags and logs collected around the YFDP (Figure 8) demonstrate that many decay class 3-5 sugar pine snags and logs died when fires were still actively burning the plot or shortly thereafter (Chapter 2). A bark beetle outbreak in the early 1990s (Guarín and Taylor 2005) left many standing sugar pine snags, most of which, after about 25 years, are only in the early stages of decay. In our model, the average age of highly decayed class 5 sugar pines is about 25 years, which is too fast, especially since many of the dead sugar pines were 100+ cm in diameter at the time of death.

Erroneous tree decay predictions could be attributed to a number of factors. Snag transition rates between decay classes and log to snag transition rates for sugar pine and white fir are based on a single study (Morrison and Raphael 1993) that investigated snag dynamics only over a short time period (10 years). This study likely did not capture the high variation in snag decay class transition and fall rates. Additionally, the rates presented in the study are not size-dependent and the mean dbh of snags was 40.6 cm (Morrison and Raphael 1993), much smaller
than many snags present on the YFDP (many of which are >100 cm dbh). In reality, however, smaller trees decay faster than larger trees (Harmon et al. 1986). Since this transition matrix determines the time in which logs transition to standing snags, logs (that decay via a separate pathway in the model until they are transferred to the snag matrix) become snags more rapidly than they would in reality. Additionally, the log decay component is also not size dependent and we had to substitute decay rates ($k$ values) for species that lacked decay data (Appendix A, Table A.1).

Although the ages of incense cedar logs and snags are based on data collected for western redcedar (*Thuja plicata*) (Daniels et al. 1997), we believe that incense cedar decay is well represented in our study. Frequent field observations of decay class 2 incense cedar logs on the YFDP with charred bases indicate it is likely these logs were already on the forest floor when fires were still actively burning, rendering our prediction that dead cedar trees of decay class 3 would not have been alive in the reference year plausible.

4.2.4 *Model variability.* Incorporating uncertainties in model parameters for both the Das and site-specific models did not introduce high levels of variability across simulations (Figure 15), and stand-level metrics remained relatively constant across all simulations for both models (Table 4), suggesting that presentation of estimated conditions for each model based on mean results across simulations is appropriate. In the Das model, certain species were more sensitive to growth and competition parameter variations than others: incense cedar and white fir showed the most variation in growth rates across simulations, as compared to sugar pine, which demonstrated much more restricted growth rates (Figure 16). Das (2012) identified that the more shade-tolerant species, namely incense cedar and white fir (Burns and Honkala 1990), varied
much more in their competitive strength than sugar pine, likely contributing to more plasticity in growth rates across simulations.

4.3 Data-driven sources of error

Using a computer-driven reconstruction model allows for exploration of large, spatially-resolved datasets such as this, in which coring all trees would be prohibitive, if not impossible. Our intention was to include all 38,928 trees ≥1 cm dbh of the contemporary dataset in the model; however, given the computational restraints our R code and computing power, we were forced to reduce the dataset to trees ≥10 cm dbh, thereby removing 21,932 trees. While we can generally assume that trees <10 cm dbh have established after the reference year, shade-tolerant trees such as white fir and stress-tolerant trees such as incense cedar can persist in the understory and have surprisingly slow growth rates, resulting in a poor correlation between age and size (Van Pelt 2008). Outright removal of trees <10 cm neglects the potential for some of these smaller trees to have been alive in 1900, growing suppressed the understory for a century. Additionally, while individual small trees do not have strong competitive influences on larger trees (Biging and Dobbertin 1992), as a combined force they can limit resource availability and induce drought-stress on competitors (Guarín and Taylor 2005) and potentially contribute to restricted growth or mortality of large-diameter trees (Lutz et al. 2009). The contemporary YFDP has a very high density of small trees <10 cm dbh (828 tph), which could exert some competitive influence on larger trees (Das 2012), especially in areas of the plot with limited water.

When we ran the Das growth model on a 2 ha subset of the plot, this did not have a substantial impact on model performance as we predicted it might (Table 3). This leads us to believe that inclusion of trees <10 cm in this particular model would not result in more
reasonable estimates of forest conditions in 1900. It is important to note, however, that while the Das model is not sensitive to the inclusion of trees <10 cm dbh, this does not mean that in reality small-diameter trees were not growing at very slow rates in the understory or do not exert influence on the growth of larger trees; this analysis simply illustrates that for the Das model, including small trees does not substantially alter the results. It is also worth noting that our initial exploration of including small trees was only for a small subset of the plot and results could be different when extrapolated out to the entire dataset. The Python version of this model, while still in the final stages of development, can handle extremely large datasets (>40,000 trees), and when combined with high-performance cluster computing power, is capable of producing high numbers of simulations in short time frames.

It was surprising that in both models, all of the Pacific dogwood trees disappeared before the reference year – it is highly unlikely that there were no dogwood trees in 1900. For both models, we calibrated the growth rates of dogwood based on published estimates of five-year radial growth rates (Hann and Hanus 2002). This likely does not accurately portray their growth over long time frames given the morphology of dogwood trees. A dogwood tree is a group of genetically identical ramets growing up from a central genet. While individual ramets will grow and die, the genet will persist since it can resprout (Brush 1948). Since we did not collect data on snags or logs <10 cm in diameter, it is highly likely that we therefore did not detect dead dogwood ramets that would provide evidence for genets persisting over the past century. By modeling the growth of only individual ramets but neglecting to capture genet change over time, we are likely underestimating historical dogwood presence.

Given that white fir trees and small diameter trees have fast decay rates (Harmon et al. 1986, 1987), it is highly likely that we were not able to detect the presence of trees that may have
been alive in the reference year but have died and decayed substantially since, which would cause us to underestimate historical tree density. Our investigation of this “missing tree” component reveals that there is a high probability of not detecting a substantial number of trees (Figure 17) (however, since our estimates of decay rates are too fast, our estimates of these probabilities are high). The lack of evidence and our inability to quantify what we are missing represents a potentially large source of error inherent to forest reconstructions dependent on contemporary evidence of all historical trees. For example, the low 1930 tree density predicted by the site-specific model (100 tph ≥10 cm dbh) compared to the 1929 historical empirical data collected in STEF (315 tph ≥10 cm dbh) (Knapp et al. 2013) could likely be due to missing evidence of historical small diameter trees on the YFDP. In 1929, there were 154 tph between 10 and 20 cm dbh on STEF; many of these trees alive in 1929 on the YFDP were probably already decayed by 2010.

4.4 Levels of confidence

Given the fast growth rates of the Das model, the fast decay rates in both models, and the possibility of missing evidence, our models predict a minimum estimate of the historical tree population. As such, we have a high confidence in our predictions about individual trees with high probabilities of presence in 1900 across simulations, since despite overestimates of growth and decay rates, these trees were consistently present in the reference year. Our greatest confidence, therefore lies in predictions about the largest size classes – the largest trees are consistently present in 1900 (Figure 14). There appears to be a distinct diameter threshold at which this shift occurs, which differs for each species.
Similarly, we can be relatively confident in our predictions about the smallest diameter trees, although we have lower confidence in the presence or absence of individual trees of smaller classes and are only able to make more general assumptions. Many shade-tolerant trees, namely white fir, are able to persist at very slow growth rates in the understory and can be much older than their size might indicate (Gersonde and O’Hara 2005), so we cannot confidently assume a specific smaller tree was either present or absent in the reference forest. We can assume, however, that most trees of the smallest size classes have established during the fire suppression era. Based on these assumptions, our greatest uncertainties involve trees in the middle size classes.

4.5 Evaluation of other reconstruction studies

4.5.1 Decay. We identified that the use of a decay model based on integrating available decay data for Sierra Nevada mixed-conifer tree species are not sufficient for accurately modeling tree decay over long periods of time. Reconstruction studies over-simplify the tree decay process, and while we understand little about tree decay in Sierra Nevada mixed-conifer forests, we know it is much more complex than our modeling efforts imply.

The use of the decay class rating system for snags and logs (Thomas et al. 1979) is useful for field surveys, estimations of coarse woody debris amounts, and describing general decay trajectories and biomass loss over time (Grove et al. 2011). It was not, however, developed for assigning a specific calendar year to tree death. While the decay class system is used in most reconstructions (Fulé et al. 1997), the validity of this approach is largely untested. Furthermore, employing a simple decay class system to estimate tree ages across the different size classes is not accurate, as trees of smaller size classes will reach advanced stages of decay more rapidly
than larger trees (Vanderwel et al. 2006). Models that capture some of the complexities associated with decay, such as that developed by Vanderwel et al. (2006), would be more appropriate.

Reconstruction studies should acknowledge the significant limitations of decay rate estimates due to lack of sufficient decay data. For example, a number of studies in the Sierra Nevada (see North et al. 2007, Van de Water and North 2011), including our study, estimate snag decay rates based on the Morrison and Raphael (1993) study. A possible result, as demonstrated in our study, is an overestimation of decay rates and obfuscation of inherent variation in decay across different species and size classes. Other studies in the region (e.g. Scholl and Taylor 2010) use decay rates that are further generalized and parameterized for ponderosa pine (Rogers 1984) and/or are based on decay rates of fire-killed timber (Kimmey 1955), which decay much differently than trees that die in the absence of fire (Harmon et al. 1986). Furthermore, for those studies that did include hardwoods (Scholl and Taylor 2010, Van de Water and North 2011), neither reference any decay data used to model the decay of black oak, the implications of which are a likely misrepresentation of historical black oak populations. Reconstruction studies in low-elevation ponderosa pine forests also oversimplify tree decay (Fulé et al. 1997, Mast et al. 1999, Bakker et al. 2008). However, we at least have a better understanding of decay rates in these systems, the dendrochronological record is more intact, and we have more empirical historical data with which to validate reconstructed estimates (Moore et al. 2004).

4.5.2 Loss of evidence. While some reconstruction studies mention the loss of evidence of historical trees as a potential bias in the results, this missing evidence effect has never been quantified for reconstructions of historical trees in Sierra Nevada mixed-conifer forests. Given
that white fir, a ubiquitous species in these forests (Fites-Kaufman et al. 2007), can decay quite rapidly (Harmon et al. 1987), it is highly likely we are missing evidence of a substantial number of historical trees. A possible effect of this omission includes underestimating historical tree densities and misrepresenting historical species composition. This is problematic, because many restoration strategies seek to remove shade-intolerant trees such as white fir (North et al. 2009). If we base our restoration targets on inaccurate historical reference data, we may remove an inappropriate number of shade-tolerant trees, the ecological results of which are largely unknown.

4.5.3 Exclusion of hardwoods. Many assessments of historical forest conditions in the Sierra Nevada neglect to account for the presence of hardwoods (North et al. 2007, Van de Water and North 2011, Collins et al. 2011, Lydersen et al. 2013), although angiosperms are indisputably important for biodiversity in mixed-conifer forest ecosystems (Schowalter and Zhang 2005, Fontaine et al. 2009). A number of rare and threatened wildlife species depend on hardwoods for nesting, foraging, and cover: black oak, in particular, is important habitat for dusky-footed woodrats (Innes et al. 2007), the California fisher (Zielinski et al. 2004, Purcell et al. 2009), the spotted owl (Irwin et al. 2012), as well as other wildlife in decline (Purcell 2007). Pacific dogwood trees are important forage for ungulates (Lawrence and Biswell 1972) and their flowers are attractive to many insects and birds (Michael 1928). Given the ecological importance of hardwoods, we cannot overlook how their population distributions have changed during the fire suppression era and restoration efforts to reintroduce fire should also take into account impacts on populations of trees other than conifers. For example, black oak has been found to be declining in Yosemite (Ripple and Beschta 2008). Pacific dogwood may be particularly threatened due to its susceptibility to the invasive fungal pathogen anthracnose
(Brown et al. 1996) as well as its limited genetic diversity, which could result in poor population adaptability as climate changes (Keir et al. 2011). While we do consider the historical presence of black oak and dogwood trees in this reconstruction study, we admit to excluding many other important angiosperms from our dataset, such as Scouler’s willow (*Salix scouleriana*) and chokecherry (*Prunus virginiana*).

4.6 *Future research opportunities*

This study demonstrates the clear need to expand research efforts regarding tree decay in Sierra Nevada mixed-conifer forests. More decay data could substantially improve forest reconstruction studies in the Sierra Nevada, thereby allowing us to expand the availability of defensible reference information. Furthermore, snags and coarse woody debris are crucial for ecosystem functioning, providing habitat and nutrition for wildlife and microorganisms and sites for nutrient fixation (Harmon et al. 1986, 1987) and more research on tree decay can help us understand the ecological roles of decaying wood and how these roles change over time.

Tree decay research can also help improve other forest modeling projects, such as forest growth and fuels models that predict forest changes in the future. For example, the Forest Vegetation Simulator (FVS) is a widely used forest growth model that is utilized to make management decisions and predict changes to forests across the United States (Crookston and Dixon 2005). However, careful investigation of the decay components in the model reveals that it too is limited by a lack of relevant decay data. In the Fire and Fuels Extension (FFE) of FVS, snag and log decay in the Sierra Nevada variant is a simplification of decay rates derived from “some rates for Douglas-fir snags” taken from an unpublished study in Oregon (Reinhardt and Crookston 2003). Rates for specific species are slightly faster or slower than Douglas-fir, based
on assumptions regarding species fall and decay rates, but many species, such as whitebark pine
(*Pinus albicaulis*), lodgepole pine, and sugar pine are assigned the same decay rates. If outputs
from models such as FVS are being used to make management decisions, we need make
improvements to the decay components of the model.

We can take advantage of long-term forest research studies (Lindenmayer et al. 2012),
specifically those in the Sierra Nevada (Stephenson et al. 2004, Lutz et al. 2012) to collect this
valuable decay information. Useful field surveys might include tracking the height of snags over
time and making more detailed observations of dead tree volume losses, rather than using only a
simple decay class rating system. Annual photography of snags and logs decaying *in situ* could
help us better track structural changes over time. We have a tremendous amount of technology
at our disposal that makes more sophisticated tracking of individual trees over long time periods
feasible.

Tree growth models can also continue to be improved. While the Das growth model is
quite complex, it does not take into account site characteristics, such as productivity, it cannot
differentiate between trees growing on different substrates, and does not take into account short
or long term climatic variables that would impact tree growth. In our reconstruction framework,
the complex Das growth model produces less accurate results than the more parsimonious site-
specific model. Development of growth models that capture more of the site-specific factors
associated with tree growth would benefit forest modeling projects and our ability to predict
forest change over time, both in the past and future.
5. CONCLUSIONS

One of the main objectives of this study was to develop a new reconstruction methodology to be utilized in Sierra Nevada mixed-conifer forests. Computer reconstruction models, such as used in this study, represent a unique tool for estimating historical forest conditions across large study areas at a high spatial resolution, where collection of trees cores from each living tree is not feasible. We feel that this methodology deserves future development and improvement where we have indicated and that given these improvements can be a viable manner to obtain new reference information across the Sierra Nevada region.

The site-specific model is most believable when compared to the highest standard of calibration data, the historical empirical datasets (Collins et al. 2011, Knapp et al. 2013). As such, we use these results to continue our exploration of changes to forest conditions during the fire suppression era (Chapter 4). We acknowledge, however, that even the results from the site-specific model are a minimum estimate of historical forest conditions. While we have the most confidence in our predictions about the current large-diameter trees, we recognize that the predicted density and size of even these large trees in the early 1900s is likely underestimated due to fast decay rates, particularly for sugar pine. Additionally, we cannot overcome the lack of evidence of small trees that may have been alive in the early 1900s, especially for fast-decaying species such as white fir.

The other main objective of this study was to develop estimates of historical forest structure and composition on the YFDP and to explore the temporal sequence of changes since the onset of fire suppression. Given our understanding of the biases present in the Das model and its unreasonably low predictions of historical tree density, we know that the results likely do
not accurately represent historical conditions. However, given the limitations of the decay model present in both the Das and site-specific models, we want to be clear that we would not recommend results from either model to be utilized directly to guide restoration efforts – for example, we are not suggesting that managers thin fire-suppressed stands to 84.5 tph and justify such an action based on our results.

The exploration of uncertainties in this study elucidated important findings about how assumptions inherent to forest reconstructions can affect results. We hope that scientists performing reconstruction studies in the future will take into the account the possible effects that inaccurate decay information and missing evidence can have on estimated historical forest conditions. When implementing reconstruction studies without the concomitant development of more refined tree decay models, researchers should more adequately portray study limitations and provide more refined interpretation of the possible effects of these limitations. The current level of recognition given to these limitations and lack of indications of data used to drive the reconstruction of dead trees is unacceptable, especially when these reconstruction-derived reference conditions to directly inform management.

More research regarding how ecological processes have shifted during the fire suppression era is required to better grasp how forest dynamics, rather than just structure and composition, has been altered in the absence of fire. Given our confidence in our site-specific model results, we have a reasonable understanding of which trees likely did establish prior to the onset of fire suppression and which trees have established during the fire suppression era. Investigating the patterns of tree invasion over the past century can provide a richer ecological understanding of how the exclusion of fire can influence other ecological processes in the forest.
ACKNOWLEDGEMENTS

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### Table 2

Modeled ages (time since death) of snags and logs on the YFDP, showing results across 100 simulations of the decay model.

<table>
<thead>
<tr>
<th>Decay Class in 2010</th>
<th>Status in 2010</th>
<th>Log Mean age (SD)</th>
<th>Snag Mean year alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>White fir</td>
<td></td>
<td>6 (2.2)</td>
<td>2004 N=2</td>
</tr>
<tr>
<td>Sugar pine</td>
<td></td>
<td>8 (3.9)</td>
<td>2002 N=1</td>
</tr>
<tr>
<td>Incense cedar</td>
<td></td>
<td>5 (1.5)</td>
<td>2005 N=1</td>
</tr>
</tbody>
</table>

Table 2 shows the modeled ages (time since death) of snags and logs on the YFDP, with data across 100 simulations of the decay model.
Table 3. Results of the growth sensitivity analysis showing 1900 reconstructed forest conditions predicted by the Das model (1), the site-specific model (2), and two modified versions of the Das model (3-4). Standard deviation and ranges are calculated across 30 simulations of all models.

