REFERENCE CONDITIONS AND SPATIAL DYNAMICS IN A SOUTHWESTERN DRY MIXED-CONIFER FOREST

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ABSTRACT

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Structural conditions in southwestern “frequent-fire” forests, or forests that have a history of frequent, low-severity fire, have changed considerably since Euro-American settlement (ca. late 1800's); these changes are primarily due to excessive livestock grazing, extractive logging, road construction, and organized fire suppression. As a result of these land-use changes, forest densities in many locations have increased, contributing to increases in fire size and severity and alterations to ecosystem function. A recognition of these impacts has prompted interest in forest restoration treatments across broad swaths of the landscape. Forest restoration attempts to mimic the natural range of variability - or the structure and function inherent to intact natural ecosystems - but many aspects of these ecosystems are poorly understood. In combination with studies of the natural disturbance regime, reference conditions and studies of the natural range of variability also provide an ecological basis for silvicultural treatments. Spatial pattern, or the horizontal distribution of trees, is an important component of the natural range of variability and influences a wide array of ecological processes.

With this study, we reconstructed historical structure (density and spatial pattern) and species composition for four dry mixed-conifer stands on the Mogollon Rim, Arizona, USA. We reconstructed conditions from the year 1879, the time of the widespread cessation of fire in the area. We found that these forests showed evidence of increased tree density between 1879 and 2014 with major increases in density in the smaller size classes. During this time period, the number of live trees ha^{-1} increased from an average of 129.5 to 744.3, basal area increased from 10.1 to 41.9 m^{2} ha^{-1}, and mean canopy cover increased from 14.8 to 54.7 percent. Our results also showed shifts in species composition to a higher relative proportion of *Abies concolor*, and *Pseudotsuga menziesii*, and a lower relative proportion of *Pinus ponderosa* and *Quercus gambelii*. Mean group size, or the average number of trees in explicit tree groups, also increased as tree canopy cover became more continuous. Finally, we investigated the roles of different species groups within fine-scale spatial pattern. Species groups showed distinctly different patterns, suggesting that the patterns of individual species are an important consideration during the implementation of silvicultural treatments that are meant to mimic natural patterns and processes. Mechanical treatments and thinning operations in dry mixed-conifer forests on the Mogollon Rim should target an aggregated spatial structure of leave trees with a range of group sizes within a given site. Treatments based on the natural range of variability are likely to increase resistance and resilience of these ecosystems in the face of uncertain future conditions.

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Dedication

To my grandparents Hubert and Carita Rodman. You lived long and incredible lives. Having you as a part of mine for the last 24 years helped motivate me to study the sciences and to pursue my passions. Thanks for making this all possible.

Preface

This thesis is written in a “manuscript format”, a format endorsed by the Northern Arizona University School of Forestry and the Northern Arizona University Graduate College. Chapter 3 is formatted for direct submission and eventual publication in the peer-reviewed journal *Ecological Applications*. For this reason, I also use the term “we” instead of “I” throughout the text; upon submission, this manuscript will have multiple authors. There may be some repetition and redundancy of information between chapters. Chapter 3 is intended to “stand alone”, but greater detail on relevant literature and implications to land management can be found in Chapters 2 and 4 respectively.

Chapter 1

Introduction

Ecological patterns and process are closely related and interact at multiple spatial scales (Urban et al. 1987, Turner 1989, Levin 1992); therefore, a shift in the structure of an ecosystem is likely to cause substantial changes to its ecological function. Overstory forest conditions and spatial pattern (the horizontal distribution of trees) are known to exert strong control over conditions in the understory, including light infiltration (Battaglia et al. 2002), species composition (Bigelow et al. 2011), understory diversity and productivity (Laughlin et al. 2006, Moore et al. 2006), tree recruitment (Sánchez Meador et al. 2009), water availability (O'Hara and Nagel 2006, Dore et al. 2012), and the variability of fuels and associated fire behavior (Thaxton and Platt 2006, Fry and Stephens 2010). Frequent-fire ecosystems in the West exhibited, historically, a heterogeneous structure that led to functional diversity at fine-, intermediate-, and coarse-scales (Larson and Churchill 2012, Reynolds et al. 2013). At the fine-scale (< 4ha extent), forests had a mix of individual trees and groups of trees with interlocking crowns, discrete openings, and grassy interspaces (Larson and Churchill 2012, Reynolds et al. 2013). At the intermediate-scale (4-400 ha extent; hereafter referred to as “stand-scale”), trees could be arranged in an aggregated spatial distribution (trees tending to grow in groups), a random spatial distribution, or, less commonly, in a uniform spatial distribution (evenly spaced) (Abella and Denton 2009, Reynolds et al. 2013). At a coarse-scale (> 400 ha extent; hereafter referred to as the “landscape-scale”), forests probably had a variety of densities, seral stages, and species compositions. These differences were based on disturbance history, aspect, slope position, soils, and many other factors (Evans et al. 2011, Reynolds et al. 2013).

Land use changes following Euro-American settlement in the southwestern United States excluded fire from many frequent-fire forests, altering local tree carrying capacities (Bond et al. 2005) and increasing rates of recruitment (Covington and Moore 1994, Jones 1994, Mast et al. 1999, Allen et al. 2002). This, in turn, led to dramatic increases in forest density, shifts in species composition to a greater proportion of shade-tolerant and fire-intolerant species (in mixed-species forests), and decreases in average nearest neighbor distance (Cooper 1960, Covington and Moore 1994, Fulé et al. 2002, Sánchez Meador et al. 2009). Pure ponderosa pine (*Pinus ponderosa*) and pine-oak (*Pinus ponderosa/Quercus gambelii*) forests have deviated most substantially from their natural conditions, but these changes have also occurred in some mixed-conifer forests (Cocke et al. 2005). Mixed-conifer forests lie between ponderosa pine forests (typically a frequent, low-severity fire regime) and spruce-fir forests (typically an infrequent, high-severity fire regime) on a gradient of temperature and moisture (driven by elevation, aspect, and other factors; Evans et al. 2011). Forest structural changes over the last 150 years are more pronounced in the lower warm/dry mixed-conifer forests (hereafter referred to "dry" mixed-conifer) than the cool/wet mixed-conifer forests due to a comparatively greater deviation from the natural disturbance regime (Mast and Wolf 2006, Romme et al. 2009, Evans et al. 2011). Southwestern dry mixed-conifer forests are typically dominated by *Pinus ponderosa* var. *scopulorum* (Engelm.) with other tree species present including: *Pseudotsuga menziesii* var. *glauca* (Mayr) Franco, *Abies concolor* var. *concolor* (Gordon) Lindley ex Hildebrand, *Populus tremuloides* Michx., *Pinus strobiformis* Engelm., *Pinus flexilis* E.James, and *Quercus gambelii* Nutt. (Romme et al. 2009, Evans et al. 2011, Reynolds et al. 2013).

Dry mixed-conifer ecosystems are both complex and poorly understood (Reynolds et al. 2013), however, many of these forests are the target of forest management activities that aim to restore natural ecosystem structure and function (e.g. Four Forests Restoration Initiative, 4fri.org). Many southwestern dry mixed-conifer forests experienced fire regimes that were historically frequent, burning at least 25% of the landscape every 4-30 years (Dieterich 1983, Swetnam and Baisan 1996, Brown et al. 2001, O'Connor et al. 2014, Huffman et al. 2015). These frequent, low-severity fire regimes maintained low forest densities, and the interruption of this process altered forest structure. Dendrochronological reconstructions and historical plot data suggest that overstory densities in these forests ranged 51-246 trees ha^{-1} and 9-28.5 m^2 of basal area ha^{-1} in the late 1800's (Fulé et al. 2002, Matonis et al. 2013) and have increased by nearly one order of magnitude relative to historical densities. In recent years, these forests have been found to have as many as 1613 live trees ha^{-1} and as much as 51 m^2 of basal area ha^{-1} in the overstory (Heinlein et al. 2005). Mixed-conifer forests, as a whole, cover approximately 1,000,000 ha in the Southwest (Dieterich 1983), but this is probably a greater area than was present historically. Johnson (1994) found that the mixed-conifer cover type increased by about 400,000 hectares between 1962 and 1986, primarily due to the encroachment of shade-tolerant and mid-tolerant conifers into many pure *Pinus* *ponderosa* and *Populus tremuloides* stands.

Efforts to quantify forest structure and spatial heterogeneity can provide useful information to land managers both through greater knowledge of the natural range of variability (NRV: the range of conditions present in naturally functioning ecosystems; Swanson et al. 1994), and through an improved understanding of ecological processes such as disturbance dynamics (Thaxton and Platt 2006), competitive and facilitative interaction, and patch formation (Mast and Veblen 1999, Mast and Wolf 2004, Stephens and Fry 2005). An understanding of these factors allows managers to more closely align silviculture with the ecology of the areas being managed (O'Hara 2002). Multi-scaled heterogeneity, a common component of the structure of these ecosystems historically, is thought to increase ecosystem resistance and resilience (Larkin et al. 2006, O'Hara and Ramage 2013, Reynolds et al. 2013). These terms reflect the ability of ecosystems to experience disturbance with only minimal change to structure (resistance), or maintain similar functional attributes following disturbance (resilience; DeRose and Long 2014). Resistance and resilience are especially important in a rapidly changing environment in which fire occurrence and drought-related disturbance are increasing (Westerling et al. 2006, Allen et al. 2010, Garfin et al. 2013). Lower stand densities and a heterogeneous forest structure allow ecosystems to better persist in an uncertain future (Fulé 2008) by reducing fire hazard (Stephens et al. 2009), and decreasing drought stress (O'Hara and Nagel 2006, Dore et al. 2012). Heterogeneity may also increase genetic diversity at the population level (Li et al. 2001, Huang et al. 2002) due to the presence of a wider range of environmental conditions in the understory (Meyer et al. 2001). This genetic diversity may facilitate in-situ adaptation under uncertain future conditions (Hoffman and Sgrò 2011). Forest management partially informed by the NRV is still relevant in light of these climatic changes because these natural structural conditions and disturbance regimes reflect the evolutionary history under which many current tree populations and forest communities have developed (Fulé 2008).

Our study uses a combination of spatial analyses to quantify historical fine-scale heterogeneity in dry mixed-conifer forests of the Southwest, a recognized gap in scientific knowledge (Reynolds et al. 2013) that will help inform future land management strategies. The spatial and temporal relationships discussed in this study also help to describe inter and intraspecific competition and facilitation (e.g. Mast and Wolf 2004), ecological niche theory, and gap-partitioning in mixed-species forests (Canham 1989).

This study is primarily concerned with the spatial ecology and NRV of dry mixed-conifer forests in the Southwest. Chapter two, a comprehensive literature review, covers: a) the importance of fine-scale and stand-scale spatial pattern in influencing ecosystem function, b) the factors that drive spatial pattern formation and maintenance in forests, c) the current state of knowledge regarding dry mixed-conifer forests in the Southwest, d) methods of identifying reference conditions and the NRV, and e) methods for quantifying spatial pattern. Chapter three describes a spatially explicit reconstruction of forest structure and composition for several forest stands in dry mixed-conifer ecosystems on the Mogollon Rim in central Arizona, USA. Chapter four provides an overview of results and conclusions from this study and other similar studies in the Southwest, specifically focusing on the implications of these findings to the management of public lands.

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Chapter 2

Literature Review of Southwestern Mixed-Conifer Forests and Spatial Dynamics

Ecosystem pattern and ecological processes are intimately intertwined (Urban et al. 1987, Turner 1989), and species composition, vertical structure, density, and the horizontal spatial distribution of trees (hereafter referred to as spatial pattern) all play important roles in the ecological function of forested ecosystems (Oliver and Larson 1996, Larson and Churchill 2012). Many aspects of ecosystem structure in frequent-fire forests of the southwestern United States have shifted quite considerably over the last 150 years (Covington and Moore 1994, Cocke et al. 2005, Sánchez Meador et al. 2009, Sánchez Meador et al. 2010a, Reynolds et al 2013). Dry mixed-conifer forests lie at the upper range of these frequent-fire forests (on a gradient of elevation and moisture) in the Southwest. In the absence of widespread, low-severity fire (Swetnam and Baisan 1996), many dry mixed-conifer forests have had increases in density, shifts in composition to a greater proportion of shade-tolerant (and fire-intolerant) species (Heinlein et al. 2005, Fulé et al. 2009). As a result of these structural changes, many forests have become more susceptible to uncharacteristically severe wildfire (reviewed in Evans et al. 2011) and have experienced alterations to ecosystem function (reviewed in Reynolds et al. 2013).

A combination of mechanical thinning treatments and prescribed fire has been proposed as a potential solution to these problems, and can, under all but the most extreme climatic conditions, be very effective in reducing the occurrence of severe wildfire in Southwestern forests (Fulé et al. 2001, Fulé et al. 2012). The nature of silvicultural treatments has changed in recent years, as managers have begun to focus on uneven-aged management techniques (O'Hara 2002) that attempt to restore systems and mimic natural patterns of disturbance and regeneration (Franklin et al. 2002). Uneven-aged management is also thought to decrease the susceptibility of many forests to disturbance (O’Hara and Ramage 2013). As stated by O'Hara (2002), “Successful uneven-aged management in the future will require practices that recognize the disturbance and stand dynamics of individual ecosystems and use these to guide management.” These concepts align well with the ideas of restoration ecology, using knowledge of the natural range of variability (NRV, the range of structure and function present in natural systems; Swanson et al. 1994) and disturbance dynamics to manage forest systems in ways that more closely mirror their evolutionary history. The natural stand structure (especially spatial pattern) and many aspects of the ecological function of dry mixed-conifer forests in the Southwest are not thoroughly understood (Reynolds et al. 2013).

In this review, I will discuss the ecological importance of spatial pattern, the environmental factors that influence forest spatial pattern, methods of identifying reference forest structure, methods of quantifying spatial patterns at multiple scales. Because of the relatively small number of studies (of this type) in the Southwest, I will also discuss our current state of knowledge regarding the NRV in dry mixed-conifer forests in the western United States.

Ecological Importance of Spatial Pattern

Land managers often attempt to target “heterogeneity” in forest systems, because heterogeneity may increase ecosystem resistance and resilience to disturbance (Larkin et al. 2006, O’Hara and Ramage 2013). Resistance allows for the persistence of ecosystems (largely unchanged) following disturbance, while resilience allows forests to “absorb inevitable [disturbances] without fundamentally changing the system at the landscape scale” (DeRose and Long 2014). Unfortunately, heterogeneity is a relatively ambiguous term. It can be expressed at multiple scales (Reynolds et al. 2013), and in a variety of ways. In recent years, studies have attempted to quantify this heterogeneity in a way that can be explicitly incorporated into silvicultural treatments (Sánchez Meador et al. 2011, Churchill et al. 2013). Forest spatial pattern has long been recognized as a structural component of forests in the Southwest (see Cooper 1961), but an understanding of its ecological importance is still relatively new. Spatial pattern has a number of influences on climate change adaptation (both by species within forests and by humans reliant on them), the effects of fire and other disturbances, understory plant diversity and composition, tree regeneration, and wildlife habitat.

Climate Change Adaptation

Climate in the southwestern United States is becoming warmer and drier, and these changes are expected to continue in upcoming years (Seager et al. 2007, Garfin et al. 2013). Climate change-induced drought can lead to dramatic shifts in disturbance patterns and tree mortality (Westerling et al. 2006, Allen et al. 2010). These shifts in climate and disturbance have already had noticeable ecological impacts on species phenologies and ranges (Walther et al. 2002). While the ability of many species to adapt to a changing climate is unknown, it is believed that a variety of micro-environmental conditions (like that provided by a spatially heterogeneous overstory, Meyer et al. 2001) may promote genotypic (Li et al. 2001, Huang et al. 2002) and phenotypic (Nicotra et al. 2010, Laughlin et al. 2011, Auger and Shipley 2013) diversity within species. This diversity may facilitate future adaptation of plant species at the population level. Local adaptation is especially important when range shifts are not feasible because of topographic limitations or limitations of dispersal (Jump and Peñuelas 2005).