<table>
<thead>
<tr>
<th>Model</th>
<th>Input data</th>
<th>Diameter cutoff</th>
<th>Density (trees ≥10 cm dbh/ha) (SD) (Range)</th>
<th>Basal area (m²/ha) (SD) (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Das (1)</td>
<td>25.6 ha (entire plot)</td>
<td>trees ≥10 cm dbh</td>
<td>27.1 (0.45) {26.1-28.1}</td>
<td>3.6 (0.16) {3.3-3.9}</td>
</tr>
<tr>
<td>Site-specific (2)</td>
<td>25.6 ha (entire plot)</td>
<td>trees ≥10 cm dbh</td>
<td>84.5 (0.42) {90.1-92.0}</td>
<td>25.7 (0.13) {25.5-26.0}</td>
</tr>
<tr>
<td>Das subset (3)</td>
<td>2 ha subset</td>
<td>trees ≥10 cm dbh</td>
<td>32.1 (1.21) {30.2-35.1}</td>
<td>2.10 (0.20) {1.54-2.88}</td>
</tr>
<tr>
<td>Das high-resolution subset (4)</td>
<td>2 ha subset</td>
<td>trees ≥1 cm dbh</td>
<td>33.0 (1.66) {29.2-36.0}</td>
<td>2.17 (0.24) {1.60-2.64}</td>
</tr>
</tbody>
</table>
Table 4. Comparison of the contemporary (2010) and historical (1900) tree population on the YFDP using two different reconstruction model approaches: the Das model and the site-specific model. Trees <10 cm dbh as well as trees that fall within the buffer zone around the plot are excluded.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Density (stems/ha)</th>
<th>Basal area (m²/ha)</th>
<th>% Total basal area</th>
<th>Total stems ≥ 10 cm dbh</th>
<th>Total stems ≥ 100 cm dbh</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Stems ≥10 cm dbh</td>
<td>Stems ≥10 cm dbh</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Trees:</td>
<td>2010</td>
<td>539.3</td>
<td>62.6</td>
<td>–</td>
<td>11,572</td>
<td>410</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>27.1 (0.44) {25.9-28.4}</td>
<td>3.59 (0.14) {3.3-3.9}</td>
<td>–</td>
<td>584.5 (9.46) {560-614}</td>
<td>15.6 (2.38) {10-23}</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>84.5 (0.39) {83.7-85.4}</td>
<td>23.9 (0.12) {23.1-24.1}</td>
<td>-</td>
<td>1825.4 (8.5) {1808-1844}</td>
<td>171.3 (3.90) {165-179}</td>
</tr>
<tr>
<td>White fir</td>
<td>2010</td>
<td>384.6</td>
<td>28.2</td>
<td>45.0%</td>
<td>8,253</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>4.2 (0.17) {3.8-4.6}</td>
<td>0.5 (0.03) {0.4-0.6}</td>
<td>13.9%</td>
<td>91.7 (3.70) {82-99}</td>
<td>0.1 (0.34) {0-1}</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>33.7 (0.34) {32.9-34.2}</td>
<td>4.6 (0.04) {4.5-4.7}</td>
<td>19.4%</td>
<td>728 (7.44) {711-738}</td>
<td>4.6 (1.4) {2-8}</td>
</tr>
<tr>
<td>Sugar pine</td>
<td>2010</td>
<td>85.2</td>
<td>28.7</td>
<td>45.9%</td>
<td>1,829</td>
<td>288</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>17.7 (0.31) {16.7-18.4}</td>
<td>2.24 (0.11) {2.0-2.6}</td>
<td>62.7%</td>
<td>382.2 (6.71) {361-398}</td>
<td>8.3 (2.14) {4-14}</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>43.1 (0.24) {42.6-43.5}</td>
<td>18.0 (0.10) {17.8-18.2}</td>
<td>75.3%</td>
<td>931.5 (5.1) {920-940}</td>
<td>159.6 (3.7) {153-166}</td>
</tr>
<tr>
<td>Incense cedar</td>
<td>2010</td>
<td>26.6</td>
<td>4.4</td>
<td>7.0%</td>
<td>570</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>2.3 (0.18) {1.9-2.7}</td>
<td>0.77 (0.10) {0.6-1.0}</td>
<td>21.5%</td>
<td>48.9 (3.82) {42-59}</td>
<td>7.2 (1.39) {5-12}</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>4.7 (0.13) {4.4-5.0}</td>
<td>1.23 (0.07) {1.1-1.4}</td>
<td>5.1%</td>
<td>102 (2.75) {94-109}</td>
<td>7.2 (1.27) {5-10}</td>
</tr>
<tr>
<td>Black oak</td>
<td>2010</td>
<td>30.1</td>
<td>1.1</td>
<td>1.8%</td>
<td>647</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>2.9 (0.16) {2.5-3.3}</td>
<td>0.08 (0) {0.1-0.1}</td>
<td>2.2%</td>
<td>61.8 (3.54) {53-72}</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>2.9 (0.2) {2.4-3.3}</td>
<td>0.08 (0) {0.1-0.1}</td>
<td>0.03%</td>
<td>62.5 (4.42) {52-72}</td>
<td>0</td>
</tr>
<tr>
<td>Pacific dogwood</td>
<td>2010</td>
<td>12.3</td>
<td>0.2</td>
<td>0.3%</td>
<td>264</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Das 1900</td>
<td>0</td>
<td>0</td>
<td>0%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Site-specific 1900</td>
<td>0</td>
<td>0</td>
<td>0%</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
**Table 5.** Comparison of other studies investigating historical conditions in Sierra Nevada mixed-conifer forests to estimates produced by our two model versions using the same year and diameter cutoff presented in each study.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Year of historical data</th>
<th>Diameter cutoff</th>
<th>Historical conditions Density</th>
<th>Basal area</th>
<th>Das model Density</th>
<th>Basal area</th>
<th>Site-specific model Density</th>
<th>Basal area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scholl and Taylor (2010)</td>
<td>Yosemite</td>
<td>1899</td>
<td>≥10 cm</td>
<td>160 tph</td>
<td>30 m²/ha</td>
<td>27.1 tph</td>
<td>3.6 m²/ha</td>
<td>84.5 tph</td>
<td>25.7 m²/ha</td>
</tr>
<tr>
<td>Van de Water and North</td>
<td>N. Sierra Nevada</td>
<td>1900</td>
<td>≥5 cm</td>
<td>201 tph</td>
<td>21.4 m²/ha</td>
<td>36.7 tph</td>
<td>3.8 m²/ha</td>
<td>97.2 tph</td>
<td>26.5 m²/ha</td>
</tr>
<tr>
<td>(2011)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collins et al. (2011)</td>
<td>Yosemite</td>
<td>1911</td>
<td>≥15.2 cm</td>
<td>60 tph</td>
<td>n.a.</td>
<td>20.0 tph</td>
<td>3.5 m²/ha</td>
<td>72.7 tph</td>
<td>23.7 m²/ha</td>
</tr>
<tr>
<td>Knapp et al. (2013)</td>
<td>Stanislaus Nat’l</td>
<td>1929</td>
<td>≥10 cm</td>
<td>315 tph</td>
<td>53.9 m²/ha</td>
<td>58 tph</td>
<td>10.4 m²/ha</td>
<td>120 tph</td>
<td>34.2 m²/ha</td>
</tr>
<tr>
<td>Forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North et al. (2007)</td>
<td>Teakettle Experimental Forest</td>
<td>1865</td>
<td>≥5 cm</td>
<td>67 tph</td>
<td>56.4 m²/ha</td>
<td>36.7 tph</td>
<td>3.8 m²/ha</td>
<td>97.2 tph</td>
<td>26.5 m²/ha</td>
</tr>
</tbody>
</table>
Figure 9. Snags and logs on the YFDP were classified into 1 of 5 decay classes based on a field rating of decay. During model simulations, logs transitioned between decay classes and became snags based on published snag fall rates. Figure adapted from Thomas et al. (1979).

Figure 10. Field assistant Erin Costello estimates a dead tree’s “original dbh”, using structural clues to account for bole loss due to decay since tree death.
Figure 11. Flowchart demonstrating the structure of the computer-driven forest reconstruction model used to estimate historical conditions on the YFDP.
**Figure 12.** Top panels: Empirical tree growth derived from tree cores collected on the Yosemite Forest Dynamics Plot (grey) and predicted tree growth of 50 random trees derived from the Das model (colored) for the three most prominent tree species on the plot. Bottom panels: Empirical tree growth derived from tree cores collected on the YFDP (grey) and modeled tree growth for 50 random trees based on the site-specific model (colored).
Figure 13. Predicted changes to tree density and basal area of the all live trees ≥10 cm dbh on the YFDP from 1900 to 2010 for four different model versions. Calculations are based on mean values across 30 simulations of each model version.
Figure 14. The probability of contemporary (2010) live trees on the YFDP being alive in 1900 based on both the Das and site-specific models. Error bars represent the standard error across each size class from all simulations; text above bars displays the number of trees in each size class.
Figure 15. Contemporary (2010) and reconstructed (1900) diameter distribution of live trees ≥10 cm dbh on the YFDP, all species pooled, based on two different model approaches (the Das and site-specific models). Error bars represent the standard error across simulations.
Figure 16. Predicted historical (1900) dbh of contemporary (2010) live trees on the YFDP based on two different reconstruction model approaches. Each point represents the estimated dbh from a single simulation; all simulations are displayed to show variability in reconstructed diameter across simulations.
Figure 17. Probabilities of not detecting trees that may have been alive in 1900 but have died between 1900 and 2010 on the YFDP based on 100 forward simulations of the decay component of our reconstruction models.
CHAPTER 3 REFERENCES


Dunn, C. J. 2011. Coarse woody detritus dynamics, variable decay rates and their contribution to wildland fuel succession following high-severity fire disturbance in dry-mixed conifer forests of Oregon’s eastern Cascades. Ph.D Dissertation, Oregon State University, Corvallis, OR.


[USFS]. USDA Forest Service, Forest Inventory and Analysis Program.


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CHAPTER 4
SPATIAL PATTERNS OF TREE ESTABLISHMENT DURING THE FIRE SUPPRESSION ERA

1. INTRODUCTION

Frequent fires once shaped the heterogeneous structure of dry western coniferous forests, creating variable patterns of tree species and age classes across landscapes (Hessburg et al. 1999, Kaufmann et al. 2007, Williams and Baker 2012) and within forest stands (Larson and Churchill 2012, Lydersen et al. 2013). Fire suppression has homogenized conditions in dry forests across the West, causing dramatic changes to species composition and structural diversity (Stephens and Ruth 2005). Such changes have been well documented in the Sierra Nevada mixed-conifer forests of California (Ansley and Battles 1998, Scholl and Taylor 2010). While numerous studies have identified changes to Sierra Nevada mixed-conifer forest size structure and composition between the onset of fire suppression and the present (Kilgore 1973, Parsons and DeBenedetti 1979, Collins et al. 2011, Lydersen et al. 2013), fewer have investigated fine-scale ecological processes that have contributed to these changes during the fire suppression era (Scholl and Taylor 2010). Static views of contemporary and historical forest conditions allow us to quantify forest change between two points in time, but require us to make assumptions regarding what has contributed to these changes. Investigating the processes that have influenced forest structural and compositional shifts during the fire suppression era will provide ecologists with a deeper understanding of forest development in the absence of fire (Fry and Stephens 2010). Given the ecological impacts of fire suppression, there has been substantial effort to restore these forests using mechanical thinning and prescribed and natural fire (Stephens and Ruth 2005, North et al. 2012) and better understanding of how processes have influenced
forest change in the absence of fire can help improve the effectiveness of our management strategies.

1.1 Spatial patterns in Sierra Nevada mixed-conifer forests

Fire-frequent forests were historically characterized by a predictable patch-mosaic pattern of spatial components which typically manifested at scales <0.4 ha (Larson and Churchill 2012). In Sierra Nevada mixed-conifer forests, historical fire patterns resulted from and maintained this complex pattern of trees (Bonnicksen and Stone 1982, North et al. 2009). Mixed-severity fires shaped Sierra Nevada forests by differentially thinning tree populations, leaving some areas more or less severely burned and produced scattered openings within a matrix of surviving trees (Stephenson et al. 1991, van Wagendonk and Fites-Kaufman 2006, Beaty and Taylor 2007). From the limited number of studies that have investigated historical Sierra Nevada mixed-conifer within-stand spatial patterns, we have learned that fire suppression has in part homogenized the mosaic by reducing the amount of open space, increasing the size and density of tree clumps, and decreasing the nearest neighbor distance between trees (Knapp et al. 2012, Lydersen et al. 2013, Fry et al. 2014), following a similar trend in other fire-suppressed historically fire-frequent forest types (Larson et al. 2012, Churchill et al. 2013) (Appendix C). These changes can contribute to increased fire size and severity (Kilgore and Sando 1975), added drought stress on ecologically important large-diameter trees (Guarín and Taylor 2005, Lutz et al. 2009), and loss of the diverse habitat needed to sustain many sensitive wildlife species (Weatherspoon et al. 1992).

Patterns of tree invasion during the fire suppression era appear to be inconsistent throughout mixed-conifer forests of the Sierra Nevada. While Lydersen et al. (2013) found that forest gaps in the central Sierra Nevada have become infilled during the fire suppression era, North et al. (2004) and Fry et al. (2014) demonstrate that, despite the exclusion of fire, gaps in
the southern Sierra Nevada have persisted. These differences could be attributed to local edaphic factors, such as parent material and soil thickness (Meyer et al. 2007) which influence tree establishment. Furthermore, in the absence of fire, forest gaps may also be shrub maintained (Lutz et al. 2014). Prior to fire suppression, shrub distribution in Sierra Nevada mixed-conifer forests was likely restricted to moist refugia (Kolden et al. 2012), yet without fire, shrub patches can be quite extensive and limit tree establishment (Lutz et al. 2014).

1.2 Intertree relationships

Spatial relationships between different tree (sub)populations and how they change through time provide insight into mechanisms that drive forest change in the absence of fire. Spatial analysis of where ingrowth trees (those that have established since the onset of fire suppression) have established in relation to legacy trees (those that established during an active fire regime) provides valuable evidence regarding forest dynamics in the absence of fire (Figure 19). While we know that forest spatial patterns in Sierra Nevada mixed-conifer forests are shifting, changes are not consistent from site to site and our understanding of the ecological processes that are driving these changes is limited. Analysis of intertree dynamics is one way to investigate the mechanisms behind observed changes in order to refine our understanding of forest dynamics in the absence of fire. Increasing our understanding of tree recruitment processes in the absence of fire can allow us to better gauge the relative importance of fire in the creation of specific recruitment patterns and further our understanding about drivers of forest structural heterogeneity (Lutz et al. 2013).

Forest spatial patterns can be driven by both endogenous factors, such as competition and facilitation between trees, and exogenous factors, such as substrate quality, disturbances,
topography, and climate variability (Larson and Franklin 2006). In western coniferous forests, endogenous factors tend to result in spatial patterns at the scale of the zone of influence of a single tree (0-10 m), which corresponds roughly to the crown radius of a mature conifer (Abella et al. 2007, Lydersen et al. 2013). Both facilitation (Baumeister and Callaway 2006) and competition (Canham et al. 2006) between conifers occur at these small scales. In addition, for conifers, dispersal of seeds is generally highest directly beneath seed tree canopies (Keeton and Franklin 2005). If biological relationships are at least in part a driving mechanism behind tree pattern formation, we would expect to see small scale spatial repulsion between competing trees and spatial attraction between trees where facilitation is present (Larson and Franklin 2006). While small scale tree spatial patterns can be influenced by both intertree relationships and exogenous factors, large scale patterns (10+ m), are more likely a result of environmental heterogeneity. If edaphic factors and past disturbance effects, for example, are driving mechanisms behind forest pattern, trees would exhibit spatial segregation at scales beyond the zone of influence of an individual tree (North et al. 2004).

Forest openings (i.e., areas with little to no trees) can be created and maintained disturbances, such as windthrow, fire, and grazing, or can instead be the result of belowground factors limiting tree establishment (Sánchez Meador et al. 2009). In the case of Sierra Nevada mixed-conifer forests, disturbance-mediated openings would likely have been maintained by frequent fires. While the absence of fire can provide fire-intolerant trees with an opportunity to recruit in openings that are no longer fire-maintained, openings that are a result of poor site conditions can persist despite the exclusion of fire (Nagel and Taylor 2005). Patch regeneration (i.e., ingrowth occurring as tree clusters in forest openings) would result in spatial segregation of
canopy strata (Boyden et al. 2005) and would be evidenced by spatial patterns between ingrowth and legacy trees occurring at large scales.

Recent research in Sierra Nevada mixed conifer forests has demonstrated that large forest gaps were present historically and were maintained by processes other than fire, because in the absence for fire these gaps have persisted (North et al. 2004). Recruitment into openings is likely limited due to edaphic factors, such as shallow soils or rocky outcroppings (Meyer et al. 2007) (Figure 18). Canopy cover of existing trees may play an important role in facilitating post-suppression tree recruitment (North et al. 2004). However, this pattern does not seem to be consistent throughout the Sierra Nevada mixed-conifer region. Other studies have found that gaps are indeed be colonized by trees in the absence of fire, with ingrowth occurring between, rather than underneath, existing trees (Nagel and Taylor 2005, Scholl 2008, Lydersen et al. 2013). Similar patterns of tree recruitment in the absence of an historical fire regime have been observed in other old-growth coniferous forests in the West (Youngblood et al. 2005, Abella and Denton 2009).

Spatial patterns of tree invasion are relevant to the design and implementation of forest restoration prescriptions (see Appendix C). Studies investigating change in Sierra Nevada mixed-conifer forests over the past century have demonstrated that the populations of historically dominant shade-intolerant tree species, such as sugar pine and ponderosa pine are declining (Ansley and Battles 1998, van Mantgem et al. 2004, Lutz et al. 2009). These trees preferentially recruit in sunny forest openings, many of which were historically created or maintained by fire (Zald et al. 2008). Given these declines, restoration treatments in Sierra Nevada mixed-conifer forests should promote the establishment of shade-intolerant species. Knowing where shade-intolerant trees have naturally recruited in the absence of fire and how this recruitment relates to
legacy trees can give insight into how interactions between established trees facilitate or hinder shade-intolerant tree recruitment in a fire-free ecosystem.