Forests may also help to offset some of the immediate effects of climatic change, both through direct carbon sequestration in woody biomass (Marland and Shlamadinger 1997) and through soil carbon storage (Lal 2005). In a study of spruce-dominated (*Picea* spp.) forests in New Brunswick, Canada, Wang et al. (2011) found that increases in structural diversity increased the potential for carbon storage. Additionally, in a review summarizing even-aged and uneven-aged management of ponderosa pine (*Pinus ponderosa*), O'Hara and Nagel (2006) found that uneven-aged stands with greater spatial variability exhibited less summer water stress and slightly higher growth efficiency than even-aged stands with less spatial variability. Battaglia et al. (2002) found that spatially aggregated overstories in longleaf pine (*Pinus palustris*) forests allowed greater overall light infiltration into the understory than evenly spaced thinning treatments with similar residual densities. This increase in resource availability was also shown to benefit seedling growth efficiency (Palik et al. 2003).

Disturbance Dynamics

The spatial distribution of trees within forests can influence the effects of disturbance. In a study of Jeffrey pine (*Pinus jeffreyi*)-dominated mixed-conifer forests in Sierra San Pedro Martir, Mexico, Fry and Stephens (2010) found a strong relationship between overstory structure and the spatial distribution of fine fuels. Greater levels of fine fuels were associated with populations of *Abies* concolor, and lower levels of fine fuels were found near *Pinus jeffreyi* trees. The study suggests that the spatial pattern and species composition of the overstory can have important influences on variations in fine-scale burn severity. In *Pinus palustris* forests in Louisiana, Thaxton and Platt (2006) demonstrated that variability in local fuel loading led to more heterogeneous burns. This fine-scale heterogeneity of disturbance resulted in greater understory species richness and diversity. Many fire-modeling projects (reviewed in Reynolds et al. 2013) indicate that heterogeneous forest canopies are less susceptible to active crown fire, instead forcing the fire to the surface after small flare-ups. Because forest restoration is often concerned with returning natural ecosystem function, understanding the effects of residual tree patterns on disturbance is of paramount importance.

Spatial pattern can also affect the behavior of other disturbances beyond fire. In mixed-conifer forests in the Sierra Nevada, trees in dense groups die more frequently from insects and pathogens than do those in more open areas (Smith et al. 2005). Large trees also die more frequently than expected from these disturbances (Smith et al. 2005). Dwarf mistletoes *(Arcuethobium* spp.), common parasitic plants in Southwestern forests, tend to spread more quickly in open and uneven-aged forests, but more slowly through dense groups of larger trees (Castello et al. 1995, Conklin and Fairweather 2010). This positive affect on spread may only be true up to a point because of limitations of dispersal (Mathiasen 1996). Western spruce budworm (*Choristonuera occidentalis*), a native species that is one of the most common and destructive defoliating insects in the West, tends to spread “top-down” from tree canopies and causes more damage in uneven-aged stands with vertical complexity (Brookes et al. 1987). White pine blister rust, an non-native tree disease caused by the pathogen *Cronartium ribicola*, is more likely to affect trees in riparian areas or cool and moist abiotic environments (Geils et al. 2010). Dense, closed-canopy tree groups with vertical heterogeneity are associated with cooler, wetter, understory conditions (Rambo and North 2009), and could facilitate the establishment and success of white pine blister rust. The spatial distribution of large trees may increase the susceptibility of adjacent trees to colonization and mortality in mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Mitchell and Preisler 1991).

Growth and Composition

From a silvicultural perspective, the sizes of canopy gaps and tree groups have important implications for tree growth form, growth efficiency, and future species composition of forested stands. In a study of spatial pattern in *Pinus ponderosa* forests in northern Arizona, Sánchez Meador et al. (2011) found that trees within groups had, on average, smaller diameters than trees on the edges of groups or within openings. York et al. (2004) found that trees adjacent to harvested openings had 41% greater growth efficiency than those within the unharvested matrix. In old-growth *Picea abies* forests in

Sweden, Fraver et al. (2014) demonstrated that competition intensity reduced growth rates of individual trees. Heterogeneous growing conditions create a variety of competitive environments. These environments then promote differential selective pressures on the individuals within a stand.

The gap-partitioning hypothesis as discussed in Canham (1989), is particularly applicable to mixed-species stands in the western United States. The success of tree seedlings and germinants depends not only on the overstory density, but also on the spatial arrangement of overstory trees. Changes in resource availability and competitive interactions (between seedlings) occur with alterations to forest spatial pattern (Palik et al. 2003). Light thresholds limit the trees that can regenerate in the understory, and shade intolerant species (e.g. *Pinus ponderosa*, *Pinus jeffreyi*, *Populus tremuloides*) may need larger gaps than shade-tolerant species (e.g. *Abies concolor, Abies lasiocarpa, Picea engelmanii*, *Acer grandidentatum*) to establish and persist (Burns and Honkala 1990a, 1990b, Bigelow et al. 2011). Mid-tolerant species (e.g. *Pinus strobiformis, Pseudotsuga menziesii, Quercus gambelii*) are somewhere in the middle of this spectrum. A diversity of disturbance types and gap sizes likely promotes species diversity on a site.

Tree spatial patterns influence subsequent regeneration patterns in forests. Stephens and Fry (2005) found that the combination of overstory structure and heterogeneous fire behavior in *Pinus jeffreyi* forests leads to the creation of regeneration patches ranging from 6-650 square meters; the majority of regeneration patches were in the smaller end of this range. Group sizes reported by Stephens and Fry (2005) are similar to others summarized in Larson and Churchill (2012), and Reynolds et al. (2013), suggesting that this regeneration mechanism may also occur in other western forests.

Fine-scale patterns and processes have an important role in the patterns of tree recruitment. York et al. (2004) demonstrated that seedlings grew more efficiently when they were in openings and not in close proximity to established overstory trees. Sánchez Meador et al. (2009) found a negative relationship between *Pinus ponderosa* recruitment and established overstory trees, suggesting that these individuals first colonized the centers of openings after the onset of fire exclusion. In mixed-conifer forests in the Sierra Nevada, North et al. (2004) found conflicting results, instead demonstrating that openings may have inhibited tree regeneration. Location within the canopy gap is an important factor in determining the success of tree regeneration (Gray and Spies 1996), and competition with the herbaceous understory (Puhlick et al. 2012) is one possible explanation for this effect. Broad-scale climatic conditions are known to affect tree recruitment (Brown and Wu 2005). These conditions could interact with overstory and understory conditions to affect the patterns of tree recruitment.

Understory Communities

Overstory structure has dramatic influences on understory community structure and composition. In forests in southwestern Colorado, Korb et al. (2007) found that percent understory cover was highest beneath *Populus tremuloides,* and lowest beneath *Pinus ponderosa*. Moore et al. (2006) found that restored *Pinus ponderosa* forests in northern Arizona had significantly greater C3 graminoid biomass in the first few years after treatment than did untreated control plots. After a 4-5 year lag, the biomass of forbs and legumes were also greater than levels in control plots. Laughlin et al. (2006) suggested that grassy openings and interspaces may have (historically) covered as much as 70% of the understory in many *Pinus ponderosa* forests in the Southwest. These frequent-fire ecosystems probably had characteristics of both forest and grassland communities. Reductions in tree density and the creation of overstory gaps in *Pinus ponderosa* forests lead to increased overall herbaceous standing crop biomass and understory species richness (Griffis et al. 2001, Laughlin et al. 2006, Moore et al. 2006, Thomas and Waring 2014).

Implications for Wildlife

Differing forest structures can (simultaneously) be beneficial to certain types of wildlife while being detrimental to others. The Mexican spotted owl (*Strix occidentalis lucida*; a threatened species) prefers to nest or roost in areas that have high canopy cover (Grubb et al. 1997), and many large trees (May et al. 2004). These types of forest are also selected by the northern goshawk (*Accipter gentilis*), but competitive interaction plays an equally important role in nest site selection for the goshawk (Reich et al. 2004). Avian species differ in their responses to treatments at a fine-scale. Using multi-species occupancy models, White et al. (2013) suggested that heterogeneous fuel reduction treatments in the Sierra Nevada would have higher avian species richness than more homogeneous treatments, however the effects differed between species. Though results from a similar study were not conclusive in northern Arizona, the distribution of snags, large trees, and areas of low canopy cover appear to be important contributors to avian habitat quality (Kalies and Rosenstock 2013).