1.3 Study goals

In this study, we utilize a large, spatially-explicit dataset from a forest research plot in Yosemite National Park (Yosemite) to investigate the spatio-temporal patterns of tree recruitment during the fire suppression era. Specifically, we test alternative hypotheses (Table 6) about the dominant ecological processes influencing the spatial-temporal pattern of tree invasion by quantifying spatial relationships between legacy trees and different age classes of ingrowth trees. We define legacy trees in our study area as those estimated as being alive in 1930 with a forest reconstruction model (see Chapter 3). We considered two classes of suppression-era ingrowth: early ingrowth are those trees with reconstructed recruitment dates between 1930 and 1970, while late ingrowth are those that established between 1970 and 2010.

This study is organized around three broad questions:

1) Do the spatial locations of ingrowth trees depend on legacy trees?

2) Do the spatial relationships between legacy trees and early ingrowth differ from that of legacy trees and late ingrowth?

3) Does the spatial relationship between ingrowth and legacy trees differ for the principle shade-tolerant species, white fir, and the principle shade-intolerant species, sugar pine?

For each of these questions we tested alternative hypotheses reflecting different biological mechanisms expected to influence spatio-temporal patterns of tree establishment in the absence of fire (Table 6).
2. METHODS

2.1 Study site

The Yosemite Forest Dynamics Plot (YFDP) is a 25.6 ha permanent sample plot located in the Rockefeller sugar pine grove – an old-growth mixed-conifer stand in Yosemite, California (Lutz et al. 2012, Gabrielson et al. 2012) (Figure 3). Dominant tree species include sugar pine, white-fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and Pacific dogwood (*Cornus nuttallii*), with some sugar pine > 200 cm diameter at breast height (dbh). Shrub cover is dominated by beaked hazel (*Corylus cornuta* var. *californica*), bush chinquapin (*Chrysolepis sempervierns*), and northern bilberry (*Vaccinium uliginosum*). All live trees ≥1cm dbh are tagged and mapped, including all snags ≥10 cm dbh and ≥1.8 m tall and all downed logs > 30 cm in diameter, for a total inventory of about 38,000 live and dead trees. Historically, the YFDP experienced a regime of non-stand-replacement fire, with a point fire return interval of 29.5 years, until 1900, after which all widespread fires were suppressed (see Chapter 2).

2.2 Historical data

We reconstructed estimates of tree presence, absence, size, and status on the YFDP from 2010 to 1900 using a forest reconstruction model. We used reconstructions obtained from the site-specific growth model variant of the reconstruction model described in Chapter 3. We obtained 30 simulations of the reconstructed forest; each simulation resulted in tree lists of live trees on the YFDP at five year intervals from 2010 to 1900. For each simulation, we classified each tree in the contemporary dataset as either being either legacy (established before and alive in 1930), early ingrowth (established between 1930 and 1970), or late ingrowth (established
between 1970 and 2010). We chose 1930 as the cutoff year for legacy trees because the last widespread fire on the YFDP was in 1900 and 30 years represents approximately one fire return interval for the YFDP (Chapter 2); thus 1930 represents the estimated outer bound of the historical range of variability for this site. Furthermore, the 1930 cutoff year helps offset the effects of the rapid decay rates in the site-specific reconstruction model (Chapter 3). It is important to note that we define ingrowth trees are those that established during the fire suppression era and have survived until the present day – not trees that may have established but have subsequently died (and decayed) during the past 80 years. Each reconstructed forest (i.e., each tree list produced by running the reconstruction model) was unique due to the stochastic representation of growth and decay in the reconstruction model (Chapter 3).

2.4 Statistical analysis

To test the spatial relationship between legacy and ingrowth trees, we employed the bivariate form of the pair-correlation function $g(r)$. The pair correlation function is defined as

$$g(r) = \frac{K'(r)}{2\pi r}$$

where $K'(r)$ is the derivative of Ripley’s $K$ function. The estimate $\hat{g}_{1,2}(r)$ describes the number of type 2 (ingrowth) trees occurring within a ring of radius $r$ centered on the $i$th type 1 (legacy) tree, summed over all type 1 trees in the plot (Wiegand and Moloney 2004). Unlike the commonly used bivariate form of the Ripley’s K function, which describes the number of ingrowth trees within a circle of radius $r$, the pair-correlation function describes the number of ingrowth trees at a distance $r$ from a given legacy tree. The benefit of using pair-correlation function over the K function arises because the K function is cumulative and estimates at larger
distances are cofounded by effects at shorter distances. Using the pair-correlation function allows one to isolate spatial patterns at each distance of $r$ (Wiegand and Moloney 2004).

Since the pair-correlation statistic is non-parametric in nature, it requires a null model with which to test for spatial independence in a given point pattern. Typically, the observed pattern is compared to the patterns of a large number of Monte Carlo simulations of the null model – observed values that deviate significantly from the envelope generated from the simulations of the null model indicate a spatial relationship other than random (Wiegand and Moloney 2004). In choosing a null model, we must acknowledge that direct environmental factors such as topography and soil type can exert strong controls over where trees can and will grow, masking the role of intertree dynamics in determining tree spatial patterns (Getzin et al. 2006). Since tree spatial distribution is strongly controlled by these exogenous “first-order” effects, our null model must take into account that the intensity of trees across the plot is not spatially uniform – that is, that intensity varies from region to region. Therefore, we chose to use a torodial shift null model, which preserves the underlying second-order structure of the type 2 (ingrowth) pattern and shifts this pattern randomly in relation to the type 1 (legacy) pattern.

We ran a separate test for each of eight relationships of interest (e.g., legacy sugar pine and early ingrowth sugar pine, (Figures 20-23). For each test, we selected the appropriate data from each reconstructed stem map. We then calculated the empirical value of $\hat{g}_{1,2}(r)$ for each reconstructed stem map at a given distance $r$, and then simulated 15 torodial shifts of each ingrowth tree pattern. This resulted in 450 realizations of the null model for each test (30 stem maps x 15 torodial shift simulations). For each value of $r$, we calculated the mean and 95% confidence intervals of the empirical value for $\hat{g}_{1,2}(r)$ across the 30 reconstructed stem maps and the mean and 95% confidence intervals of $\hat{g}_{1,2}(r)$ for all 450 realizations of the null model.
We employed isotropic edge correction (Diggle 2003) to account for trees located less than \( r \) from plot edges.

Based on initial results, we chose to also investigate the spatial relationship between early ingrowth sugar pine and heterospecific legacy trees (white fir and incense cedar) to provide insight into observed patterns between early ingrowth sugar pine and both legacy sugar pine and all legacy trees.

3. RESULTS

During the early stages of fire suppression on the YFDP, seedling establishment of sugar pine occurred in the vicinity of legacy trees, evidenced by spatial attraction between legacy trees and ingrowth sugar pine at small spatial scales (<10 m) (Figure 24 A₁; Figure 26 C₁). Late sugar pine ingrowth exhibited the opposite pattern with sugar pine ingrowth occurring less frequently than expected in the vicinity of legacy trees, as demonstrated by the small scale spatial repulsion between legacy trees and late ingrowth sugar pine (Figure 24, A₂; Figure 26, C₂). Additionally, there is evidence for spatial attraction between all legacy trees and late ingrowth sugar pine at large scales: empirical \( \hat{g}_{1,2}(r) \) values at all scales fall outside of the 95% confidence envelope generated from 450 simulations of the torodial shift null model between about 35-50 m (Figure 24, A₂). There was no spatial relationship between early ingrowth sugar pine and legacy heterospecifics (white fir and incense cedar) – the empirical pattern \( \hat{g}_{1,2}(r) \) pattern falls within the 95% confidence envelope generated by the random torodial shifts (Figure 28).

Early white fir ingrowth trees are spatially attracted to legacy trees at very small spatial scales (<2 m) (Figure 25, B₁; Figure 27 D₁). Contrary to sugar pine, however, as fire suppression has progressed, the location of late white fir ingrowth appears to be random with respect to
legacy trees: empirical $\hat{g}_{1,2}(r)$ values at all scales fall within the 95% confidence envelope generated from the null model (Figure 25 B₂; Figure 27, D₂). These results demonstrate a substantial shift of intertree dynamics as fire suppression has progressed over the past century.

4. DISCUSSION

Historically, the spaces around the vicinity of large, seed-producing trees were likely open, because fine fuels such as needles, bark, and cones collecting at the base of trees would have promoted fire and limited seedling recruitment (Stephens et al. 2008, Gabrielson et al. 2012). After the onset of fire suppression, these open areas under legacy trees were quickly colonized, evidenced by the spatial attraction between legacy and early ingrowth trees at a scale that corresponds roughly to the radius of mature conifer crowns (0-10 m) (Figure 24 A₁; Figure 25, B₁; Figure 26 C₁; Figure 27 D₁) (Sánchez Meador et al. 2011). We hypothesized that this attraction could be the results of a seed source effect, whereby seeds from parent trees tended to established within the vicinity of the parent trees (Keeton and Franklin 2005), and/or a facilitative effect, whereby the legacy trees provided habitat amelioration in some way that encouraged seedling establishment (Baumeister and Callaway 2006) (Table 6).

While we found evidence for spatial attraction between early ingrowth sugar pine and all species of legacy trees (Figure 24, A₁) as well as solely legacy conspecifics (Figure 26, C₁), when we analyzed the relationship between early ingrowth sugar pine and heterospecific legacy trees (white fir and incense cedar), the pattern was random (Figure 28). This indicates that conspecific legacy sugar pine trees have a strong influence on the observed pattern of attraction between early ingrowth sugar pine and legacy trees and therefore attraction is most likely due to a seed source effect. We also observed spatial attraction between early ingrowth white fir and
conspecific legacy trees (Figure 27, D₁); this pattern was much weaker, however, when all legacy trees were included (Figure 25, B₁), also indicating a possible seed source effect of legacy white fir trees.

As fire suppression progressed, spatial patterns of tree establishment shifted. There is no evidence of spatial attraction between late ingrowth and legacy trees; instead, we see spatial repulsion between late ingrowth sugar pine and legacy trees at small scales (Figure 24 A₂; Figure 26, C₂) and random establishment of late ingrowth white fir in relation to legacy trees (Figure 25 B₂; Figure 27, D₂). The spatial repulsion between late ingrowth sugar pine and legacy trees is likely a result of infilling of the spaces in the vicinity of legacy trees by earlier ingrowth, with which late ingrowth could not compete. It is possible that the increased density of conspecifics at the base of legacy sugar pines has contributed to increased sugar pine seedling morality, due to Janzen-Connell-type effects, which has been observed in Sierra Nevada mixed-conifer forests for sugar pine (Das et al. 2008). It is also possible that the invasive pathogen white pine blister rust (*Cronartium ribicola*), which was introduced to the Sierra Nevada in the early 1960s, also contributes to density-mediated mortality of late ingrowth around the bases of large trees (van Mantgem et al. 2004, Waring and O’Hara 2009). Another explanation is that despite open spaces beneath legacy trees, the large accumulation of duff and other fine fuels at the bases of legacy trees that accumulated in the absence of fire restricts sugar pine seed germination (Lutz et al. 2012). Establishment of the late arrivers, therefore, has been limited to elsewhere in the plot.

On the contrary, late ingrowth white fir are not spatially repulsed from legacy trees, likely because as a shade tolerant species, white fir can recruit underneath and compete with the earlier ingrowth (Burns and Honkala 1990). White fir appears to be less restricted by low light levels and competition than sugar pine, and in the absence of fire, can establish on a wide variety
of sites. Furthermore, unlike sugar pine, white fir survival has been found to increase with density of conspecific neighbors, possibly because closely spaced white fir benefit from increased mycorrhizal associations (Das et al. 2008).

We found some weak evidence for spatial attraction between all legacy trees and late ingrowth sugar pine at large scales (35-50 m), which is potentially indicative of exogenous factors, such as substrate quality or suitability of forest openings, driving late ingrowth sugar pine spatial patterns (Sánchez Meador et al. 2009). Although we did not find any evidence for attraction at large spatial scales for any other ingrowth trees, it is not to say that tree invasion during the fire suppression era has not occurred in forest openings or that substrate quality does not at all mediate where tree establish. Rather, exogenous factors such as these may not be particularly important in determining the locations of ingrowth trees, and that establishment is instead mainly density-mediated (i.e., trees establish simply because there is unoccupied growing space). Observed random patterns of establishment at scales outside of the zones of individual tree influence observed for both early and late ingrowth of both species could be a result of the decoupling between above and belowground resources, especially light, which tends to occur in tall temperate forests in at middle and high latitudes (Van Pelt and Franklin 2000).

Our results demonstrate that in the absence of fire, tree establishment on the YFDP has occurred both underneath and between legacy trees, indicating that forest gaps are neither less nor more conducive to tree establishment than other areas of the forest. Is likely that while there are some persistent substrate-mediated gaps and shrub-maintained gaps on the YFDP (Lutz et al. 2014) (Figure 18), there are not substantially more of these types of openings than those once historically maintained by fire – as such we see very little evidence for spatial repulsion or
attraction at large scales. It is also possible that the effects of these two different types of gaps on tree spatial patterns obscure each other in the statistical approach we present here.

It appears that patterns of tree establishment in Sierra Nevada mixed-conifer forests may be strongly influenced by the underlying substrate. A number of studies in Sierra Nevada mixed-conifer forests investigating changes in trees spatial patterns during the fire suppression era have demonstrated an increase in the size of tree clumps and a decrease in amount of open space, indicating tree invasion into open spaces (Nagel and Taylor 2005, Lydersen et al. 2013). However, North et al. (2004) and Fry et al. (2014) found that forest openings at the Teakettle Experimental Forest in the southern Sierra Nevada have been maintained despite more than a century of fire suppression. Teakettle’s soils are of granitic parent material, in contrast to the metamorphic-derived soils of the YFDP. It is likely that poor soil quality as a result of shallow, dry soils with limited bedrock fracture restricts colonization of openings at Teakettle (North et al. 2004), which is not the case on the YFDP.

It is important to acknowledge that our classifications of trees as legacy, early ingrowth, or late ingrowth are based on a forest reconstruction model, not on individual tree cores that would provide empirical evidence of tree establishment dates. One of the benefits of classifying the tree population in large decadal bins (i.e., 1900-1930, 1930-1970, and 1970-2010) is that we “smooth over” some of the uncertainty inherent to our approach in determining tree presence and absence at specific years in the past. We recognize that we may have misclassified individual trees, but feel that given the large number of trees, the overall effect of a few misclassifications is likely minimal.
5. CONCLUSIONS

In this study, we found evidence for a clear spatiotemporal structure to the patterns of tree invasion after the beginning of fire exclusion on the YFDP and demonstrate the importance of viewing the continuum of change during the fire suppression era. While comparing both historical and contemporary spatial patterns are useful for identifying changes to the structure and composition of forests in the absence of fire, static views provide little insight into the ecological processes that have driven these changes. Had we simply analyzed the spatial relationship between all ingrowth trees and legacy trees instead of the early versus late invaders, we likely would not have detected the important relationships between legacy trees and the early invaders. Without fire, forest spatial patterns have shifted, which may affect important aspects of forest functionality. Much of the current pattern we see today is a result of tree establishment during the fire suppression era (>25,000 ingrowth trees) and this establishment has, in part, shifted tree spatial patterns to the point where they are well outside of the bounds of historical patterns.