Landscape variability is well-understood to affect animal movement (Fahrig 2007), but fine-scale and stand-scale habitat components may also be more important to smaller or less mobile organisms. Meyer and Sisk (2001) found that variability in *Pinus ponderosa* forest cover can influence insect behavior, primarily through dramatic changes to the understory microclimate across relatively short distances. Converse et al. (2006) and Kalies et al. (2012) found that small mammals were often associated with open-canopied *Pinus ponderosa* forests with greater understory productivity, more snags, and higher levels of coarse woody debris. Biological legacies (Franklin et al. 2002) and the spatial distribution of tree groups and openings are important functional components of fine-scale and stand-scale structural heterogeneity.

Factors Driving Spatial Pattern in Forests

The processes that drive forest heterogeneity are complex and variable, causing considerable differences between and within forest types. Numerous factors probably play important roles, particularly species composition, site productivity, seral state, and disturbance.

Species Composition

Species composition can influence forest spatial pattern through competitive and facilitative interactions, as well as through the growth strategies of individual species. In some species, allelopathic effects can limit tree recruitment. For example, *Picea* *engelmanii* can inhibit the growth of its own seedlings, as well as those of *Pinus contorta* in close proximity to established overstory trees (Taylor and Shaw 1983). Understory plants can also express this trait, and the western bracken fern (*Pteridium aquilidum*) may inhibit the growth of Douglas-fir seedlings (*Pseudotsuga menzeisii)*, though this relationship has only been effectively demonstrated in laboratory settings (Stewart 1975). Facilitation is also an important process governing the patterns of establishment of trees (Bruno et al. 2003). Overstory trees can strongly influence the understory microclimate (Meyer et al. 2001, Rambo and North 2009), which, in the absence of fire, facilitates the growth of late-seral species (Fulé et al. 2009). This same process also reduces the success of regeneration by shade-intolerant, early-seral tree species (Fulé et al. 2009, Bigelow et al. 2011). Ecological theory suggests that harsh sites may require facilitation for any successful tree regeneration to occur (Bertness and Callaway 1994).

Pinus ponderosa can demonstrate aggregated (closer than expected distance between trees), random, or uniform (evenly spaced) tree distributions, based on local site conditions (Abella and Denton 2009). Group membership can be beneficial to shallow-rooted species such as *Picea pungens* or *Picea engelmanii* to prevent windthrow mortality (Jones 1974). This might create an adaptive pressure that prevents individual tree establishment in open areas. *Populus tremuloides, Acer spp., Quercus gambelii, Robinia spp.*, all reproduce, at least partially, from sprouting and suckering (Jones 1974, Burns and Honkala 1990b) and commonly occur in groups. If these species are a dominant component of a forested stand, it makes sense that the forest would be more likely to demonstrate aggregation. Less is known about the spatial distributions of many other species; this is an important area for future research.

Site Productivity

Climate, topography, and soils interact to help determine the productivity of a given site. Abella and Denton (2009) demonstrated that forests with different soil types can have very different spatial patterns. Spatial pattern was less sensitive to site differences (than measurements of tree density), but both pattern and density were influenced by climate and soil type (Abella and Denton 2009). In southwestern forests, more productive sites typically have a higher tree density than less productive sites (Abella and Denton 2009, Reynolds et al. 2013).

Site productivity also influences the herbaceous understory, which could exclude the regeneration of some trees due to competitive effects (Abella and Denton 2009, Puhlick et al. 2012). Studies have shown that *Pinus ponderosa* forests growing on the less-productive basalt and cinder soils of the Southwest had aggregated patterns historically (Dyer et al. 2008, Sánchez Meador et al. 2009, Sánchez Meador et al. 2011). In these forests, aggregation could be an expression of a limited number of sites with greater water availability or the prevalence of slightly rockier areas that are less prone to grass establishment (and therefore better suited to tree regeneration). It could also reflect the “patchier” nature of fires, when a flammable understory may not cover the entire site. These findings contrast with *Pinus ponderosa* stands on more productive soils (sedimentary-derived) that primarily have random spatial patterns (Schneider 2012). Stands underlain by sedimentary soils may have had more “uniformly good” site conditions, with fewer barriers to tree establishment. Low-severity fire may also have burned more continuously throughout the understory because of greater herbaceous cover.

Temporal Dynamics

In many parts of the United States, spatial analysis of forest patterns began in the 1950’s and 1960’s; much early work on this topic focused on the changes in forest structure as stands progressed through the stages of stand development (Oliver and Larson 1996). In southwestern *Pinus ponderosa* forests, Cooper (1961) demonstrated that tree patterns are initially aggregated, as groups of small seedlings establish in openings or in advantageous microsites. However, as the new cohort ages tree patterns begin to shift towards random or uniform distributions. Williamson (1975) found similar dynamics in old-growth beech/maple forests in Indiana. Peet and Christensen (1987) describe a possible mechanism for these changes: self-thinning after initial cohort establishment leads to substantial tree mortality, resulting in only a handful of trees surviving in each tree group. In *Pinus ponderosa* forests in the Front Range of Colorado, Mast and Veblen (1999) demonstrated that trees established in small, even-aged groups, and that pattern shifted with age. Many *Pinus ponderosa* forests show the presence of even-aged groups even in later stages of stand development, suggesting that more than one individual usually survives after self-thinning of the initially dense regeneration patches (Mast and Wolf 2004), but tree size becomes more variable with cohort age (Mast and Veblen 1999). Temporal patterns of tree growth are tied to community structure and successional processes; spatial patterns of forests are a reflection of both deterministic and stochastic components (Halpern 1989, Sánchez Meador et al. 2009).

Disturbance

Patterns of disturbance play a very important role in determining overstory pattern and subsequent regeneration (Moustakas 2015). This is especially true for fire-related disturbance, but is also the case for insects and pathogens. In Sequoia National Park, CA, Rice (1993) demonstrated that burn severity and microtopographic variation have important influences on post-fire establishment of vegetation, primarily through effects on soil nutrient availability. Small areas of high-severity fire had less vegetative cover than low-severity areas following a year of recovery (Rice 1993). In the Sierra Nevada, areas that had more frequent and intense fire typically had fewer tree seedlings and a greater level of shrub cover (Lydersen and North 2012). Fry et al. (2014) found that areas with intact low-severity fire regimes did not have significantly larger openings than forests that had experienced long-term fire suppression. These findings suggest that persistent meadows and disturbance types other than fire can also contribute to fine-scale variability in spatial pattern. Fire can also create landscape-scale heterogeneity of burned and unburned patches in large mixed or high severity fire events (Romme 1982).

Similarly, insects, parasitic plants, and disease can have a variety of effects on the patterns of growth and mortality in western forests (Wilson and Tkacz 1993). Due to methods of spread, root diseases, dwarf mistletoes, and some insect species can cause tree mortality in an aggregated fashion (Wilson an Tkacz 1993, Smith et al. 2005, Bruhn et al.

1996). However, Silver et al. (2013) show that recent mortality (from root rot fungi, drought, windthrow, and other factors) in stands dominated by *Pinus resinosa* occurred randomly across the forest, and snags were only aggregated at very small scales (2-4m). *Phellinus weirii* (laminated root rot), creates slowly expanding gaps of mortality, maintaining open areas for long periods of time (Hansen and Goheen 2000). Western spruce budworm (*Choristenuera occidentalis*) tends to outbreak periodically and preferentially targets certain species (notably *Pseudotsuga menziesii*) in mixed-conifer forests (Swetnam and Lynch 1993). Considering the importance of species composition to spatial pattern, this has important implications. Both dwarf mistletoe (*Arceuthobium* spp.) and western spruce budworm spread top-down, and cause more rapid mortality in smaller trees (Swetnam and Lynch 1993, Conklin and Fairweather 2010). Though this mortality is more likely to affect vertical heterogeneity and size structure, it probably also has important effects on horizontal spatial pattern and may limit tree recruitment in openings.