Forest managers seeking to restore fire-suppressed Sierra Nevada mixed-conifer forests should consider historical tree spatial patterns when designing and implementing silvicultural prescriptions and prescribed burning (Appendix C) (Churchill et al. 2013). Active fires would likely have maintained space beneath large-diameter seed source trees, but in the absence of fire, these areas have become and remained occupied by ingrowth. In order to shift tree spatial patterns back within their historical range and variability, thus maintaining ecological functions associated with these patterns, managers might consider removing some of the ingrowth located in the vicinity of large trees and removing duff mounds around tree bases (Nesmith et al. 2010). Our study also further demonstrates the importance of avoiding generalizations regarding where
trees have invaded during the fire suppression era in Sierra Nevada mixed-conifer forests – some sites have experienced less change than the YFDP with regard to tree spatial patterns because of the persistence of environmentally-mediated (i.e., substrate quality) openings. Tree removal efforts perhaps should be concentrated at sites where historical openings have now become infilled in the absence of fire, as opposed to sites where these openings have been maintained despite fire suppression. We should consider a specific site’s soil parent material to inform our development of target conditions for restoration.
### Table 6. Summary of hypotheses to explain the spatial relationship of legacy trees and ingrowth trees on the YFDP. N values are based on mean values across 30 reconstructions of the YFDP

<table>
<thead>
<tr>
<th>Test</th>
<th>Species</th>
<th>Hypotheses</th>
<th>Rationale</th>
<th>Expected statistical results</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>Legacy: all (n=4,500) Ingrowth: early sugar pine (n=704)</td>
<td>HAa: Ingrowth has occurred in the canopy openings between legacy trees.</td>
<td>Legacy trees compete with ingrowth and inhibit establishment; ingrowth able to occupy open areas once maintained by fire (Lutz 2012, Scholl 2008).</td>
<td>Spatial repulsion at small (0-10 m) scales; spatial attraction at larger scales</td>
</tr>
<tr>
<td>A1</td>
<td>Legacy: all (n=4,500) Ingrowth: late sugar pine (n=3,330)</td>
<td>HAb: Ingrowth has occurred underneath legacy tree canopies; substrate restricts colonization of openings.</td>
<td>Legacy trees facilitate the establishment of ingrowth by ameliorating germination environment (i.e., providing shade, water) and/or by acting as a seed source (North et al. 2004, Fry et al. 2014, Keeton and Franklin 2007)</td>
<td>Spatial attraction at small scales (0-10 m); spatial repulsion at larger scales</td>
</tr>
<tr>
<td>A2</td>
<td>Legacy: all (n=4,500) Ingrowth: early white fir (n=3,949)</td>
<td>HBa: Ingrowth has occurred beneath legacy tree canopies</td>
<td>White fir are shade tolerant, exogenous factors limit colonization of openings. Legacy trees act as seed source (North et al. 2004, Fry et al. 2014, Keeton and Franklin 2007).</td>
<td>Spatial attraction at small scales (0-10 m); spatial repulsion at larger scales</td>
</tr>
<tr>
<td>A2</td>
<td>Legacy: all (n=4,500) Ingrowth: late white fir (n=20,504)</td>
<td>HBo: Legacy trees and ingrowth trees are spatially independent.</td>
<td>Unoccupied space colonized equally by both cohorts.</td>
<td>Empirical $g_{1,2}(r)$ overlaps envelope from randomized simulations</td>
</tr>
<tr>
<td>B1</td>
<td>Legacy: sugar pine (n=1,510) Ingrowth: early sugar pine (n=704)</td>
<td>HCa: Ingrowth occurs in forest openings between legacy trees</td>
<td>Sugar pine tend to recruit in sunny openings (Zald et al 2008). Legacy sugar pine facilitate recruitment of ingrowth sugar pine and/or produce seed source effects, but duff mounds at the base of legacy trees restrict germination in close proximity to tree boles (Lutz et al. 2012).</td>
<td>Spatial repulsion at small (0-10 m) scales; spatial attraction at larger scales</td>
</tr>
<tr>
<td>B2</td>
<td>Legacy: sugar pine (n=1,510) Ingrowth: late sugar pine (n=3,330)</td>
<td>HCb: Ingrowth occurs near legacy trees but not in immediate vicinity.</td>
<td>Unoccupied space colonized equally by both cohorts.</td>
<td>Empirical $g_{1,2}(r)$ overlaps envelope from randomized simulations</td>
</tr>
<tr>
<td>C1</td>
<td>Legacy: white fir (n=2,170) Ingrowth: early white fir (n=3,949)</td>
<td>HDa: Ingrowth has occurred beneath legacy tree canopies</td>
<td>White fir are shade tolerant, exogenous factors limit colonization of openings. Legacy trees may produce seed source effect (North et al. 2004, Fry et al. 2014, Keeton and Franklin 2007).</td>
<td>Spatial attraction at small scales (0-10 m); spatial repulsion at larger scales</td>
</tr>
<tr>
<td>C2</td>
<td>Legacy: white fir (n=2,170) Ingrowth: late white fir (n=20,564)</td>
<td>HDb: Ingrowth has occurred both underneath legacy tree canopies and in forest openings</td>
<td>White fir can grow well in shade but can also tolerate sun; fire no longer maintains openings (Lydersen et al. 2013).</td>
<td>Spatial attraction at both small (0-10 m) and large scales</td>
</tr>
<tr>
<td>C2</td>
<td>Legacy: white fir (n=2,170) Ingrowth: late white fir (n=20,564)</td>
<td>HDc: Legacy trees and ingrowth trees are spatially independent.</td>
<td>Unoccupied space colonized equally by both cohorts.</td>
<td>Empirical $g_{1,2}(r)$ overlaps envelope from randomized simulations</td>
</tr>
</tbody>
</table>
Figure 18. The YFDP harbors a number of large forest openings that are dominated by shrubs on rocky outcroppings. It is likely that openings such as these are substrate mediated and will persist despite the lack of frequent fires. This photo shows a large persistent shrub patch (Cornus sericea) on the southwest corner of the plot. *Photo by M.A.F. Barth.*
Figure 19. The YFDP is characterized by large-diameter trees, both living and dead, many of which established prior to the onset of fire suppression. Ingrowth trees crowd the understory in places, yet forest openings with few trees still persist. *Photo by J. Lutz.*
Figure 20. Stem maps of the YFDP displaying the spatial relationships between all legacy trees and ingrowth sugar pine. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. DBH represents diameter in 1930 (legacy), 1970 (early) or 2010 (late). Panel labels refer to hypotheses in Table 6.
Figure 21. Stem maps of the YFDP displaying the spatial relationships between all legacy trees and ingrowth white fir. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. DBH represents diameter in 1930 (legacy), 1970 (early) or 2010 (late). Panel labels refer to hypotheses in Table 6.
Figure 22. Stem maps of the YFDP displaying the spatial relationships between sugar pine legacy trees and ingrowth sugar pine. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. DBH represents diameter in 1930 (legacy), 1970 (early) or 2010 (late). Panel labels refer to hypotheses in Table 6.
Figure 23. Stem maps of the YFDP displaying the spatial relationships between white fir legacy trees and ingrowth white fir. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. DBH represents diameter in 1930 (legacy), 1970 (early) or 2010 (late). Panel labels refer to hypotheses in Table 6.
Figure 24. Panels display the $g(r)_{1,2}$ values for the empirical spatial relationships between all legacy trees and ingrowth sugar pine (blue) and $g(r)_{1,2}$ values from randomized simulations (red). Dashed lines represent 95% confidence intervals (CI) across 30 reconstructions of the YFDP (blue) and 450 randomized simulations using the torodial shift method (red); solid lines are mean values. Empirical values outside of the population independence CI interval >1 indicate spatial attraction and values <1 indicate spatial repulsion between the two populations. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. Panel labels refer to hypotheses in Table 6.
Figure 25. Panels display the $g(r)_{1,2}$ values for the empirical spatial relationships between all legacy trees and ingrowth white fir (blue) and $g(r)_{1,2}$ values from randomized simulations (red). Dashed represent 95% confidence intervals (CI) across 30 reconstructions of the YFDP (blue) and 450 randomized simulations using the torodial shift method (red); solid lines are mean values). Empirical values outside of the population independence CI interval >1 indicate spatial attraction and values <1 indicate spatial repulsion between the two populations. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. Panel labels refer to hypotheses in Table 6.
Figure 26. Panels display the $g(r)_{1,2}$ values for the empirical spatial relationships between sugar pine legacy trees and ingrowth sugar pine (blue) and $g(r)_{1,2}$ values from randomized simulations (red). Dashed represent 95% confidence intervals (CI) across 30 reconstructions of the YFDP (blue) and 450 randomized simulations using the torodial shift method (red); solid lines are mean values. Empirical values outside of the population independence CI interval $>1$ indicate spatial attraction and values $<1$ indicate spatial repulsion between the two populations. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. Panel labels refer to hypotheses in Table 6.
Figure 27. Panels display the $g(r)_{1,2}$ values for the empirical spatial relationships between white fir legacy trees and ingrowth white fir (blue) and $g(r)_{1,2}$ values from randomized simulations (red). Dashed represent 95% confidence intervals (CI) across 30 reconstructions of the YFDP (blue) and 450 randomized simulations using the torodial shift method (red); solid lines are mean values). Empirical values outside of the population independence CI interval $>1$ indicate spatial attraction and values $<1$ indicate spatial repulsion between the two populations. All legacy trees were alive in 1930. All early ingrowth trees established between 1930 and 1970; all late ingrowth trees established between 1970 and 2010. Panel labels refer to hypotheses in Table 6.
Figure 28. Comparison of the spatial relationship between legacy sugar pine and early ingrowth sugar pine (top panel) to that of heterospecific legacy tree species (white fir and incense cedar) and early ingrowth sugar pine (bottom panel). Empirical values outside of the population independence CI interval >1 indicate spatial attraction and values <1 indicate spatial repulsion between the two populations. Differences in empirical g(r)_{1,2} values at small spatial scales provide evidence for a potential seed source effect of legacy sugar pine trees. Legacy trees were alive in 1930, early ingrowth trees established between 1930 and 1970. Panel labels refer to hypotheses in Table 6.
CHAPTER 4 REFERENCES


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CHAPTER 5
CONCLUSION

The overall goal of this research was to investigate changes to Sierra Nevada mixed-conifer forests during the fire suppression era. This work was motivated by the need to better understand the ecological processes driving forest change in the absence of fire, and to inform restoration efforts. We chose to frame our research around the Yosemite Forest Dynamics Plot, a newly established permanent forest research site located in heart of the Sierra Nevada mixed-conifer forests, because of the vast potential learning opportunities afforded by extensive continuing research efforts at this site. We hoped that in reconstructing historical forest stand structure and composition of the YFDP as well as the site-specific historical fire regime, we could better interpret the contemporary dataset and gain insight into the ecological processes that have given rise to the forest we see today. We also sought to evaluate and improve reconstruction-based approaches for assessing forest change.

The historical fire regime of the YFDP was characterized by frequent, non-stand replacing fires, similar to other mixed-conifer forests in the region. Prior to the last widespread fire in 1900, the YFDP a point fire return interval (PFRI) of about 29 years. Fires burned most frequently late in the growing season and during dormancy and were generally small and confined, although larger fires across the landscape were not uncommon. The YFDP had a longer PFRI than Big Oak Flat (BOF) a drier, less productive site downslope and north of the YFDP, which had a PFRI of only 12 years. This could mean that the fire return interval departure is lower on the YFDP than similar, less productive sites, and that the YFDP may be able to naturally harbored higher, or perhaps more variable, tree densities and fuel loads. In designing and implementing restoration prescriptions for fire-suppressed Sierra Nevada mixed-
conifer forests, managers should take into account the possibility for heterogeneity in historical fire regimes across a landscape.

Forest reconstruction studies represent our best way to obtain new historical reference information. We feel that a computer-based forest reconstruction approach can be a valid method for expanding the availability of historical reference information, given the improvements addressed in this study are addressed. We developed two forest reconstruction models, parameterized specifically for Sierra Nevada mixed-conifer forests, which can predict forest stand structure and composition of a given stand at some point in the past. Our in depth assessment of model performance demonstrated that the regionally-parameterized Das growth model results in inaccurate estimates of historical forest conditions and that a simpler site-specific growth model based on tree growth rates derived from tree cores collected near the YFDP produces more reasonable results that are in general agreement with historical datasets from nearby forests of similar composition. Tree growth rates derived from local tree cores integrate complexities of tree growth that are difficult to predict in a modeling framework, such as site productivity, substrate characteristics, competition, resource availability, and climatic variables, which likely contributes to improved model performance.

Without a substantial increase in decay data available for Sierra Nevada tree species, our limited understanding of tree decay will continue to be a major constraint in forest reconstruction studies and other forest models that predict tree decay over long time scales. The current decay data available for Sierra Nevada mixed-conifer forests are not adequate for use in forest reconstruction studies or forest modeling exercises that are used to plan and justify management, such as the Forest Vegetation Simulator (FVS). Also, there may be a substantial amount of missing evidence of historical trees in contemporary forests, which is an inherent limitation to all
reconstruction studies. We feel that other reconstruction studies, especially those in Sierra Nevada mixed-conifer forests, should better acknowledge the limitations and biases associated with inadequate tree decay models and loss of evidence to avoid the potential for inappropriate use of reconstruction-derived reference information.

Our investigation of the spatial relationships between legacy trees and early and late ingrowth trees provides evidence for a clear spatiotemporal structure to the patterns of tree invasion after the beginning of fire exclusion on the YFDP. Investigating the spatial patterns of tree invasion in the absence of fire allows us to understand how dynamic ecological processes have influenced changes to forest structure and composition. In the early stages of fire suppression, ingrowth white fir and sugar pine established in the immediate vicinity of legacy tree crowns, indicating a possible seed source effect. However, as fire suppression has progressed, ingrowth sugar pine no longer establish in the vicinity of legacy trees, likely because these spaces were occupied by the early ingrowth, or perhaps because of Janzen-Connell effects. In contrast, late arriving white fir can still establish near legacy trees, most likely because of their ability to tolerate competition with the earlier arrivers. These results highlight a substantial shift in forest spatial patterns in the fire suppression era, which may affect important aspects of forest functionality.

This project highlights notable considerations for assessment of forest change in Sierra Nevada mixed-conifer forests during the fire suppression era. Historical fire regimes between two adjacent sites can be quite different and therefore assumptions regarding the historical fire regime of a specific site and the degree to which forest conditions at that site have changed in the absence of fire may be incorrect. Forest reconstruction studies that use limited decay data and do not account for loss of evidence may misrepresent historical forest conditions, specifically the
small-diameter and shade-tolerant tree component. Static views of contemporary and historical forest condition allow us to quantify forest change between two points in time, but require us to make assumptions regarding the ecological processes effecting these changes. As we work to reintroduce fire to Sierra Nevada mixed-conifer forests, it is important that we make management decisions using the best available scientific evidence. Restoration efforts should increase forest resiliency to disturbances, and in doing so, prepare these forests to adapt to uncertain future while maintaining important ecological functions and services. This will require an ongoing effort to reduce the uncertainties regarding how these ecosystems functioned prior to human alteration.
APPENDIX A: DECAY MODEL DATA

Table A.1. Specific decay data used to “undecay” snags and logs in the forest reconstruction model. “Forest type” and “target species” are where, and for which species, the decay rates were originally derived in the source study. *Density by decay class estimates derived from Harmon et al. (2008).

<table>
<thead>
<tr>
<th>YFDLP species</th>
<th>Decay data used</th>
<th>Density data (g/cm³)</th>
<th>Target species</th>
<th>Sample tree sizes</th>
<th>Forest type</th>
<th>Source</th>
<th>Limitations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Logs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>White fir</strong></td>
<td>Log mineralization rate: k=0.049</td>
<td>DC 1: ≤ 0.340, &gt;0.305 DC 2: ≤ 0.305, &gt; 0.212 DC 3: ≤ 0.212, &gt; 0.178 DC 4/5: &lt;0.178</td>
<td>White fir</td>
<td>&gt; 20 cm diameter</td>
<td>Dry mixed-conifer (CA)</td>
<td>Harmon et al. (1987)</td>
<td>Small sample size (n = 20)</td>
</tr>
<tr>
<td><strong>Sugar pine</strong></td>
<td>Log mineralization rate: k=0.024</td>
<td>DC 1: ≤ 0.369, &gt;0.269 DC 2: ≤ 0.269, &gt; 0.221 DC 3: ≤ 0.221, &gt;0.113 DC 4/5: &lt;0.113</td>
<td>Ponderosa pine</td>
<td>&gt; 23 cm diameter</td>
<td>Dry mixed-conifer (CA)</td>
<td>Dunn (2011)</td>
<td></td>
</tr>
<tr>
<td><strong>Incense cedar</strong></td>
<td>Log age estimated by decay class</td>
<td></td>
<td>Western redcedar</td>
<td>Range: 79-250 cm dbh</td>
<td>Coastal rainforest, BC</td>
<td>Daniels et al. (2011)</td>
<td>Small sample size (n = 15)</td>
</tr>
<tr>
<td><strong>Black oak</strong></td>
<td>Log mineralization rate: k=0.0295</td>
<td>DC 1: ≤ 0.611, &gt;0.450 DC 2: ≤ 0.450, &gt; 0.382 DC 3: ≤ 0.382, &gt;0.241 DC 4/5: &lt;0.241</td>
<td>White oak, eastern black oak, northern red oak combined</td>
<td>Range: 10-80 cm diameter</td>
<td>Deciduous (ID)</td>
<td>Macmillian (1981)</td>
<td></td>
</tr>
<tr>
<td><strong>Snags</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>White fir</strong></td>
<td>Snag fall rates by decay class</td>
<td></td>
<td>White fir and red fir combined</td>
<td>Mean dbh: 40.6</td>
<td>Sierra Nevada mixed-conifer</td>
<td>Morrison and Raphael (1993)</td>
<td>Base on single 10 year study</td>
</tr>
<tr>
<td><strong>Sugar pine</strong></td>
<td>Snag fall rates by decay class</td>
<td></td>
<td>Jeffery pine, sugar pine, lodgepole pine combined</td>
<td>Mean dbh: 40.6</td>
<td>Sierra Nevada mixed-conifer</td>
<td>Morrison and Raphael (1993)</td>
<td>Base on single 10 year study</td>
</tr>
<tr>
<td><strong>Incense cedar</strong></td>
<td>Snag age estimated by decay class</td>
<td></td>
<td>Western redcedar</td>
<td>Range: 115-312 cm cm dbh</td>
<td>Southwest coastal rainforest, British Columbia</td>
<td>Daniels et al. (2011)</td>
<td>Small sample size (n = 17)</td>
</tr>
<tr>
<td><strong>Black oak</strong></td>
<td>Snag fall rates stochastic: equal likelihood of staying in same decay class or transitioning to earlier decay class.</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix A. References


Dunn, C. J. 2011. Coarse woody detritus dynamics, variable decay rates and their contribution to wildland fuel succession following high-severity fire disturbance in dry-mixed conifer forests of Oregon’s eastern Cascades. Ph.D Dissertation, Oregon State University, Corvallis, OR.


library(spatstat)

# Load functions

#******************************NCI FUNCTION******************************#
# function to calculate the crowding index for a given focal tree
nci <- function(input.list, focal.tree, lambda.matrix, competitors){
  #input.list: dataframe containing the focal tree's id, spp, dbh, and x,y location
  #focal.tree: the row number of the focal tree
  #lambda.matrix: matrix of interspecific competition values (0-1).
  #competitors is a data frame, which represents the live competitors surrounding the focal tree.

  if (nrow(competitors)>0){
    comp.exuded <- vector()
    target <- lambda.matrix[as.character(input.list$spp[focal.tree]),]
    for (j in 1:nrow(competitors)){
      if (competitors$distances[j]==0){comp.exuded[j]<-0}
      else {lambda <- target[,as.character(competitors$spp[j])]
    }
    nci.focal <- input.list$dbh[focal.tree]^input.list$gamma[focal.tree]*sum(comp.exuded) #crowding index for the focal tree
  }
  return(nci.focal)
}