Methods of Identifying Reference Forest Structure

A combination of historical plot data (e.g. Moore et al. 2004), studies of reference sites with intact fire regimes (e.g. Fulé et al. 2003a, Stephens and Fulé 2005), and historical reconstructions (e.g. Fulé et al. 1997) are often used to quantify the NRV in disturbed or degraded forests. In many western forests, data (referred to as historical plot data) were collected on federal lands beginning in the early 1900's to monitor the effects of silvicultural treatments over time. Data were often collected for all live trees above a given diameter (usually 9.14 cm diameter at 1.37m above ground level). Historical plot data can be useful because these data were relatively accurate, and were collected and recorded thoroughly and at regular intervals (Moore et al. 2004, Sánchez Meador and Moore 2010, Vankat 2011a, 2011b). Unfortunately, the number of these historical data sets is relatively minimal. Also, these plots may only be representative of a small subsample of all the ecosystem types in the Southwest (Bell et al. 2009). Additionally, collection of historical plot data began in the early 1900's, 2-4 decades after the initial onset of fire exclusion (Moore et al. 2004, Sánchez Meador et al. 2009, Lydersen et al. 2013); it is possible that forests on these plots had already undergone substantial changes due to Euro-American settlement by this point. While studies using these historical plot data can provide very useful information, they are not without limitations. Studies of current reference sites with intact fire regimes are especially useful because they provide data within the context of current environmental conditions (Stephens and Fulé 2005), and there is greater certainty associated with current conditions than past ones. But, like historical data, these sites only exist in a small number of locations. In the Southwest, these sites include the Gila Wilderness in New Mexico, some remote mesa tops in the Grand Canyon, AZ, and parts of Mexico (Fulé et al. 2003a, Stephens and Fulé 2005). Much like historical plot data, the applicability of these sites to the entirety of the southwestern forests is limited.

Reconstruction of historical structure helps to fill some gaps in knowledge of the NRV. On sites where “historical remnant” (snags, logs, stumps, etc.) is still present, forest structure prior to Euro-American settlement can be effectively reconstructed (Fulé et al. 1997, Moore et al. 2004). Because decomposition rates are slow in the arid Southwest and many species are relatively long-lived, these methods demonstrate minimal bias (Moore et al. 2004).

Many techniques have been utilized by scientists for the purpose of forest reconstruction. Youngblood et al. (2004), Abella and Denton (2009), Dickinson (2014), and Greco and Sensibaugh (2014) all present methods of historical reconstruction that are based, primarily, on size-age relationships. With this “size-age relationship method”, all live trees and historical remnants above a given diameter threshold, or showing old growth characteristics, are considered to have been present prior to Euro-American settlement. Any trees or evidences smaller than this threshold are not believed to have been present historically. These data can be quickly collected, leading to a broad census across many sites in a short time-period. Size-age relationships can vary both within and between sites (Oliver and Larson 1996), leading to inaccuracy in the results presented in these studies.

More accurate results are presented in studies where the majority of live trees and historical remnants are dated using standard dendrochronological techniques (Stokes and Smiley 1968). Mast et al. (1999), Brown and Wu (2005), and Brown et al. (2012) are three such studies. Mast et al. (1999) and Brown and Wu (2005) crossdated all historical remnants on their plots. Brown et al. (2012) determined age structure of dead trees with a small subplot within each larger plot. Though these methods are highly accurate, they are also very time-consuming in the field and the laboratory, leading to a very small sample size relative to the number of person-hours invested. Our approach (outlined in Chapter

3, slightly modified from Sánchez Meador et al. 2011) is a hybrid of dendrochronology and size-age relationships. When using this method, we sacrifice some of the accuracy presented by Mast et al. (1999) and Brown and Wu (2005) (especially in historical remnants) for a larger sample size.

Methods of Quantifying Spatial Patterns at Multiple Scales

Point pattern analyses, statistics quantifying spatial autocorrelation, and geostatistics, are useful methods that are the basis for many ecological studies concerned with the relationship of events within space (Perry et al. 2002). Point pattern analysis is typically concerned with the pattern of events, solely based on their location relative to other events in one-dimensional, two-dimensional, or three-dimensional space (Baddeley et al. 2014). Spatial autocorrelation and geostatistics focus on the relationship of a variable (such as age, size, genotype, etc.) across space (e.g. Fry and Stephens 2010). Methods of spatial autocorrelation and geostatistics often assume that events that occur in close proximity to one another (spatially or temporally) have greater similarity than events that occur far from one another (Tobler 1970).

Point Pattern Analysis

Point pattern analysis, broadly, can be broken down into three categories: first order methods, second order methods, and local indicators of spatial association (LISA, Anselin 1995). First order methods, such as those described by the the Clark and Evans' R index (Clark and Evans 1954), and Pielou's Alpha statistic (Pielou 1959), describe the overall pattern of events at the plot extent with one numerical value. The Clark and Evans' R index is a ratio of observed mean nearest neighbor (the average of the distances from each point to its closest neighbor) distance divided by the “expected mean distance” with a given point density (Clark and Evans 1954). This expected distance is a function of the number of events and the total area surveyed. The difference between observed and expected is often tested with a Z-test to determine statistical significance (Baddeley and Turner 2005).

Pielou's α index (Pielou 1959) is an improvement upon the method of Clark and Evans (1954). With this method, the researcher performs the analysis in two steps. During the first step in Pielou's method, one calculates the mean nearest neighbor distance in the observed dataset. Then a set of points (with the same intensity), representing complete spatial randomness (CSR) is simulated. The interpattern nearest neighbor distance is calculated for each individual in the observed pattern (the distance to the closest of the random points). The mean of these values (the expected value for CSR) is then compared to the mean nearest neighbor distance between points in the observed pattern (Pielou 1959).

For either first order method, if events are closer in space than would be expected under randomness then the pattern can be described as aggregated. Aggregation implies that events occur close to one another, suggesting that there is some ecological benefit or underlying process driving events to occur in this way. If events are uniformly distributed (evenly spaced), such as in a plantation, they are further than expected under CSR. In a natural ecological setting, uniform spatial distributions are the result of some ecological benefit or process that makes events occur far from one another. Strong competition between individuals or allelopathy are two possible explanations for this type of pattern. Clark and Evans' R index is the most widely used first-order point pattern statistic in the study of tree spatial patterns (Larson and Churchill 2012)

Second-order analyses, such as the univariate Ripley's K (Ripley 1977) and the Paired Correlation Function (PCF, Stoyan and Stoyan 1994) also test questions relating to the distance between events, but the use of these methods adds the complexity of changes in spatial scale. The Ripley's K analysis is cumulative, meaning that observed patterns at a short distances can influence the observed patterns at a larger distances. The PCF gives very similar results to Ripley's K, but it is non-cumulative. For this reason, the results of the PCF (at a given lag distance) may be more easily interpreted than the Ripley's K (Loosmore and Ford 2006). Both tests are statistically valid if interpreted correctly (Baddeley et al. 2014). Historically, Ripley's K analysis has been the most widely used measure to quantify forest spatial pattern (Larson and Churchill 2012), but the PCF has seen increased use recently (e.g. Fry et al. 2014).

Hypothesis tests for these second order methods are based on Monte Carlo simulations of a random Poisson point process (Baddeley et al. 2014). For these simulations (if the assumption of isotropy or site homogeneity is not rejected), each location within the study area is equally likely to have a simulated point within it; the intensity parameter for the Poisson distribution is based on expected number of points per unit area. Two-tailed confidence envelopes are then developed by simulating a large number of patterns (often 999), and taking the 2.5th and 97.5th quantile values at each point in the tested interval (Baddeley et al. 2014).

Because comparisons between the observed pattern and the simulation envelopes are being made at each tested distance, statistical significance must be interpreted carefully to prevent α-inflation (Loosmore and Ford 2006). If the observed pattern exceeds this envelope at a given distance, either more aggregated or more uniform than random, it is assumed that the observed point pattern is significantly different from random at a given scale, but this assumption should also be tested with a goodness of fit test (Loosmore and Ford 2006). The most commonly used goodness of fit tests are the Diggle, Cressie, Loomis, and Ford test (DCLF) or the Maximum Absolute Deviation (MAD) test (Baddeley et al. 2014). The MAD test is more powerful than the DCLF test when there is no prior knowledge of the expected scale of a relationship, though the DCLF is preferable when the researcher has an *a priori* hypothesis of interaction distance (Baddeley et al. 2014).

Local indicators of spatial interaction (LISA; Anselin 1995), such as those described by Plotkin et al. (2002) and Getis and Ord (1992), do more than quantify the mean patterns of a data set. LISA can tell us about the effect of each event on the overall pattern, or the distribution of events within the pattern, and can be used to quantify the number of tree groups, the range in group sizes, and the number of isolated individuals (Larson and Churchill 2012). These aspects of pattern are crucial in the development of silvicultural prescriptions that target heterogeneity (See Larson and Churchill 2012, and Churchill et all. 2014). Quantifying the size and number of openings or empty space between events, is valuable and an important area for future research (Larson and

Churchill 2012, Lydersen et al. 2013, Dickinson 2014).

The continuum percolation method (described in Plotkin et al. 2002) determines group size and distribution by searching for points within a given lag distance of other points (Plotkin et al. 2002, Larson and Churchill 2008). Though previous studies have used a wide range of lag distances, a commonly used lag distance is 6m (Larson and Churchill 2008, Sánchez Meador et al. 2011, Lydersen et al. 2013). This value corresponds to the 75th percentile crown diameter of historical trees in *Pinus ponderosa* forests of northern Arizona (Sánchez Meador et al. 2011). In this case, any trees within 6m of another tree are considered to be a part of the same group. Because the biological definition of tree groups is multiple trees with overlapping crowns (Larson and Churchill 2012, Reynolds et al. 2013), methods that incorporate tree crown size have also been developed (Sánchez Meador et al. 2011, Lydersen et al. 2013). The methods of Sánchez Meador et al. (2011) correct a bias that may predispose large trees (beyond the 75th percentile of size) to be isolated individuals rather than members of groups. If using this method, the lag distance for a given tree is 6m unless the estimated crown diameter exceeds this value. If crown diameter exceeds 6m, then the crown diameter becomes the lag distance for this tree when assigning group membership. Methods presented in Lydersen et al. (2013), Fry et al. (2014), and Chapter 3 also determine group size and membership based on measured or estimated crown radius. Use of a fixed lag distance estimates the “biotic potential” of trees to become members of groups (Sánchez Meador et al. 2011), while methods based solely on crown overlap determine if a tree is a member of a group at that given point in time.

Measures of Spatial Autocorrelation

Tests of spatial autocorrelation measure the relationship of a variable in space, and determine if events close to one another are likely to have similar values. Moran's I (Cliff and Ord 1981), a measure of spatial autocorrelation, is a commonly used method for the analysis of spatial pattern in forests (Larson and Churchill 2012). Mast and Veblen (1999), Mast and Wolf (2004, 2006), and Sánchez Meador et al. (2009) use this metric to quantify the patch size of even-sized and even-aged groups of trees. Because point pattern analyses are solely based on the proximity of points to one another, spatial autocorrelation may provide more insight into the underlying ecological processes driving spatial pattern. When using Moran's I, variables tested for autocorrelation must be continuous. The Join Count Statistic (Cliff and Ord 1981) provides a test of spatial autocorrelation for binary categorical variables (such as species groups or size-classes). These global methods test the hypothesis (H_o) of “no significant autocorrelation of the given variable at the plot extent.” H_a: points with similar values are more likely to occur near one another.

Autocorrelograms are a local adaptation of the Moran's I statistic. These analyses typically include a Bonferroni correction (Bonferroni 1936) of pointwise p-values for multiple comparisons. Autocorrelograms allow one to go beyond the hypothesis test of “spatial autocorrelation at the extent” to ask questions relating to spatial autocorrelation at a given scale. These differences are analogous to the first-order (Clark and Evans' R, Pielou's α) and second-order (Ripley's K, PCF) tests within Point Pattern Analysis.

Geostatistics

Geostatistics compare observations of a given variable between events to create predictive surfaces. Hessl et al. (2007) provides a good overview of some of these analyses, and describe the use of Kriging, Inverse Distance Weighting, and Thiessen/Vorronoi Polygons to predict values around sample locations of fire occurrence. These methods all have benefits and drawbacks, discussed at length by Hessl et al. (2007), and will not be discussed at length here. Geostatistics can prove useful for visualizing data and can be utilized in presenting temporal relationships such as regeneration dates in different spatial locations (Sánchez Meador et al. 2009). Some of these methods, such as semivariogram analysis, can be particularly useful in making connections between pattern and process (e.g. Fry and Stephens 2010). Certain geostatistical methods can also be utilized for hypothesis testing (e.g. kriging; Perry et al. 2002).

Collection of Spatial Point Pattern Data at Multiple Scales

Studies of forest spatial pattern most commonly rely on field-based stem-mapping at stand-scales (Larson and Churchill 2012), but new remote sensing-based methods (such as airborne LiDAR) may provide an additional way to collect and analyze spatial data in forests (e.g. Swetnam 2013). Because many methods of spatial analysis are vulnerable to edge effects (Ripley 1988), collection of data in plots that maximize the ratio of inner area:outer edge, may be best for the purpose of maximizing the efficiency of data collection. Circles have the highest ratio of area:edge of any standard shape, so circular plots are the best shape for this purpose. However, circular plots can also be logistically difficult to establish when plot sizes are large. Most studies of forest spatial pattern use plots that are square (e.g. Sánchez Meador et al. 2009, Lydersen et al. 2013, Fry et al. 2014). Spatial analyses can only be performed for ½ the length of the shortest plot diameter, with some form of edge correction either eliminating observations near the plot edge (reduced sample/guard correction) or reducing the weight of the outermost points (isotropic edge correction, translation correction) towards the observed pattern (Ohser 1983, Ripley 1988). These methods of edge correction account for the fact that there is no knowledge of events outside the plot perimeter.

The Current State of Knowledge for Southwestern Mixed-Conifer Forests

Mixed-conifer forests are one of the most diverse and productive cover types in the Southwest and cover approximately 1,000,000 hectares in this region (Dieterich 1983, Korb et al. 2007). Southwestern mixed-conifer has been defined as the intermediate zone between ponderosa pine forests (at lower elevations) and spruce-fir forests at higher elevations, sharing species and environmental characteristics of both adjacent forest types, but often with a higher overstory species richness (Romme et al. 2009, Evans et al. 2011). This species richness is perhaps the most recognizable aspect of the ecosystem. Mixed-conifer is commonly grouped into cool/wet and warm/dry categories based on relative species composition and historical disturbance regimes (Romme et al. 2009). It is believed that cool and wet mixed-conifer forests have a history of mixed-severity fire and structure within these forests has not substantially changed as a result of fire exclusion

(Evans et al. 2011). Contrarily, warm and dry mixed-conifer forests (with a history of frequent low-severity fire) have seen substantial structural changes since Euro-American settlement (summarized in Evans et al. 2011, Reynolds et al. 2013). In the Southwest, dry mixed-conifer forests are typically dominated by *Pinus ponderosa*, but also commonly include components of: *Pseudotsuga menziesii, Abies concolor, Quercus gambelii, Populus tremuloides, Acer* spp., *Quercus gambelii, Pinus flexilis, Pinus strobiformis,* and occasionally *Abies bifolia*, *Picea engelmanii*, or *Picea pungens*. (Dieterich 1983, Romme et al. 2009, Evans et al. 2011). In other regions of the western United States, *Pinus jeffreyi, Larix occidentalis, Abies grandis, Tsuga* spp., *Thuga* spp., *Calocedrus* spp., *Sequoia* spp., and *Quercus* spp. may also be important components of these ecosystems (Evans et al. 2011, Larson et al. 2012, Fry et al. 2014).

Southwestern mixed-conifer forests may occupy a greater area today than they did historically due to the effects of fire suppression. Johnson (1994) found substantial decreases in the cover of ponderosa pine and aspen forests, and associated increases in mixed-conifer cover in the Southwest between the 1960's and 1980's. These changes are due, in large part, to increases in forest densities, favoring regeneration of shade tolerant species (see also: Dahms et al. 1997). Though mixed-conifer forests may cover only a small portion of the total area for southwestern forests, they are sanctums of biodiversity, providing important habitat for many plant and animal species. For example, the Mexican spotted owl (*Strix occidentalis lucida*) preferentially nests in mixed-conifer forests over other cover types (May and Gutiérrez 2002). See: Battaglia and Shepphard (2007), Evans et al. (2011), Margolis et al. (2013), Looney and Waring (2013), and Reynolds et al.

(2013) for recent reviews of structural and functional characteristics in these ecosystems.