#**************************************** NCI auxiliary function****************************************#
# function to calculate the crowding index for a given focal tree with neighbors' dbh @ t-1 already known.
nci.neighbors.known <- function(input.list, focal.tree, lambda.matrix, competitors){
  #input.list: dataframe containing tree id, species/group, dbh, x,y location,
  #lambda: matrix of interspecific competition values (0-1)
  #focal.tree: the row number of the focal tree
  #competitors: the output of the grow.neighbors function
  comp.exuded <- vector() #empty vector

  for (i in 1:nrow(competitors)){
    if (competitors$distances[i]==0){comp.exuded[i]<-0}
    else {target <- lambda.matrix[as.character(input.list$spp[focal.tree]),]
      lambda <- rnorm(1, mean=target[,as.character(competitors$spp[i])],
      sd=target[,paste(as.character(competitors$spp[i])," .SD", sep="" ))) #pull out the lambda value (and randomize) given the
      competitor's species
      comp.exuded[i] <- lambda*(competitors$dbh.begin[i]^competitors$alpha[i]/competitors$distances[i]^competitors$beta[i])}
  }
  nci.focal <- input.list$dbh[focal.tree]^input.list$gamma[focal.tree]*sum(comp.exuded) #crowding index for the focal tree
  return(nci.focal)
}
#******************************************************************************************
#******************************* F(competition) Function ************************************
#******************************************************************************************
f.competition<-function(tree.list, focal.tree){
  #tree.list: dataframe containing tree id, species/group, dbh, x,y location, parameters c and d, nci
  #focal.tree: the row number of the focal tree
  if(tree.list$spp[focal.tree]=="ABCO" | tree.list$spp[focal.tree]=="ABMA"){  #got these maxNCI values directly from Adrian
    nci.max<-1129.908
  } else if(tree.list$spp[focal.tree]=="PILA" | tree.list$spp[focal.tree]=="PIPO" | tree.list$spp[focal.tree]=="PSME"){
    nci.max<-1436.893
  } else if (tree.list$spp[focal.tree]=="CADE"){
    nci.max<-873.6522
  }
  f.comp<-exp(-tree.list$c[focal.tree]*(tree.list$nci.begin[focal.tree]/nci.max)^tree.list$d[focal.tree])
  return(f.comp)
}

#**************************************************
#**************************PRG Function******************************************
#**************************************************
prg<-function(tree.list, focal.tree){
  #where tree.list is a df containing dbh and (previously defined) a, b1, b2, c1, c2, intercept, and focal.tree is the row number of the focal tree
  intercept<-tree.list$Intercept[focal.tree]
  a<-tree.list$a[focal.tree]
  b1<-tree.list$b1[focal.tree]
  c1<-tree.list$c1[focal.tree]
  b2<-tree.list$b2[focal.tree]
  c2<-tree.list$c2[focal.tree]
  dbh<-tree.list$dbh[focal.tree]
  prg<-intercept+a*(dbh+0.01)^((b1*exp(-c1*dbh)-b2*exp(-c2*dbh))
  return(prg)
}

#*******************************************************************************************
#****************Grow neighbors function***********************************************
#this function will calculate the "dbh.begin" (dbh at the beginning of the timestep) for all the competitive neighbors of a given focal tree.
#*******************************************************************************************
grow.neighbors<-function(input.list, focal.tree, timestep, compeditors){
  #where input list is the dataframe of trees, and focal.tree is the row number of the focal tree
  #timestep is the number of years in the timestep (ie, 1,5,10)
  if(nrow(compeditors)>0){
    compeditors$comp<-0
    compeditors$prg<-0
    compeditors$rg<-0
  } else {
    for (i in 1:nrow(compeditors)){
      #loop to assign the proper mean.nci based on each neighbor tree's spp and dbh
      spp<-compeditors$spp[i]  #shortcut to make coding easier
      dbh<-compeditors$dbh[i]  #shortcut to make coding easier
      if(compeditors$update[i]==1){  #if a dbh has already been updated to a more accurate value, use this.
        dbh<-compeditors$dbh[i]  #dbh calc is the most updated dbh available during each repeat
      } else if (compeditors$spp[i]=="QUKE"){
        dbh<-compeditors$dbh[i]-2*(rnorm(1, mean=4.96, sd=0.88))  #subtract diameter growth for 5 years based on avg. quke radial growth!if ts changes this needs to change
      } else {
        if (spp=="ABCO" | spp=="ABMA"){
          nci.max<-1129.908
        } else if (spp=="PILA" | spp=="PIPO" | spp=="PSME"){
          nci.max<-1436.893
        } else if (spp=="CADE"){
          nci.max<-873.6522
        }
        f.comp<-exp(-spp*(nci.begin/spp)^d)
        return(f.comp)
      }
    }
  }
}

#******************************************************************************************
if (dbh<10){
    mean.nci< abco1.10
  }
else if (dbh>=10 & dbh<20){
    mean.nci< abco10.20
  }
else if (dbh>=20 & dbh<30){
    mean.nci< abco20.30
  }
else if (dbh>=30 & dbh<40){
    mean.nci< abco30.40
  }
else if (dbh>=40 & dbh<50){
    mean.nci< abco40.50
  }
else if (dbh>=50 & dbh<60){
    mean.nci< abco50.60
  }
else if (dbh>60 & dbh<70){
    mean.nci< abco60.70
  }
else if (dbh>=70 & dbh<80){
    mean.nci< abco70.80
  }
else if (dbh>=80 & dbh<90){
    mean.nci< abco80.90
  }
else if (dbh>=90 & dbh<100){
    mean.nci< abco90.100
  }
else if (dbh>=100 & dbh<110){
    mean.nci< abco100.110
  }
else if (dbh>=110 & dbh<120){
    mean.nci< abco110.120
  }
else if (dbh>=120 & dbh<130){
    mean.nci< abco120.130
  }
else if (dbh>=130 & dbh<140){
    mean.nci< abco130.140
  }
else if (dbh>=140 & dbh<150){
    mean.nci< abco140.150
  }
else if (dbh>=150 & dbh<160){
    mean.nci< abco150.160
  }
else if (dbh>=160 & dbh<170){
    mean.nci< abco160.170
  }
else {
    mean.nci< abco170
  }
}
else if (spp=="PILA" | spp=="PSME" | spp=="PIPO"){
  if (dbh<10){
    mean.nci< pila1.10
  }
else if (dbh>=10 & dbh<20){
    mean.nci< pila10.20
  }
else if (dbh>=20 & dbh<30){
    mean.nci< pila20.30
  }
else if (dbh>=30 & dbh<40){
    mean.nci< pila30.40
  }
else if (dbh>=40 & dbh<50){
    mean.nci< pila40.50
  }
else if (dbh>=50 & dbh<60){
    mean.nci< pila50.60
  }
else if (dbh>=60 & dbh<70){
    mean.nci< pila60.70
  }
else if (dbh>=70 & dbh<80){
    mean.nci< pila70.80
  }
else if (dbh>=80 & dbh<90){
    mean.nci< pila80.90
  }
else if (dbh>=90 & dbh<100){
    mean.nci< pila90.100
  }
else if (dbh>=100 & dbh<110){
    mean.nci=pila100.110
}
else if (dbh>=110 & dbh<120){
    mean.nci=pila110.120
}
else if (dbh>=120 & dbh<130){
    mean.nci=pila120.130
}
else if (dbh>=130 & dbh<140){
    mean.nci=pila130.140
}
else if (dbh>=140 & dbh<150){
    mean.nci=pila140.150
}
else if (dbh>=150 & dbh<160){
    mean.nci=pila150.160
}
else if (dbh>=160 & dbh<170){
    mean.nci=pila160.170
}
else if (dbh>=170 & dbh<180){
    mean.nci=pila170.180
}
else if (dbh>=180 & dbh<190){
    mean.nci=pila180.190
}
else if (dbh>=190 & dbh<200){
    mean.nci=pila190.200
}
else if (dbh>=200 & dbh<210){
    mean.nci=pila200.210
}
else if (dbh>=210 & dbh<220){
    mean.nci=pila210.220
}
else if (dbh>=220 & dbh<230){
    mean.nci=pila220.230
}
else {
    mean.nci=pila230
}
}
else if (spp=='CADE'){
    if (dbh<10){
        mean.nci=cade1.10
    }
    else if (dbh>=10 & dbh<20){
        mean.nci=cade10.20
    }
    else if (dbh>=20 & dbh<30){
        mean.nci=cade20.30
    }
    else if (dbh>=30 & dbh<40){
        mean.nci=cade30.40
    }
    else if (dbh>=40 & dbh<50){
        mean.nci=cade40.50
    }
    else if (dbh>=50 & dbh<60){
        mean.nci=cade50.60
    }
    else if (dbh>=60 & dbh<70){
        mean.nci=cade60.70
    }
    else if (dbh>=70 & dbh<80){
        mean.nci=cade70.80
    }
    else if (dbh>=80 & dbh<90){
        mean.nci=cade80.90
    }
    else if (dbh>=90 & dbh<100){
        mean.nci=cade90.100
    }
    else if (dbh>=100 & dbh<110){
        mean.nci=cade100.110
    }
    else if (dbh>=110 & dbh<120){
        mean.nci=cade110.120
    }
    else if (dbh>=120 & dbh<130){
        mean.nci=cade120.130
    }
    else if (dbh>=130 & dbh<140){
        mean.nci=cade130.140
    }
    else if (dbh>=140 & dbh<150){
        mean.nci=cade140.150
    }
    else if (dbh>=150 & dbh<160){
        mean.nci=cade150.160
    }
    else if (dbh>=160 & dbh<170){
        mean.nci=cade160.170
    }
    else if (dbh>=170 & dbh<180){
        mean.nci=cade170.180
    }
    else if (dbh>=180 & dbh<190){
        mean.nci=cade180.190
    }
    else if (dbh>=190 & dbh<200){
        mean.nci=cade190.200
    }
    else if (dbh>=200 & dbh<210){
        mean.nci=cade200.210
    }
    else if (dbh>=210 & dbh<220){
        mean.nci=cade210.220
    }
    else if (dbh>=220 & dbh<230){
        mean.nci=cade220.230
    }
    else {
        mean.nci=cade230
    }
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else if (dbh>=130 & dbh<140){
    mean.nci<-cade130.140
}
else if (dbh>=140 & dbh<150){
    mean.nci<-cade140.150
}
else if (dbh>=150 & dbh<160){
    mean.nci<-cade150.160
}
else if (dbh>=160 & dbh<170){
    mean.nci<-cade160.170
}
else {
    mean.nci<-cade170
}
}

compeditors$nci.begin[i]<-mean.nci
compeditors$comp[i]<-f.competition(compeditors, i)
compeditors$prg[i]<-prg(compeditors, i) #growth. not really appropriate.

compeditors$rg[i]<-compeditors$prg[i]*compeditors$comp[i] #radial growth rate in cm/year

compeditors$dbh.begin[i]<-compeditors$dbh[i]-(timestep*(2*compeditors$rg[i])) #the dbh of focal neighbor i at the
beginning of the timestep based on its calculated rg rate

return(compeditors) #returns a dataframe with compeditors and their estimated dbh's at the beginning of the ts
}

#******************************************
#******************************************
#**********************RECONSTRUCTION MODEL CODE***************************************
#******************************************
#******************************************

data<-read.csv("yfdp_database_2013.csv", header=T) #read in all tree data
data<-subset(data, spp!="SASC" & spp!="SALIX" & spp!="RHCA" & spp!="PRVI" & spp!="PREM" & spp!="COCOC" &
dbh>=10) #remove all species not relevant to this study

lambda.yfdp<-read.csv("yfdp_lambda_matrix.csv", header=T, row.names=1) ## lambda.matrix is a matrix with target
species as rows and competitor species as columns and stan.dev of competitor's competitive strength as columns

#####set values before starting the simulations
start.year<-2010
timestep<-5 #the number of years of the timestep.
n.timestep<-(2010-1900)/5 #set the number of timesteps.
n.sim<-0 #start with 0 simulations
results<-list() #create an empty list to store the results of each timestep
total.sim<-100 # set the desired number of simulations

###### Buffer the plot to eliminate edge effects. Assign new plot corners
max.radius<-18.5
minx<-0+max.radius
maxy<-800-max.radius
maxy<-320-max.radius

#assign trees to within or out of buffered plot
cat("Assigning trees to buffer")
within<-subset(data, x>=minx & x<=maxx & y<=maxy & y>=miny) #all trees that are within the buffered plot
out<-subset(data, x<minx | x>maxx | y>maxy | y<miny)
within$buffer<-as.character("in")
onbuffer<-as.character("out")
trees.for.sim<-rbind(within, out) #bind back together

rm(data)
rm(within)
rm(out)

###assign radii for distance/neighbor list building ####################
abco<-subset(trees.for.sim, spp=="ABCO" | spp=="ABMA")
pila<-subset(trees.for.sim, spp=="PILA" | spp=="PSME" | spp=="PIPO")
cade<-subset(trees.for.sim, spp=="CADE")
quke<-subset(trees.for.sim, spp=="QUKE")
unkn<-subset(trees.for.sim, spp=="UNKN")
conu<-subset(trees.for.sim, spp=="CONU")

abco$radius<-18.5
pila$radius<-11.5
cade$radius<-7.5
unkn$radius<-12.5
quke$radius<-0

original.treelist<-rbind(abco, pila, cade, quke, unkn)
rm(abco, pila, cade, quke, unkn)

######################################################################## CREATE THE COMPEDITORS LIST (only done once)########################################################################

#Note: "Original.treelist" is only used to create and access the distances and neighborhood lists.
cat("populating neighborhood and distances list", "\n")

df of the focal tree

distances<-pairdist(neighbors.in.radius)[,foc.tree]####distances associated with neighbors
neighbor.df<-as.data.frame(original.treelist[neighbors.index [,]])
neighbor.df<-cbind(neighbor.df, distances)
compeditors.list[[i]]<-subset(neighbor.df, orig.index!=original.treelist$orig.index[i])
cat(paste("tree", i, "is a q and lists complete ", "\n"))

#add extra columns to conu
conu$orig.index<-0
conu$radius<-0

trees.for.sim<-rbind(original.treelist, conu)
rm(original.treelist)
while(n.sim<total.sim){ #controls the number of total number reconstructions.
trees<-trees.for.sim #refreshes the treelist to start all over again at the beginning of each reconstruction
tyrees<-
trees.for.sim  #refreshes the treelist to start all over again at the beginning of each reconstruction
year.now<-2010
timestep.executed<-1

start simulations

while(n.sim<total.sim){ #controls the number of total number reconstructions.
trees<-trees.for.sim #refreshes the treelist to start all over again at the beginning of each reconstruction
year.now<-2010
timestep.executed<-1

assign Species and dbh to UNKN trees (once per sim)

if(nrow(unkn)>0){
  for(i in 1:nrow(unkn)){
    if(unkn$dbh[i]>0){unkn$sd[i]<-
unkn$dbh[i]}
    if(unkn$sd[i]<60){
      prob<-
c(0.63, 0.03, 0.14, 0.19) #defines probabilities of UNKN being a certain species
      unkn$spp[i]<-
sample(c("ABCO", "CADE", "QUKE", "PILA"), size=1, prob=prob)
    }
  }
  trees<-
  rbind(unkn, allelse)
  rm(unkn, allelse)
}

assign parameters to all live and dead trees (once per sim)

abco<-
subset(trees, spp="ABCO" | spp="ABMA")
pila<-
subset(trees, spp="PILA" | spp="PSME" | spp="PIPO")
cade<-
subset(trees, spp="CADE")
quke<-
subset(trees, spp="QUKE")
conu<-
subset(trees, spp="CONU")

abco.alpha<-
rnorm(nrow(abco), mean=1.32, sd=0.01785714)
abco.beta<-
rnorm(nrow(abco), mean=1.09, sd=0.005102041)
abco.gamma<-
rnorm(nrow(abco), mean=-0.18, sd=0.007653061)
abco.c<-
rnorm(nrow(abco), mean=3.80, sd=0.280612)
abco.d<-
rnorm(nrow(abco), mean=1, sd=0.00255102)
abco.a<-
rnorm(nrow(abco), mean=2.57, sd=0.005102041)
abco.b1<-
rnorm(nrow(abco), mean=0.60, sd=0.005102041)
abco.c1<-
rnorm(nrow(abco), mean=0.9567, sd=1.0)
abco.b2<-
rnorm(nrow(abco), mean=0.65, sd=0.005102041)
abco.c2 <- rm(nrow(abco), mean = 0.04637, sd = (5.102041 * 10^-6))
abco.intercept <- rm(nrow(abco), mean = -2.18, sd = 0.01530612)
abco.complete <- cbind(abco, abco.alpha, abco.beta, abco.gamma, abco.c, abco.d, abco.a, abco.b1, abco.c1, abco.b2, abco.c2, abco.intercept)
colnames(abco.complete) <- c("id", "spp", "status", "dc", "dbh", "x", "y", "year.sampled", "buffer", "radius", "orig.index", "alpha", "beta", "gamma", "c", "d", "a", "b1", "c1", "b2", "c2", "intercept")
rm(abco, abco.alpha, abco.beta, abco.gamma, abco.c, abco.d, abco.a, abco.b1, abco.c1, abco.b2, abco.c2, abco.intercept)

abco.complete <- cbind(abco, abco.alpha, abco.beta, abco.gamma, abco.c, abco.d, abco.a, abco.b1, abco.c1, abco.b2, abco.c2, abco.intercept)
colnames(abco.complete) <- c("id", "spp", "status", "dc", "dbh", "x", "y", "year.sampled", "buffer", "radius", "orig.index", "alpha", "beta", "gamma", "c", "d", "a", "b1", "c1", "b2", "c2", "intercept")
rm(abco, abco.alpha, abco.beta, abco.gamma, abco.c, abco.d, abco.a, abco.b1, abco.c1, abco.b2, abco.c2, abco.intercept)

pila.alpha <- rnorm(nrow(pila), mean = 0.84, sd = 0.02806122)
pila.beta <- rnorm(nrow(pila), mean = 0, sd = 0.1071429)
pila.gamma <- rnorm(nrow(pila), mean = -0.48, sd = 0.0127551)
pila.c <- rnorm(nrow(pila), mean = 7.08, sd = 0.01785714)
pila.d <- rnorm(nrow(pila), mean = 1.03, sd = 0.02551012)
pila.a <- rnorm(nrow(pila), mean = 0.34, sd = 0.0240816)
pila.b1 <- rnorm(nrow(pila), mean = 5.42, sd = 0.1020408)
pila.c1 <- rnorm(nrow(pila), mean = 0.22354, sd = 0.04244898)
pila.b2 <- rnorm(nrow(pila), mean = 7.25, sd = 0.09693878)
pila.c2 <- rnorm(nrow(pila), mean = 0.11917, sd = 0.00655102)
pila.intercept <- rnorm(nrow(pila), mean = 0.28, sd = 0.01020408)
pila.complete <- cbind(pila, pila.alpha, pila.beta, pila.gamma, pila.c, pila.d, pila.a, pila.b1, pila.c1, pila.b2, pila.c2, pila.intercept)
colnames(pila.complete) <- c("id", "spp", "status", "dc", "dbh", "x", "y", "year.sampled", "buffer", "radius", "orig.index", "alpha", "beta", "gamma", "c", "d", "a", "b1", "c1", "b2", "c2", "intercept")
rm(pila, pila.alpha, pila.beta, pila.gamma, pila.c, pila.d, pila.a, pila.b1, pila.c1, pila.b2, pila.c2, pila.intercept)

#add 'dummy' values for quke to keep columns the same
quke.alpha <- 0
quke.beta <- 0
quke.gamma <- 0
quke.c <- 0
quke.d <- 0
quke.a <- 0
quke.b1 <- 0
quke.c1 <- 0
quke.b2 <- 0
quke.c2 <- 0
quke.intercept <- 0
quke.complete<-cbind(quke, quke.alpha, quke.beta, quke.gamma, quke.c, quke.d, quke.a, quke.b1, quke.c1, quke.b2, quke.c2, quke.intercept)
colnames(quke.complete)<-c("id", "spp", "status", "dc", "sd", "dbh", "x", "y", "year.sampled", "buffer", "radius", "orig.index", "alpha", "beta", "gamma", "c", "d", "a", "b1", "c1", "b2", "c2", "intercept")
rm(quke, quke.alpha, quke.beta, quke.gamma, quke.c, quke.d, quke.a, quke.b1, quke.c1, quke.b2, quke.c2, quke.intercept)

#add 'dummy' values for conu to keep columns the same
conu.alpha<-0
conu.beta<-0
conu.gamma<-0
conu.c<-0
conu.d<-0
conu.a<-0
conu.b1<-0
conu.c1<-0
conu.b2<-0
conu.c2<-0

conu.intercept<-0
conu.complete<-cbind(conu, conu.alpha, conu.beta, conu.gamma, conu.c, conu.d, conu.a, conu.b1, conu.c1, conu.b2, conu.c2, conu.intercept)
colnames(conu.complete)<-c("id", "spp", "status", "dc", "sd", "dbh", "x", "y", "year.sampled", "buffer", "radius", "orig.index", "alpha", "beta", "gamma", "c", "d", "a", "b1", "c1", "b2", "c2", "intercept")
rm(conu, conu.alpha, conu.beta, conu.gamma, conu.c, conu.d, conu.a, conu.b1, conu.c1, conu.b2, conu.c2, conu.intercept)

exist.a<-exists("abco.complete")  #the following is a work around incase there are no trees of a certain species; keeps the
code from haulting.
exist.b<-exists("pila.complete")
exist.ca<-exists("cade.complete")
exist.q<-exists("quke.complete")
exist.co<-exists("conu.complete")
exist.list<-list(c(exist.a, exist.b, exist.ca, exist.q, exist.co))

choose.list<-list(c("abco.complete", "pila.complete", "cade.complete", "quke.complete", "conu.complete"))
these<-choose.list[[1]][which(exist.list[[1]]==T)]
together<-list()
for(t in 1:length(these)){
together[[t]]<-get(these[t])
}
trees<-as.data.frame(do.call("rbind",together))
rm(together, abco.complete, pila.complete, cade.complete, quke.complete, conu.complete) #may display warning message
b/c come might not exist. it's ok.

########################################################################Figure out when CADE logs and snags were alive########################################################################
cat("Determine year CADE logs and snags were alive")
cade.logs<-subset(trees, spp=="CADE" & status=="log")
cade.snags<-subset(trees, spp=="CADE" & status=="snag")

if(nrow(cade.logs)>0){
cade.logs$year.live<-0 # add new column
for (i in 1:nrow(cade.logs)){ #the age values taken from log ages in Daniel's ppr.
  if (cade.logs$dc[i]==1){

}
age<-rnorm(1, 3.5, 0.707)
cade.logs$yea
[1] year.live[i]<-start.year-5*(round(age/5, digits=0))
else if (cade.logs$dc[i]==2){
  age<-rnorm(1, 50, 25.2)
cade.logs$year.live[i]<-start.year-5*(round(age/5, digits=0))
else if (cade.logs$dc[i]==3){
  age<-rnorm(1, 142.3, 104.4)
cade.logs$year.live[i]<-start.year-5*(round(age/5, digits=0))
else {
  age<-550
cade.logs$year.live[i]<-start.year-5*(round(age/5, digits=0))} #class 4 and 5 logs are too old
}

if(nrow(cade.snags)>0){
cade.snags$yea
[1] ar<0
for (i in 1:nrow(cade.snags)){ #these age values taken from log ages in Daniel's ppr. I calculated mean and sd
  if (cade.snags$dc[i]==1){
    age<-rnorm(1, 3, 1.41)
cade.snags$year.live[i]<-start.year-5*(round(age/5, digits=0))
  } else if (cade.snags$dc[i]==2){
    age<-rnorm(1, 122.6, 82.9)
cade.snags$year.live[i]<-start.year-5*(round(age/5, digits=0))
  } else if (cade.snags$dc[i]==3){
    age<-rnorm(1, 151.4, 37.3)
cade.snags$year.live[i]<-start.year-5*(round(age/5, digits=0))
  } else {age<-rnorm(1, 160.8, 94.7) #class 4 and 5 lumped together
   cade.snags$year.live[i]<-start.year-5*(round(age/5, digits=0))}
}

########## START  1 Timestep ############################################
while (timestep.executed<=n.timestep){
cat(paste("setting up code for live trees timestep", timestep.executed, "year", year.now), "\n")
live<-subset(trees, status=="live" & spp!="CONU")
live$update<0 #set update to 0 to start
live$neighbors.accurate<-as.character("no") #start with all neighborhood environments inaccurate
live$dbh.calc<-0 # $dbh.calc is an "intermediate" dbh
live$nci<-0 # set nci at start to 0 to avoid NAs
live$nci.begin<-0 # set nci.begin to 0 to avoid NAs. This is the nci at the end of the ts (t-5)

##########Obtain Updated Competitor List for the

live.competitors<-list()
for (i in 1:nrow(live)){
  index<-live$orig.index[i]
  possible.competitors<-compeditors.list[[index]]
  if(nrow(possible.competitors)>0){
    live.competitors[[i]]<-merge(live, possible.competitors[, c("orig.index",
    setdiff(colnames(possible.competitors),colnames(live))), by="orig.index")
cat(paste("live competitor list for tree", i, "created"), "\n")
  } #end if nrow(possible.competitors>0

### Generate NCI Metrics

#### #loop to calculate NCI for each live tree (within buffered plot) at the beginning of the timestep

```r
for (i in 1:nrow(live)) {
  cat(paste("calculating NCI for tree", i, "timestep", timestep.executed, "year", year.now), "n")
  if (live$buffer[i] == "in" & live$spp[i] != "QUKE") { # only for trees within the buffer and that are not quke
    comp.df <- as.data.frame(live.compeditors[[i]])
    nci.calc <- nci(live, i, lambda.yfdp, comp.df)
    if (nci.calc < 0) { nci.calc <- 0 }
    live$nci[i] <- nci.calc
  } else (live$nci[i] <- 0)
}
```

#### # subset out live trees within buffered plot to ensure accurate mean.nci calcs

```r
live.buffered <- subset(live, buffer == "in")
```

#### # calculate mean nci by species and size class

```r
cat(paste("Calculate mean nci by species and size class for live trees timestep", timestep.executed, year.now), "n")
abco.nci <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA"))$nci)
abco1.10 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh < 10)$nci)
if (is.nan(abco1.10) == TRUE) { abco1.10 <- abco.nci }
abco10.20 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 10 & dbh < 20)$nci)
if (is.nan(abco10.20) == TRUE) { abco10.20 <- abco.nci }
abco20.30 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 20 & dbh < 30)$nci)
if (is.nan(abco20.30) == TRUE) { abco20.30 <- abco.nci }
abco30.40 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 30 & dbh < 40)$nci)
if (is.nan(abco30.40) == TRUE) { abco30.40 <- abco.nci }
abco40.50 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 40 & dbh < 50)$nci)
if (is.nan(abco40.50) == TRUE) { abco40.50 <- abco.nci }
abco50.60 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 50 & dbh < 60)$nci)
if (is.nan(abco50.60) == TRUE) { abco50.60 <- abco.nci }
abco60.70 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 60 & dbh < 70)$nci)
if (is.nan(abco60.70) == TRUE) { abco60.70 <- abco.nci }
abco70.80 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 70 & dbh < 80)$nci)
if (is.nan(abco70.80) == TRUE) { abco70.80 <- abco.nci }
abco80.90 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 80 & dbh < 90)$nci)
if (is.nan(abco80.90) == TRUE) { abco80.90 <- abco.nci }
abco90.100 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 90 & dbh < 100)$nci)
if (is.nan(abco90.100) == TRUE) { abco90.100 <- abco.nci }
abco100.110 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 100 & dbh < 110)$nci)
if (is.nan(abco100.110) == TRUE) { abco100.110 <- abco.nci }
abco110.120 <- mean(subset(live.buffered, (spp == "ABCO" | spp == "ABMA") & dbh >= 110 & dbh < 120)$nci)
if (is.nan(abco110.120) == TRUE) { abco110.120 <- abco.nci }
```

if(is.nan(abco140.150)==TRUE){abco140.150<-abco.nci}
abco150.160<mean(subset(live.buffered, (spp="ABCO"|spp="ABMA") & dbh>=150 & dbh<160)$nci)
if(is.nan(abco150.160)==TRUE){abco150.160<-abco.nci}
abco160.170<mean(subset(live.buffered, (spp="ABCO"|spp="ABMA") & dbh>=160 & dbh<170)$nci)
if(is.nan(abco160.170)==TRUE){abco160.170<-abco.nci}
abco170<mean(subset(live.buffered, (spp="ABCO"|spp="ABMA") & dbh>=170)$nci)
if(is.nan(abco170)==TRUE){abco170<-abco.nci}

pila.nci<-mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO")$nci)
pila1.10<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh<10)$nci)
if(is.nan(pila1.10)==TRUE){pila1.10<-pila.nci}
pila10.20<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=10 & dbh<20)$nci)
if(is.nan(pila10.20)==TRUE){pila10.20<-pila.nci}
pila20.30<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=20 & dbh<30)$nci)
if(is.nan(pila20.30)==TRUE){pila20.30<-pila.nci}
pila30.40<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=30 & dbh<40)$nci)
if(is.nan(pila30.40)==TRUE){pila30.40<-pila.nci}
pila40.50<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=40 & dbh<50)$nci)
if(is.nan(pila40.50)==TRUE){pila40.50<-pila.nci}
pila50.60<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=50 & dbh<60)$nci)
if(is.nan(pila50.60)==TRUE){pila50.60<-pila.nci}
pila60.70<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=60 & dbh<70)$nci)
if(is.nan(pila60.70)==TRUE){pila60.70<-pila.nci}
pila70.80<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=70 & dbh<80)$nci)
if(is.nan(pila70.80)==TRUE){pila70.80<-pila.nci}
pila80.90<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=80 & dbh<90)$nci)
if(is.nan(pila80.90)==TRUE){pila80.90<-pila.nci}
pila90.100<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=90 & dbh<100)$nci)
if(is.nan(pila90.100)==TRUE){pila90.100<-pila.nci}
pila100.110<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=100 & dbh<110)$nci)
if(is.nan(pila100.110)==TRUE){pila100.110<-pila.nci}
pila110.120<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=110 & dbh<120)$nci)
if(is.nan(pila110.120)==TRUE){pila110.120<-pila.nci}
pila120.130<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=120 & dbh<130)$nci)
if(is.nan(pila120.130)==TRUE){pila120.130<-pila.nci}
pila130.140<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=130 & dbh<140)$nci)
if(is.nan(pila130.140)==TRUE){pila130.140<-pila.nci}
pila140.150<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=140 & dbh<150)$nci)
if(is.nan(pila140.150)==TRUE){pila140.150<-pila.nci}
pila150.160<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=150 & dbh<160)$nci)
if(is.nan(pila150.160)==TRUE){pila150.160<-pila.nci}
pila160.170<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=160 & dbh<170)$nci)
if(is.nan(pila160.170)==TRUE){pila160.170<-pila.nci}
pila170.180<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=170 & dbh<180)$nci)
if(is.nan(pila170.180)==TRUE){pila170.180<-pila.nci}
pila180.190<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=180 & dbh<190)$nci)
if(is.nan(pila180.190)==TRUE){pila180.190<-pila.nci}
pila190.200<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=190 & dbh<200)$nci)
if(is.nan(pila190.200)==TRUE){pila190.200<-pila.nci}
pila200.210<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=200 & dbh<210)$nci)
if(is.nan(pila200.210)==TRUE){pila200.210<-pila.nci}
pila210.220<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=210 & dbh<220)$nci)
if(is.nan(pila210.220)==TRUE){pila210.220<-pila.nci}
pila220.230<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>=220 & dbh<230)$nci)
if(is.nan(pila220.230)==TRUE){pila220.230<-pila.nci}
pila230<mean(subset(live.buffered, (spp="PILA"|spp="PSME"|spp="PIPO") & dbh>230)$nci)
if(is.nan(pila230)==TRUE){pila230<-pila.nci}
cade.nci <- mean(subset(live.buffered, spp == "CADE")$nci)
cade1.10 <- mean(subset(live.buffered, spp == "CADE" & dbh < 10)$nci)
if(is.nan(cade1.10) == TRUE) { cade1.10 <- cade.nci }
cade10.20 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 10 & dbh < 20)$nci)
if(is.nan(cade10.20) == TRUE) { cade10.20 <- cade.nci }
cade20.30 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 20 & dbh < 30)$nci)
if(is.nan(cade20.30) == TRUE) { cade20.30 <- cade.nci }
cade30.40 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 30 & dbh < 40)$nci)
if(is.nan(cade30.40) == TRUE) { cade30.40 <- cade.nci }
cade40.50 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 40 & dbh < 50)$nci)
if(is.nan(cade40.50) == TRUE) { cade40.50 <- cade.nci }
cade50.60 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 50 & dbh < 60)$nci)
if(is.nan(cade50.60) == TRUE) { cade50.60 <- cade.nci }
cade60.70 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 60 & dbh < 70)$nci)
if(is.nan(cade60.70) == TRUE) { cade60.70 <- cade.nci }
cade70.80 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 70 & dbh < 80)$nci)
if(is.nan(cade70.80) == TRUE) { cade70.80 <- cade.nci }
cade80.90 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 80 & dbh < 90)$nci)
if(is.nan(cade80.90) == TRUE) { cade80.90 <- cade.nci }
cade90.100 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 90 & dbh < 100)$nci)
if(is.nan(cade90.100) == TRUE) { cade90.100 <- cade.nci }
cade100.110 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 100 & dbh < 110)$nci)
if(is.nan(cade100.110) == TRUE) { cade100.110 <- cade.nci }
cade110.120 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 110 & dbh < 120)$nci)
if(is.nan(cade110.120) == TRUE) { cade110.120 <- cade.nci }
cade120.130 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 120 & dbh < 130)$nci)
if(is.nan(cade120.130) == TRUE) { cade120.130 <- cade.nci }
cade130.140 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 130 & dbh < 140)$nci)
if(is.nan(cade130.140) == TRUE) { cade130.140 <- cade.nci }
cade140.150 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 140 & dbh < 150)$nci)
if(is.nan(cade140.150) == TRUE) { cade140.150 <- cade.nci }
cade150.160 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 150 & dbh < 160)$nci)
if(is.nan(cade150.160) == TRUE) { cade150.160 <- cade.nci }
cade160.170 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 160 & dbh < 170)$nci)
if(is.nan(cade160.170) == TRUE) { cade160.170 <- cade.nci }
cade170.180 <- mean(subset(live.buffered, spp == "CADE" & dbh >= 170)$nci)
if(is.nan(cade170.180) == TRUE) { cade170.180 <- cade.nci }
rm(live.buffered)