In the context of this project, we define dry mixed-conifer as, historically, having a dominant component of *Pinus ponderosa* with at least one other more shade-tolerant and fire-intolerant coniferous species (commonly occurring at a more mesic or high-elevation site) in a dominant or codominant position in the overstory. This is an important distinction, because many contemporary mixed-conifer forests were historically ponderosa pine, or pine-oak forests with the site potential to become mixed-conifer (Johnson 1994). Our analysis focused on ecosystems that were historically mixed-conifer.

Reference Conditions- Fire History

Swetnam and Baisan (1996) developed fire chronologies for 63 sites across the Southwest; 24 of these sites included at least some mixed-conifer forest. The 25% mean fire return interval (filtered: at least 25% of samples for a site scarred in a given year) for these mixed-conifer sites ranged from 7.8-26.1 years. This is generally less frequent than fire regimes in ponderosa pine ecosystems (Swetnam and Baisan 1996). In *Pinus ponderosa* forests, years with widespread fire occurrence are typically dry years that are preceded by 2-3 wet years (Swetnam and Baisan 1996, Brown et al. 2001). These preceding years of moist conditions help to develop a lush herbaceous understory, providing greater levels of fine fuels for fire to ignite and carry (Swetnam and Baisan 1996, Brown et al. 2001). Contrarily, fires in mixed-conifer forests are less likely to be limited by fuels, rather they are controlled by top-down climatic factors (Swetnam and Baisan 1996, Brown et al. 2001). Years of widespread fire occurrence in mixed-conifer forests are typically those with abnormally low PDSI (Palmer Drought Severity Index), and are often preceded by dry years (Swetnam and Baisan 1996). Dry mixed-conifer forests in the Southwest are probably somewhere in the middle of this spectrum, being affected by both bottom-up and top-down controls (Huffman et al. 2015).

Other studies of historical fire regimes in mixed-conifer forests of the Southwest have corroborated Swetnam and Baisan (1996). In the White Mountains in eastern Arizona, Dieterich (1983) reported 22 year fire intervals of “landscape wide” fires in mixed-conifer forests. In the Sacramento Mountains of southern New Mexico, Brown et al. (2001) reported a 4-14 year mean fire return interval (MFRI) on their mixed-conifer sites (unfiltered), and stated that fire occurrences were primarily due to top-down controls. In the Pinaleños Mountains of southern Arizona, Grissino Mayer et al. (1994) found an unfiltered MFRI of 5 years, and O’Connor et al. (2014) reported that more than 80% of this landscape has transitioned from forests typified by low-mixed severity to mixed-high severity (33% filtered MFI 9.3 years). In northern New Mexico, Touchan et al. (1996) reported a 25% mean fire return interval of 10-22 years on their mixed-conifer sites. Sakulich and Taylor (2007) reported a 25% MFRI of 16.3 years for Sky Island forests in the Guadalupe Mountains in west Texas. Fulé et al. (2003a), Heinlein et al. (2005), and Huffman et al. (2015) all reported relatively frequent fire regimes on their mixed-conifer sites in northern Arizona with 9, 9-10, and 8.5 years respectively (all 25% filtered MFRI). Much evidence exists to justify the hypothesis that dry mixed-conifer forests in the Southwest experienced a relatively frequent and low-severity fire regime. All studies cited showed a near-total elimination of fire in the late 1800's or early 1900’s.

Other studies focusing on forest stand structure have suggested that less frequent, higher severity fire could also be an important factor in dry mixed-conifer forests (Williams and Baker 2012, Odion et al. 2014). Higher elevation sites (Fulé et al. 2003b) and those closer to the Rocky Mountains (Grissino Mayer et al. 2004, Fulé et al. 2009) may burn with a lower relative frequency, though filtered mean fire return intervals on these sites are often less than 30 years. In the Madrean Sky Islands of central and souther n Arizona, Margolis et al. (2011) demonstrated that there is considerable variability in fine-scale fire frequency in mixed-conifer forests, especially those with topographic diversity. The authors suggest that south-facing slopes (often the warm/dry subtype) burn at least every ten years, while north facing slopes and more mesic areas (often the cool/wet subtype) may burn much less frequently (Margolis et al. 2011). Mixed-conifer forests have a wide range of disturbance histories. This is an important consideration for managers when planning future treatments.

Reference Conditions- Density and Composition

The elimination of fire from much of the landscape has had dramatic impacts on stand structure and species composition in many southwestern forests. Reynolds et al. (2013) provide a summary of forest structure from current reference sites, historical plot data, and historical reconstructions (similar to: Fulé et al. 1997) in the ponderosa pine, pine-oak forests, and dry mixed-conifer forests in the Southwest. In dry mixed-conifer forests, reference sites ranged from about 50-250 live trees ha^{-1} and 9-29 m^{2} of basal area ha^{-1}. Contemporary densities are generally much higher than historical densities. Mast and Wolf (2004), Heinlein (2005), and Fulé and others (2009) reported ranges in contemporary densities of 584-1700 live trees ha^{-1} per hectare, and 24.3-51.5 m^2 of basal area ha^{-1} (Mast and Wolf do not report contemporary basal area). Data from the San Francisco Peaks and the Mogollon Rim in Arizona show similar patterns (Sánchez Meador et al. unpublished data; Chapter 3 - Table 3). The wide variability (both historically and contemporarily) in density reflects the heterogeneity of these dry mixed-conifer forests, and probably relates to variations in site productivity, differing disturbance histories, and human land use history in these ecosystems across the Southwest. A better understanding of the drivers of this variability may be necessary to encourage more site-specificity in management.

The exclusion of fire (in addition to other Euro-American influences) has also led to a decrease in the prevalence of shade-intolerant species such as *Pinus ponderosa* and *Populus tremuloides* in many dry mixed-conifer forests (Reynolds et al. 2013). Historically, the importance of these species, especially *Populus tremuloides*, varied across the landscape however. Some dry mixed-conifer forests had a large component of *Populus tremuloides* historically (Heinlein et al. 2005, Fulé et al. 2009), though in other forests the species may have been a less important component (Chapter 3). Shade-tolerant species and mid-tolerant species, such as *Pinus strobiformis*, *Pinus flexilis*, *Abies concolor*, and *Pseudotsuga menziesii*, have increased quite substantially in relative abundance within many dry mixed-conifer forests of the Southwest since Euro-American settlement (Mast and Wolf 2004, Heinlein et al. 2005, Fulé et al. 2009).

Reference Conditions-Spatial Pattern

Fine-scale spatial patterns of trees in frequent-fire forests of the West are often described as consisting of individual trees, groups of trees with interlocking crowns, grassy openings, and interspaces (Larson and Churchill 2012, Reynolds et al. 2013). Depending on the ecology of a given forest stand, the relative importance of these components may vary.

As densities in dry mixed-conifer forests have increased (Chapter 3 - Fig 3), the proportion of trees in large patches has generally increased as well, and the proportion of individual trees, and those in small groups, has decreased (Sánchez Meador et al. 2011, Churchill et al. 2013, Lydersen et al. 2013). Conflicting results have been presented in regards to the size and distribution of openings. By comparing sites with ongoing fire exclusion to sites with an active fire regime, Fry et al. (2014) suggested that mean opening size may not have changed substantially due to fire exclusion. Findings of Lydersen et al. (2013) suggest otherwise. In their use of historical plot data in California, Lydersen et al. (2013) found a decrease in the size and number of openings (contemporarily) relative to historical levels. Results from the Front Range of Colorado show a decrease in the number of smaller openings since the onset of Euro-American settlement (Dickinson 2014).

Studies of spatial pattern in dry mixed-conifer forests of the Southwest are under-represented in the scientific literature (Reynolds et al. 2013). In the Appendix – Table 1, I present a summary of published studies in this ecosystem type across the western United States. Across the West, mean group sizes in dry mixed-conifer ecosystems ranged from

0.003 ha (Matonis et al. 2013) to 0.72 hectares (North et al. 2007) historically, and small groups were generally much more abundant than large groups (see Appendix-Table 1 for a detailed review of patch sizes and spatial patterns). The factors affecting this variability in patch size and patch formation are poorly understood (Larson and Churchill 2012). To date, only about 150 hectares of dry mixed-conifer forest have been studied (presented in the published literature) across the entire western United States to establish spatially explicit reference conditions; these ecosystems likely cover several million hectares across the region.