##########################################################################
## grow all live trees backwards one timestep
##########################################################################
cat(paste("growing live trees backwards", timestep.executed, "year", year.now), "n")
repeat {
  for (q in 1:nrow(live)) {
    if(live$neighbors.accurate[q] == "no") {
      if(live$spp[q] == "QUKE") {
        cat(paste("tree", q, "is a QUKE"), "n")
        growth <- rnorm(1, mean = 1.04, sd = 0.61)
        if(growth < 0) { growth <- 0 }  # prevents trees getting larger over time.
    }
live$dbh.calc[q]<-live$dbh[q]-growth # subtract 2*radial growth for 5 years. !in the event that ts changes, this needs
to change
live$update[q]<-1 #match up with the rest of repeat
live$neighbors.accurate[q]<-as.character("yes") #close the quke statement

else { #if the tree is not a quke, continue
  if(live$buffer[q]=="in"){
    cat(paste("tree", q, "is in"))
    comp.df<-as.data.frame(live.competitors[q])

    competitors.begin<-grow.neighbors(live, q, 5, comp.df) #neighbors and their dbh's at beginning of ts
    cat(paste("dbh begin for competitors for tree", q, "figured out"), "n")

    if(nrow(competitors.begin)>0){ #if a tree actually has competitors, calculate nci.begin
      cat(paste("tree", q, "has at least one competitor"), "n")
      if(all(competitors.begin$update==1)){
        cat(paste("tree", q, "neighbors all good"), "n")
        live$neighbors.accurate[q]<-as.character("yes")
      }
      if(nrow(competitors.begin)<0){ #if tree does not have competitors at beginning of ts (ie, all competitors
        cat(paste("tree",q, "has no competitors at beginning of ts"),"n")}
    }else{ #if tree is outside of the buffered plot, calculate approx dbh based on mean.nci's
      cat(paste("tree", q, "is out"))
      dbh<-live$dbh[q] #shorthand to make coding easier
      spp<-live$spp[q]
      if (spp=="ABCO" | spp=="ABMA"){
        if (dbh<10){
          mean.nci<-abco1.10
        else if (dbh>=10 & dbh<20){
          mean.nci<-abco10.20
        else if (dbh>=20 & dbh<30){
          mean.nci<-abco20.30
        else if (dbh>=30 & dbh<40){
          mean.nci<-abco30.40
        else if (dbh>=40 & dbh<50){
          mean.nci<-abco40.50
        else if (dbh>=50 & dbh<60){
          mean.nci<-abco50.60
        }
      }
      }else{ #if the tree is outside of the buffered plot, calculate approx dbh based on mean.nci's
        cat(paste("tree", q, "is out"))
        dbh<-live$dbh[q] #shorthand to make coding easier
        spp<-live$spp[q]
        if (spp=="ABCO" | spp=="ABMA"){
          if (dbh<10){
            mean.nci<-abco1.10
          else if (dbh>=10 & dbh<20){
            mean.nci<-abco10.20
          else if (dbh>=20 & dbh<30){
            mean.nci<-abco20.30
          else if (dbh>=30 & dbh<40){
            mean.nci<-abco30.40
          else if (dbh>=40 & dbh<50){
            mean.nci<-abco40.50
          else if (dbh>=50 & dbh<60){
            mean.nci<-abco50.60
          }
        }
      }
    }else{ #if the tree is not a quke, continue
      if(live$buffer[q]=="in"){
        cat(paste("tree", q, "is in"))
        comp.df<-as.data.frame(live.competitors[q])

        competitors.begin<-grow.neighbors(live, q, 5, comp.df) #neighbors and their dbh's at beginning of ts
        cat(paste("dbh begin for competitors for tree", q, "figured out"), "n")

        if(nrow(competitors.begin)>0){ #if a tree actually has competitors, calculate nci.begin
          cat(paste("tree", q, "has at least one competitor"), "n")
          if(all(competitors.begin$update==1)){
            cat(paste("tree", q, "neighbors all good"), "n")
            live$neighbors.accurate[q]<-as.character("yes")
          }
          if(nrow(competitors.begin)<0){ #if tree does not have competitors at beginning of ts (ie, all competitors
            cat(paste("tree",q, "has no competitors at beginning of ts"),"n")}
        }else{ #if tree is outside of the buffered plot, calculate approx dbh based on mean.nci's
          cat(paste("tree", q, "is out"))
          dbh<-live$dbh[q] #shorthand to make coding easier
          spp<-live$spp[q]
          if (spp=="ABCO" | spp=="ABMA"){
            if (dbh<10){
              mean.nci<-abco1.10
            else if (dbh>=10 & dbh<20){
              mean.nci<-abco10.20
            else if (dbh>=20 & dbh<30){
              mean.nci<-abco20.30
            else if (dbh>=30 & dbh<40){
              mean.nci<-abco30.40
            else if (dbh>=40 & dbh<50){
              mean.nci<-abco40.50
            else if (dbh>=50 & dbh<60){
              mean.nci<-abco50.60
            }
          }
        }
      }
    }else{ #if the tree is outside of the buffered plot, calculate approx dbh based on mean.nci's
      cat(paste("tree", q, "is out"))
      dbh<-live$dbh[q] #shorthand to make coding easier
      spp<-live$spp[q]
      if (spp=="ABCO" | spp=="ABMA"){
        if (dbh<10){
          mean.nci<-abco1.10
        else if (dbh>=10 & dbh<20){
          mean.nci<-abco10.20
        else if (dbh>=20 & dbh<30){
          mean.nci<-abco20.30
        else if (dbh>=30 & dbh<40){
          mean.nci<-abco30.40
        else if (dbh>=40 & dbh<50){
          mean.nci<-abco40.50
        else if (dbh>=50 & dbh<60){
          mean.nci<-abco50.60
        }
      }
    }else{ #if the tree is outside of the buffered plot, calculate approx dbh based on mean.nci's
      cat(paste("tree", q, "is out"))
      dbh<-live$dbh[q] #shorthand to make coding easier
      spp<-live$spp[q]
      if (spp=="ABCO" | spp=="ABMA"){
        if (dbh<10){
          mean.nci<-abco1.10
        else if (dbh>=10 & dbh<20){
          mean.nci<-abco10.20
        else if (dbh>=20 & dbh<30){
          mean.nci<-abco20.30
        else if (dbh>=30 & dbh<40){
          mean.nci<-abco30.40
        else if (dbh>=40 & dbh<50){
          mean.nci<-abco40.50
        else if (dbh>=50 & dbh<60){
          mean.nci<-abco50.60
        }
      }
else if (dbh>=50 & dbh<60){
    mean_nci<abco50.60}
else if (dbh>=60 & dbh<70){
    mean_nci<abco60.70}
else if (dbh>=70 & dbh<80){
    mean_nci<abco70.80}
else if (dbh>=80 & dbh<90){
    mean_nci<abco80.90}
else if (dbh>=90 & dbh<100){
    mean_nci<abco90.100}
else if (dbh>=100 & dbh<110){
    mean_nci<abco100.110}
else if (dbh>=110 & dbh<120){
    mean_nci<abco110.120}
else if (dbh>=120 & dbh<130){
    mean_nci<abco120.130}
else if (dbh>=130 & dbh<140){
    mean_nci<abco130.140}
else if (dbh>=140 & dbh<150){
    mean_nci<abco140.150}
else if (dbh>=150 & dbh<160){
    mean_nci<abco150.160}
else if (dbh>=160 & dbh<170){
    mean_nci<abco160.170}
else {
    mean_nci<abco170}
}
else if (spp=="PILA" | spp=="PSME" | spp=="PIPO"){
    if (dbh<10){
        mean_nci<pila1.10}
    else if (dbh>=10 & dbh<20){
        mean_nci<pila10.20}
    else if (dbh>=20 & dbh<30){
        mean_nci<pila20.30}
    else if (dbh>=30 & dbh<40){
        mean_nci<pila30.40}
    else if (dbh>=40 & dbh<50){
        mean_nci<pila40.50}
    else if (dbh>=50 & dbh<60){
        mean_nci<pila50.60}
    else if (dbh>=60 & dbh<70){
        mean_nci<pila60.70}
    else if (dbh>=70 & dbh<80){
        mean_nci<pila70.80}
    else if (dbh>=80 & dbh<90){
        mean_nci<pila80.90}
    else if (dbh>=90 & dbh<100){
        mean_nci<pila90.100}
    else if (dbh>=100 & dbh<110){
        mean_nci<pila100.110}
    else if (dbh>=110 & dbh<120){
        mean_nci<pila110.120}
    else if (dbh>=120 & dbh<130){
        mean_nci<pila120.130}
    else if (dbh>=130 & dbh<140){
        mean_nci<pila130.140}
    else if (dbh>=140 & dbh<150){
        mean_nci<pila140.150}
    }
else if (dbh>=150 & dbh<160){
    mean.nci<-pila150.160}
else if (dbh>=160 & dbh<170){
    mean.nci<-pila160.170}
else if (dbh>=170 & dbh<180){
    mean.nci<-pila170.180}
else if (dbh>=180 & dbh<190){
    mean.nci<-pila180.190}
else if (dbh>=190 & dbh<200){
    mean.nci<-pila190.200}
else if (dbh>=190 & dbh<200){
    mean.nci<-pila190.200}
else if (dbh>=200 & dbh<210){
    mean.nci<-pila200.210}
else if (dbh>=210 & dbh<220){
    mean.nci<-pila210.220}
else if (dbh>=220 & dbh<230){
    mean.nci<-pila220.230}
else if (dbh>=230 & dbh<240){
    mean.nci<-pila230}
}
else if (spp=="CADE"){
    if (dbh<10){
        mean.nci<-cade1.10}
    else if (dbh>=10 & dbh<20){
        mean.nci<-cade10.20}
    else if (dbh>=20 & dbh<30){
        mean.nci<-cade20.30}
    else if (dbh>=30 & dbh<40){
        mean.nci<-cade30.40}
    else if (dbh>=40 & dbh<50){
        mean.nci<-cade40.50}
    else if (dbh>=50 & dbh<60){
        mean.nci<-cade50.60}
    else if (dbh>=60 & dbh<70){
        mean.nci<-cade60.70}
    else if (dbh>=70 & dbh<80){
        mean.nci<-cade70.80}
    else if (dbh>=80 & dbh<90){
        mean.nci<-cade80.90}
    else if (dbh>=90 & dbh<100){
        mean.nci<-cade90.100}
    else if (dbh>=100 & dbh<110){
        mean.nci<-cade100.110}
    else if (dbh>=110 & dbh<120){
        mean.nci<-cade110.120}
    else if (dbh>=120 & dbh<130){
        mean.nci<-cade120.130}
    else if (dbh>=130 & dbh<140){
        mean.nci<-cade130.140}
    else if (dbh>=140 & dbh<150){
        mean.nci<-cade140.150}
    else if (dbh>=150 & dbh<160){
        mean.nci<-cade150.160}
    else if (dbh>=160 & dbh<170){
        mean.nci<-cade160.170}
    else if (dbh>=170 & dbh<180){
        mean.nci<-cade170}
if(is.numeric(mean.nci)==F){mean.nci<-get(paste(tolower(live.spp),".nci", sep=""))}
live$nci.begin[q]<-mean.nci # mean nci for further calculations. this is the nci at the end of the ts
comp<-f.competition(live, q)
prg.calc<-prg(live, q)
rg<-prg.calc*comp # radial growth rate in cm/year

live$sdbh.calc[q]<-live$sdbh[q]-(timestep*(2*rg))
live$supdate[q]<-1
live$sneighbors.accurate[q]<-as.character("yes"))}}

else {cat(paste("tree",q, "accurate"),"n")
} # close the main loop

live.compeditors<-list()  # refresh the compeditors list to reflect updated trees
for (y in 1:nrow(live)){
  index<-live$orig.index[y]
possible.compeditors<-compeditors.list[[index]]
  if(nrow(possible.compeditors)>0){
    live.compeditors[y]<-merge(live, possible.compeditors[, c("orig.index",
      setdiff(colnames(possible.compeditors),colnames(live)))), by="orig.index")
    cat(paste("live compeditor list for tree", y, "created"), 
      "n")
  } # end if nrow(possible.compeditors>0
  else {live.compeditors[y]<-data.frame()}
} # end loop
rm(index)

if (all(live$sneighbors.accurate=="yes")) break
} # close the repeat

live$sdbh<-live$sdbh.calc # update the dbh from the end of the ts (ie. 2010) to the dbh at the beginning (ie. 2005).

####grow back the CONU. Doesn't matter if conu are within or out of the buffered plot
conu<-subset(trees, spp=="CONU" & status=="live")
if(nrow(conu)>0){ # prevents na's when conu "runs out"
  for (i in 1:nrow(conu)){
    conu$dbh[i]<-conu$dbh[i]-(1.016) # update conu dbh by subtracting diameter growth for 5 years. In the event that the ts
    changes, this needs to change
  }
}

##
live<-live[,1:23] # remove added columns
live<-rbind(live, conu) # add the grownback CONU
live<-subset(live, dbh>1) # exclude all trees which have less than 1 cm dbh

############### end live tree growth; start dead tree

undecay#################################################

logs<-subset(trees, status=="log" & (spp=="ABCO" | spp=="ABMA" | spp=="PILA" | spp=="PIPO" | spp=="QUKE"|
  spp=="PSME"))
snags<-subset(trees, status=="snag" & (spp=="ABCO" | spp=="ABMA" | spp=="PILA" | spp=="PIPO" |
  spp=="QUKE"|spp=="PSME"))

############ Undecaying logs####################################################
cat(paste("undecaying logs for timestep", timestep.executed, "year", year.now,"n"))
if(nrow(logs)>0){ #prevents na's from occurring if logs 'run out'
  for (i in 1:nrow(logs)){
    dc<logs$dc[i]
    if(logs$spp[i]=='"PILA"' | logs$spp[i]=='"PIPO"'){ #density values from Harmon 1987, i calculated SD from n and se provided
      cat(paste("log", i, "is PILA"), "n")
      if(dc==1){do<-rnorm(1, 0.369, 0.074)} #assign do
      else if(dc==2){do<-rnorm(1, 0.269, 0)}
      else if(dc==3){do<-rnorm(1, 0.221, 0.056)} #DC 4 and 5 lumped together; no dc5 provided
      k<0.024    # from Dunn 2011; SE provided in literature.
      dt<-do*exp(-k*5)
      if (dt>0.369){
        dc.temp<-0} #update dc # the log becomes alive after this treshold, code to turn "live" at end of loop
      else if (dt<=0.369 & dt>0.269){
        dc.temp<-1 #update decay class, but use placeholder
        snag.chance<-sample(c(0.42, 0.33),1)# the chance that this log was a snag at the beginning of the ts
        #snag chance sampled from the two possible chances presented in raphael and morrison 1993 (1883-1987 and 1988-1993)
        else if(logs$spp[i]=='"ABCO"' | logs$spp[i]=='"ABMA"'){ #density values from Harmon 1987, I calculated sd from se
          if(dc==1){do<-rnorm(1, 0.369, 0.068)}
          else if(dc==2){do<-rnorm(1, 0.305, 0.071)}
          else if(dc==3){do<-rnorm(1, 0.212, 0.049)}
          k<-0.049
          dt<-do*exp(-k*5)
          if (dt>0.369){
            dc.temp<-0} #if dt is now greater the density of a dc 1 abco... # the log becomes alive after this treshold
          else if (dt<=0.369 & dt>0.305){
            dc.temp<-1 #update decay class
            snag.chance<-sample(c(0.33, 0.52),1)}
          else (dt<=0.305 & dt>0.212){
            dc.temp<-2
            snag.chance<-sample(c(0.69, 0.36),1)}
          else if (dt<=0.212 & dt>0.178){
            dc.temp<-3
            snag.chance<-sample(c(0.57, 0.18),1)}
          else{
            dc.temp<-sample(c(4,5),1) #no dc5 provided, so have R assign.
            if(dc.temp==4){snag.chance<-sample(c(0.36, 0.59),1)} #snag chance if dc4
            else {snag.chance<-sample(c(0.27, 0.94),1)}} #snag chance if dc 5
          } #snag sampled from the two possible chances presented in raphael and morrison 1993 (1883-1987 and 1988-1993)
        } #snag chance if dc 5
      } #snag chance if dc 5
    } #snag chance if dc 5
  } #snag chance if dc 5
} #snag chance if dc 5
if(dc.temp>0) {logs$status[i]<-sample(c("snag", "log"), 1, prob=c(snag.chance, 1-snag.chance))}

else { #QUKE
  cat(paste(" log", i, " is QUKE"), "n")
  if(dc==1){do <- 0.611}  # density values from Harmon 2008.
  else if(dc==2){do <- 0.45}
  else if(dc==3){do <- 0.382}
  else {do <- 0.241} # DC 4 and 5 lumped together because of high uncertainty in dc5 density
  k <- 0.0295
  dt <- do*exp(-k*-5)
  if (dt>0.611) {dc.temp <- 0} # the log becomes alive after this threshold
  else if(dt<=0.611 & dt>0.45){
    dc.temp <- 1
  }
  else if(dt<=0.45 & dt>0.382){
    dc.temp <- 2
  }
  else if(dt<=0.382 & dt>0.241){
    dc.temp <- 3
  }
  else{
    dc.temp <- sample(c(4,5),1)} # dc 4 and 5 clumped together
  logs$status[i]<-sample(c("snag", "log"),1)} # stochastic transition from log to snag b/c no data available

if (dc.temp<=logs$dc[i]){logs$dc[i]<-dc.temp}
if (logs$dc[i]==0){logs$status[i]<-as.character("live")} # make trees of dc 0 alive

#end the log loop

#--------------------------undecaying snags---------------------------------

cat(paste("undecaying snags", timestep.executed, "year", year.now),"n")
if(nrow(snags)>0){
  for(i in 1:nrow(snags)){
    if(snags$spp[i]=="PILA"| snags$spp[i]=="PIPO"| snags$spp[i]=="PSME"){ # PSME lumped in with PILA for snag
      if (snags$dc[i]==1){ # snags that are DC1 become alive
        snags$dc[i]<-0
        snags$status[i]<-as.character("live")
      }
      else if(snags$dc[i]==2){
        dc.chances<-list(c(0.60, 0.40), c(0,1))
        chance.use<-unlist(sample(dc.chances,1))
        snags$dc[i]<-sample(c(1,2, 1, prob=chance.use)} # update to new DC
      }
      else if(snags$dc[i]==3){
        dc.chances<-list(c(0.28, 0.33, 0.29), c(0, 0.26, 0.74))
        chance.use<-unlist(sample(dc.chances,1))
        snags$dc[i]<-sample(c(1,2,3, 1, prob=chance.use)}
      }
      else if(snags$dc[i]==4){
        dc.chances<-list(c(0.27, 0.23, 0.24, 0.26), c(0.40, 0.05, 0.24, 0.31))
        chance.use<-unlist(sample(dc.chances,1))
        snags$dc[i]<-sample(c(1,2,3,4, 1, prob=chance.use)}
      }
      else{
        dc.chances<-list(c(0.03, 0.02, 0.07, 0.21, 0.67), c(0, 0, 0.14, 0.29, 0.57))
        chance.use<-unlist(sample(dc.chances,1))
        snags$dc[i]<-sample(c(1,2,3,4,5, 1, prob=chance.use})
      }}# end the pila if

else if(snags$spp[i]=="ABCO"| snags$spp[i]=="ABMA"){ #snags that are DC1 become alive
  snags$dc[i]<-0
  snags$status[i]<-as.character("live")
}
else if(snags$dc[i]==2){

}}#end the log loop
```r
snags$dc[i]<-1 #only one option for ABCO dc2
else if(snags$dc[i]==3){
dc.chances<-list(c(0.23, 0.12, 0.65), c(0.23, 0.31, 0.46))
chance.use<-unlist(sample(dc.chances,1))
snags$dc[i]<-sample(c(1,2,3), 1, prob=chance.use)
}
else if(snags$dc[i]==4){
dc.chances<-list(c(0.18, 0.11, 0.16, 0.55), c(0.14, 0.25, 0.31, 0.30))
chance.use<-unlist(sample(dc.chances,1))
snags$dc[i]<-sample(c(1,2,3,4), 1, prob=chance.use)
}
else{
dc.chances<-list(c(0.22, 0, 0.28, 0.17, 0.33), c(0, 0, 0.25, 0.375, 0.375))
chance.use<-unlist(sample(dc.chances,1))
snags$dc[i]<-sample(c(1,2,3,4,5), 1, prob=chance.use)}#end the abco if
else { #QUKE
if (snags$dc[i]==1){
  snags$dc[i]<-0
  snags$status[i]<-as.character("live")
}
else if(snags$dc[i]==2){
  chance.use<-c(0.5, 0.5)
  snags$dc[i]<-sample(c(1,2), 1, prob=chance.use)
}
else if(snags$dc[i]==3){
  chance.use<-c(0.33, 0.33, 0.33)
  snags$dc[i]<-sample(c(1,2,3), 1, prob=chance.use)
}
else if(snags$dc[i]==4){
  chance.use<-c(0.25, 0.25, 0.25, 0.25)
  snags$dc[i]<-sample(c(1,2,3,4), 1, prob=chance.use)
}
else{
  chance.use<-c(0.2, 0.2, 0.2, 0.2)
  snags$dc[i]<-sample(c(1,2,3,4,5), 1, prob=chance.use)}#end the QUKE if
}
}} #end the snag loop

########################################################################
clean up before next timestep

year.now<-start.year-(timestep*timestep.executed) #the year at the beginning of the timestep

trees<-rbind(live, snags, logs, cades)  #create final tree list for next timestep
survivors<-subset(trees, status=="live")[1:10] #selects only the living trees
```
survivors<-merge(trees.for.sim, survivors, by="id")[,c("id", "spp.x", "status.x","dc.x", "dbh.x",
"x.x","y.x","dbh.y","buffer.y","spp.y")]
colnames(survivors)<-c("id", "spp","status.2010","dc.2010","dbh.2010","x","y",paste("dbh.",year.now, sep=""),"buffer",
"spp.update")
write.table(survivors, file=paste("C:\Users\molly.barth\Documents\newsimulation\survivors_",".csv"),sep="", row.names=F)

times tep.executed+1 #up the number of ts executed
)
#close the reconstruction loop
n.sim<-n.sim+1 #increase the number of simulations completed
rm(survivors)
cat(paste("simulation",n.sim,"complete"),"n")
} #close the simulation loop

#****************************************END RECONSTRUCTION MODEL*******************************************
C.1. Introduction

Recently developed range-wide restoration strategies for Sierra Nevada mixed-conifer forests highlight the need to incorporate small-scale forest heterogeneity into marking prescriptions to increase the likelihood of restoring ecosystem functionality (North et al. 2009, North 2012). We have recognized the importance of maintaining or creating heterogeneity of within-stand tree spatial patterns that corresponded with an active fire regime (Stephens et al. 2008, Larson and Churchill 2012, Boyden et al. 2012), as this is more likely to achieve restoration goals than projects that focus on exclusively on size structure and tree spacing (North and Sherlock 2012, Stephens et al. 2013). While incorporating heterogeneous spatial structure into restoration prescriptions is a relatively new strategy (Churchill et al. 2013), it has garnered considerable attention from forest scientists and managers alike, especially in the Sierra Nevada mixed-conifer forests (North et al. 2009, North 2012).

C.1.1 Importance of forest heterogeneity

Within-stand tree spatial patterns describe the frequency and distribution of small-scale pattern components, such as tree clumps, forest openings, and widely spaced individual trees (Larson and Churchill 2012). Within-stand patterns have profound effects on many forest ecosystem characteristics and processes in forest throughout the world – for example rates of snow reception and retention (Woods et al. 2006, Varhola et al. 2010), the understory light environment (Van Pelt and Franklin 2000), microclimates (Chen et al. 1999), and soil properties (Beatty 1984) and can all be attributed, at least in part, to the spatial patterns of the tree community. Heterogeneity in the distribution of tree clumps, openings, and individual trees can increase forest resilience to disturbances such as drought (Safford et al. 2012), high-severity fires (Scholl and Taylor 2010, Lydersen and North 2012), and insects outbreaks (Fettig et al. 2007), which changing climate patterns may intensify (Miller and Urban 1999). For example, high spatial variability of surface fuels and tree crown connectivity can result in diverse fire behavior and effects, thereby decreasing the likelihood of a stand-replacing event (Beaty and Taylor 2007, Stephens et al. 2008, Williams and Baker 2012).

C.1.2 Restoration of within-stand spatial patterns

Establishing spatial heterogeneity presents a new challenge to managers, because traditional silvicultural methodologies must be reworked to conceptualize and treat a stand as a mosaic of spatial components – scientists must therefore provide managers with operationally relevant metrics to facilitate this transition. A relatively new methodology, known as the ICO (individuals, clumps, and openings) approach is a framework to develop silvicultural prescriptions from historical reference information (Larson and Churchill 2008, Churchill et al.
Estimates of the frequency and size distribution of individual trees, tree clumps, and widely spaced individual trees that occurred during an active fire regime can be used to develop tree marking guidelines for a restoration project. This methodology has been proven to be operationally feasible and effective at reintroducing historical spatial heterogeneity into fire-suppressed stands (Churchill et al. 2013).

C1.3 Quantifying within-stand spatial patterns

Recent research in the Sierra Nevada to inform management and restoration has focused on quantifying pre-suppression forest size structure and composition (North et al. 2007, Scholl and Taylor 2010, Van de Water and North 2011, Collins et al. 2011, Knapp et al. 2013). While there are a few studies that have investigated historical stand-level variation in structure and composition in the Sierra Nevada mixed-conifer forests (Beaty and Taylor 2007a, Scholl and Taylor 2010), even fewer have quantified historical within-stand spatial patterns (Knapp et al. 2012, Lydersen et al. 2013). Of studies that did investigate historical spatial patterns, the majority quantified “global” spatial patterns (the dominant pattern across the study area) with statistics such as Ripley’s K or Moran’s I (Beaty and Taylor 2007a, North et al. 2007, Scholl and Taylor 2010). While global patterns are useful for interring change in landscape-level patterns over time, they do not evaluate small scale changes in forest dynamics that are closely tied to specific ecological functions, such as snow retention. Furthermore, global patterns cannot be easily translated into marking guidelines for restoration prescriptions (Larson and Churchill 2012). Quantification of contemporary and historical within-stand spatial patterns allows us to not only develop marking guidelines, but also to better assess changes to fine-scale forest dynamics to develop hypotheses as to how intertree relationships may be influencing forest change.

C1.4 Objectives

We need to increase the availability of spatial pattern reference information for the region. We utilized a large, highly spatially resolute dataset from a forest monitoring plot in Yosemite National Park (Yosemite) to investigate contemporary and historical forest spatial structure in a Sierra Nevada mixed-conifer forest. Our specific objective was to characterize the contemporary and historical within-stand spatial patterns across our study plot by quantifying the:

1. Frequency, size and species composition of tree clumps;
2. The diameter distribution and species composition of individual trees;
3. The distribution of area in forest openings.

C2. Methods

C2.1 Quantifying tree clumps and individual trees We characterized tree clumps and individual trees in the contemporary and historical datasets using a clump detection algorithm developed by Plotkin et al. (2002). The clump detection algorithm identifies tree clumps at a user-specified inter-tree distance \( t \), measured from tree center to tree center. Trees are members of the same clump if they are within \( t \) of at least one other tree in the clump. Trees with no neighbors within distance \( t \) are identified as individuals. Following Plotkin et al. (2002)
we did not use any edge correction, as this method has been shown to be valid when goals are to simply describe an observed pattern (Yamada and Rogerson 2003).

We ran the clump detection algorithm using a range of values for \( t \), from 0.5 m to 35 m at 0.5 m intervals, allowing us to investigate how different inter-tree distances affected our perception of clump size distribution and to identify the percolation threshold, at which most trees were a part of one large clump (Plotkin et al. 2002). This threshold can be identified by comparing the normalized mean clump size, which computes the probability that two random trees will be in the same clump, to \( t \), across a range of values for \( t \) (Plotkin et al. 2002). We ran the algorithm for each value of \( t \) on the contemporary dataset and each of the 1930 and 1900 simulated reconstructed datasets. We restricted analysis to include only trees \( \geq 10 \) cm dbh due to the computational constraints of calculating the difference between each tree and every other tree in the forest.

We chose to specifically investigate the clump size distributions at both a 3 and 6 m inter-tree distance. A tree clump is typically defined as including trees with interlocking crowns (Larson and Churchill 2012). Generally, mature dry-forest coniferous species have a crown radius of about 3 m, thereby forming a clump at a 6 m intertree distance (Sánchez Meador et al. 2011, Larson et al. 2012). In the absence of site-specific allometric equations relating dbh to tree crown radius, we assumed that a 6 m intertree distance would be appropriate. In addition, investigation of clumps that occur at a 6 m inter-tree distance facilitated comparison with other published studies from coniferous forests across the West (Abella and Denton 2009, Sánchez Meador et al. 2011, Larson et al. 2012, Churchill et al. 2013). Lydersen et al. (2013) developed regression equations for predicting crown radius from dbh in a mixed-conifer stand in STEF, south of the YFDP and also used the Plotkin et al. (2002) method to delineate tree clumps. They found that using a fixed intertree distance of 3 m resulted in a very similar clump distribution when using individual tree crown radii as the intertree distance. Therefore, we also analyzed tree clumps on the YFDP at an intertree distance of 3 m, not only to facilitate comparison with the Lydersen et al. (2013) study, but also because we feel 3 m is a better more accurate representation of interlocking tree crowns specifically in Sierra Nevada mixed-conifer stands. Tree clumps were categorized as small (2-4 trees), medium (4-9 trees), and large (10 or more trees) (Larson et al. 2012, Churchill et al. 2013). We calculated the number individual trees and number of trees in clumps of various sizes as well as the species and size composition of these different spatial components.

**C2.2 Detecting forest openings** To quantify forest openings in the contemporary and reference stem maps we used the empty space function \( F(r) \), which calculates point to nearest tree distances calculated from a 1 m x 1 m grid superimposed on the plot (Diggle 2003). Using \( F(r) \), we calculated the percentage of the plot that included openings of sizes <3 m, 3-6 m, 6-9 m, and 9-12 m, 12-15 m, and \( \geq 15 \) (Larson et al. 2012). We calculated the envelope of potential open space distributions for 1900 and 1930.

**C3. Results**

**C3.1 Contemporary spatial patterns**

At a 6 m intertree distance, the majority (>90%) of the trees in on the contemporary plot were assigned to one large clump, illustrating that the percolation threshold had been reached...
A 3 m intertree distance better captured the small-scale heterogeneity of tree patterns. Small clumps of 2-4 trees, primarily composed of white fir and sugar pine, were the dominant tree grouping on the plot (Table C.2). White fir dominates the composition of all spatial components in both basal area and number of stems. The majority of forest openings are small (3-6 m in size) and there are no large openings <12 m present.

C3.2 Historical spatial patterns

The reconstruction model predicted a substantial decrease in stem density over time, from 539 tph (2010) to 58 tph (1930) to only 27 tph (1900) (Chapter 3). As such, the predicted historical clump size distributions were markedly different than that of the contemporary YFDP. The percolation threshold shifted over time as a result of decreasing densities to about 16.5 in 1930 and 25 m in 1900 (Figure C.1).

Spatial patterns were predicted to be quite similar in 1930 and 1900, and both years were drastically different than 2010, as illustrated by the cumulative clump size distributions (Figure C.2). For 1930, the model predicts that at a 3 m intertree distance, the majority (80.5%) of trees were individuals and there were no medium or large clumps; similarly in 1900, 81.8% of trees were individuals and there no medium or large clumps. Increasing the intertree distance to 6 m resulted in a decrease in the number of trees designated as individuals (47.5% of trees in 1930, 65.3% in 1900). The 6 m intertree distance introduced between 9–20 medium clumps and 0–3 large clumps (depending on simulation) for 1930, but for 1900 did not introduce any large clumps and only one medium clump. The reconstructed YFDP, both in 1930 and 1900, was much more open than in the present, with a substantial increase in large openings ≥15 m (from 0 to 21.4% of the plot by 1900) and decrease in small openings <3 m (from 29.9% to 2.03% by 1900).
C4. Tables and Figures

Table C.1. Clump size distribution in the contemporary YFDP forest as expressed at a range of intertree distances using the Plotkin et al. (2002) clump detection algorithm. We chose to specifically investigate tree clumps at 3 and 6 m.

<table>
<thead>
<tr>
<th>Intertree distance (m)</th>
<th>Individuals (1)</th>
<th>Small Clumps (2-4)</th>
<th>Medium Clumps (5-9)</th>
<th>Large clumps (≥10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>95</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>79</td>
<td>21</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1.5</td>
<td>60</td>
<td>36</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>43</td>
<td>44</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>2.5</td>
<td>29</td>
<td>43</td>
<td>19</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>19</td>
<td>34</td>
<td>22</td>
<td>24</td>
</tr>
<tr>
<td>3.5</td>
<td>12</td>
<td>25</td>
<td>20</td>
<td>43</td>
</tr>
<tr>
<td>4</td>
<td>7</td>
<td>16</td>
<td>15</td>
<td>61</td>
</tr>
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<td>4.5</td>
<td>4</td>
<td>10</td>
<td>10</td>
<td>76</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>86</td>
</tr>
<tr>
<td>5.5</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>92</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>96</td>
</tr>
<tr>
<td>6.5</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>97</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>99</td>
</tr>
<tr>
<td>7.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>99</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>8.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>9.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
</tbody>
</table>
Table C.2. Tree clump characteristics of the YFDP in 2010 and 1900 reconstructed. Standard deviation and range of reconstructed estimations are calculated across 100 simulations of the forest reconstruction model.

<table>
<thead>
<tr>
<th>Intertree distance:</th>
<th>2010</th>
<th>1900 (SD) [Range]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3 m</td>
<td>6 m</td>
</tr>
<tr>
<td><strong>Single trees</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Singles /ha</td>
<td>100</td>
<td>5</td>
</tr>
<tr>
<td>Proportion of trees (% Stems)</td>
<td>19.4</td>
<td>1.0</td>
</tr>
<tr>
<td>Mean BA per ha (m²/ha)</td>
<td>19.11</td>
<td>1.68</td>
</tr>
<tr>
<td>Mean BA in clump (m²/clump)</td>
<td>0.19</td>
<td>0.33</td>
</tr>
<tr>
<td><strong>Small clumps (2-4 trees)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clumps/ha</td>
<td>67</td>
<td>4</td>
</tr>
<tr>
<td>Proportion of trees (% Stems)</td>
<td>34.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Basal Area per ha (m²/ha)</td>
<td>24.1</td>
<td>3.24</td>
</tr>
<tr>
<td>Mean BA in clump (m²/clump)</td>
<td>0.36</td>
<td>0.80</td>
</tr>
<tr>
<td>Species composition (% BA)</td>
<td>ABCO: 68.5 CADE: 7.4 PILA: 18.2 QUKE: 4.5</td>
<td>ABCO: 65.5 CADE: 12.1 PILA: 24.8 QUKE: 2.2</td>
</tr>
<tr>
<td><strong>Medium clumps (5-9)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clumps /ha</td>
<td>18</td>
<td>2</td>
</tr>
<tr>
<td>Proportion of trees (% Stems)</td>
<td>22.1</td>
<td>2.0</td>
</tr>
<tr>
<td>Basal Area per hectare (m²/ha)</td>
<td>10.6</td>
<td>2.37</td>
</tr>
<tr>
<td>Basal Area in clump ( m²/clump)</td>
<td>0.60</td>
<td>1.56</td>
</tr>
<tr>
<td>Species composition (% BA)</td>
<td>ABCO: 72.9 CADE: 3.9 PILA: 18.0 QUKE: 5.8</td>
<td>ABCO: 64.1 CADE: 12.1 PILA: 17.5 QUKE: 5.6</td>
</tr>
<tr>
<td><strong>Large clumps (≥10 trees)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clumps/ha</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Proportion of trees (% Stems)</td>
<td>24.2</td>
<td>95.0</td>
</tr>
<tr>
<td>Basal Area per ha (m²/ha)</td>
<td>8.4</td>
<td>55.02</td>
</tr>
<tr>
<td>Basal Area in clump ( m²/clump)</td>
<td>1.24</td>
<td>24.46</td>
</tr>
<tr>
<td>Species composition (% BA)</td>
<td>ABCO: 78.0 CADE: 2.1 PILA: 17.5 QUKE: 5.6</td>
<td>ABCO: 55.2 CADE: 17.5 PILA: 22.2 QUKE: 4.5</td>
</tr>
<tr>
<td><strong>Open Space (%)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;3 m</td>
<td>29.9</td>
<td>2.03 (0.05) {1.9-2.1}</td>
</tr>
<tr>
<td>3-6 m</td>
<td>61.6</td>
<td>14.3 (0.21) {13.8-14.9}</td>
</tr>
<tr>
<td>6-9 m</td>
<td>8.0</td>
<td>22.9 (0.31) {22.3-23.7}</td>
</tr>
<tr>
<td>9-12 m</td>
<td>0.3</td>
<td>22.3 (0.27) {21.6-23.0}</td>
</tr>
<tr>
<td>12-15 m</td>
<td>0</td>
<td>17.1 (0.25) {16.5-17.6}</td>
</tr>
<tr>
<td>≥15 m</td>
<td>0</td>
<td>21.4 (0.71) {19.5-22.8}</td>
</tr>
</tbody>
</table>
Figure C.1. Normalized mean clump size distribution on the YFDP calculated at a range of intertree distances for 2010 (red), 1930 (blue), and 1900 (black). 1930 and 1900 distributions represent an envelope calculated across 100 simulations of the forest reconstruction model.
Figure C.2. Cumulative clump size distribution for contemporary (red), reconstructed 1930 (blue), and reconstructed 1900 (black) forest conditions on the YFDP. 1930 and 1900 distributions represent an envelope calculated across 100 simulations of the forest reconstruction model.
C5. References