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Chapter 3

Reference Conditions and Shifting Community Dynamics in Southwestern Dry Mixed-Conifer Forests

Abstract

Structural conditions in southwestern “frequent-fire” forests, or forests that have a history of frequent, low-severity fire, have changed considerably since Euro-American settlement (ca. late 1800's); these changes are primarily due to excessive livestock grazing, extractive logging, road construction, and organized fire suppression. As a result of these land-use changes, forest densities in many locations have increased, contributing to increases in fire size and severity and alterations to ecosystem function. A recognition of these impacts has prompted interest in forest restoration treatments across broad swaths of the landscape. Forest restoration attempts to mimic the natural range of variability - or the structure and function inherent to intact natural ecosystems - but many aspects of these ecosystems are poorly understood. In combination with studies of the natural disturbance regime, reference conditions and studies of the natural range of variability provide an ecological basis for silvicultural treatments. Spatial pattern, or the horizontal distribution of trees, is an important component of the natural range of variability and influences a wide array of ecological processes.

With this study, we reconstructed historical structure (density and spatial pattern) and species composition for four dry mixed-conifer sites on the Mogollon Rim, Arizona, USA. We reconstructed conditions from the year 1879, the time of the widespread cessation of fire in the area. We found that these forests showed evidence of increased tree density between 1879 and 2014 with major increases in density in the smaller size classes. During this time period, the number of live trees ha^{-1} increased from an average of 129.5 to 744.3, basal area increased from 10.1 to 41.9 m^{2} ha^{-1}, and mean canopy cover increased from 14.8 to 54.7 percent. Our results also showed shifts in species composition to a higher relative proportion of *Abies concolor*, and *Pseudotsuga menziesii*, and a lower relative proportion of *Pinus ponderosa* and *Quercus gambelii*. Mean group size, or the average number of trees in explicit tree groups, also increased as tree canopy cover became more continuous. Finally, we investigated the roles of different species groups within fine-scale spatial pattern. Species groups showed distinctly different patterns, suggesting that the patterns of individual species are an important consideration during the implementation of silvicultural treatments that are meant to mimic natural patterns and processes. Mechanical treatments and thinning operations in dry mixed-conifer forests on the Mogollon Rim should target an aggregated spatial structure of leave trees with a range of group sizes within a given site. Treatments based on the natural range of variability are likely to increase resistance and resilience of these ecosystems in the face of uncertain future conditions.

Introduction

Ecological patterns and process are closely related and interact at multiple spatial scales (Urban et al. 1987, Turner 1989, Levin 1992); therefore, a shift in the structure of an ecosystem is likely to cause substantial changes to its ecological function. Overstory forest conditions and spatial pattern (the horizontal distribution of trees) are known to exert strong control over conditions in the understory, including light infiltration (Battaglia et al. 2002), species composition (Bigelow et al. 2011), understory diversity and productivity (Laughlin et al. 2006, Moore et al. 2006), tree recruitment (Sánchez Meador et al. 2009), water availability (O'Hara and Nagel 2006, Dore et al. 2012), and the variability of fuels and associated fire behavior (Thaxton and Platt 2006, Fry and Stephens 2010). Frequent-fire ecosystems in the West exhibited, historically, a heterogeneous structure that led to functional diversity at fine-, intermediate-, and coarse-scales (Larson and Churchill 2012, Reynolds et al. 2013). At the fine-scale (< 4ha extent), forests had a mix of individual trees and groups of trees with interlocking crowns, discrete openings, and grassy interspaces (Larson and Churchill 2012; scales defined in Reynolds et al. 2013). At the intermediate-scale (4-400 ha extent; hereafter referred to as “stand-scale”), trees could be arranged in an aggregated spatial distribution (trees tending to grow in groups), a random spatial distribution, or, less commonly, in a uniform spatial distribution (evenly spaced) (Abella and Denton 2009, Reynolds et al. 2013). At a coarse-scale (> 400 ha extent; hereafter referred to as the “landscape-scale”), forests probably had a variety of densities, seral stages, and species compositions. These differences were based on disturbance history, aspect, slope position, soils, and many other factors (Evans et al. 2011, Reynolds et al. 2013).

Land use changes following Euro-American settlement in the southwestern United States excluded fire from many frequent-fire forests, altering local tree carrying capacities (Bond et al. 2005) and increasing rates of recruitment (Covington and Moore 1994, Jones 1994, Mast et al. 1999, Allen et al. 2002). This, in turn, led to dramatic increases in forest density, shifts in species composition to a greater proportion of shade-tolerant and fire-intolerant species (in mixed-species forests), and decreases in average nearest neighbor distance (Cooper 1960, Covington and Moore 1994, Fulé et al. 2002, Sánchez Meador et al. 2009). Pure ponderosa pine (*Pinus ponderosa*) and pine-oak (*Pinus ponderosa/Quercus gambelii*) forests have deviated most substantially from their natural conditions, but these changes have also occurred in some mixed-conifer forests (Cocke et al. 2005). Mixed-conifer forests lie between ponderosa pine forests (typically a frequent, low-severity fire regime) and spruce-fir forests (typically an infrequent, high-severity fire regime) on a gradient of temperature and moisture (driven by elevation, aspect, and other factors; Evans et al. 2011). Forest structural changes over the last 150 years are more pronounced in the lower warm/dry mixed-conifer forests (hereafter referred to "dry" mixed-conifer) than the cool/wet mixed-conifer forests due to a comparatively greater deviation from the natural disturbance regime (Mast and Wolf 2006, Romme et al. 2009, Evans et al. 2011). Southwestern dry mixed-conifer forests are typically dominated by *Pinus ponderosa* var. *scopulorum* (Engelm.) with other tree species present including: *Pseudotsuga menziesii* var. *glauca* (Mayr) Franco, *Abies concolor* var. *concolor* (Gordon) Lindley ex Hildebrand, *Populus tremuloides* Michx., *Pinus strobiformis* Engelm., *Pinus flexilis* E.James, and *Quercus gambelii* Nutt. (Romme et al. 2009, Evans et al. 2011, Reynolds et al. 2013).

Dry mixed-conifer ecosystems are both complex and poorly understood

(Reynolds et al. 2013), however, many of these forests are the target of forest management activities that aim to restore natural ecosystem structure and function (e.g. Four Forests Restoration Initiative, 4fri.org). Many southwestern dry mixed-conifer forests experienced fire regimes that were historically frequent, burning at least 25% of the landscape every 4-30 years (Dieterich 1983, Swetnam and Baisan 1996, Brown et al. 2001, O’Connor et al. 2014, Huffman et al. 2015). These frequent, low-severity fire regimes maintained low forest densities, and the interruption of this process altered forest structure. Dendrochronological reconstructions and historical plot data suggest that overstory densities in these forests ranged 51-246 trees ha^{-1} and 9-28.5 m^{2} of basal area ha^{-1} in the late 1800's (Fulé et al. 2002, Matonis et al. 2013) and have increased by nearly one order of magnitude relative to historical densities; in recent years, these forests have been found to have as many as 1613 live trees ha^{-1} and as much as 51 m^{2} of basal area ha^{-1} in the overstory (Heinlein et al. 2005). Mixed-conifer forests, as a whole, cover approximately 1,000,000 ha in the Southwest (Dieterich 1983), but this is probably a greater area than was present historically. Johnson (1994) found that the mixed-conifer cover type increased by about 400,000 hectares between 1962 and 1986, primarily due to the encroachment of shade-tolerant and mid-tolerant conifers into many pure *Pinus ponderosa* and *Populus tremuloides* stands.

Efforts to quantify forest structure and spatial heterogeneity can provide useful information to land managers both through greater knowledge of the natural range of variability (NRV: the range of conditions present in naturally functioning ecosystems; Swanson et al. 1994), and through an improved understanding of ecological processes such as disturbance dynamics (Thaxton and Platt 2006), competitive and facilitative interaction, and patch formation (Mast and Veblen 1999, Mast and Wolf 2004, Stephens and Fry 2005). An understanding of these factors allows managers to more closely align silviculture with the ecology of the areas being managed (O’Hara 2002). Managing for multi-scaled heterogeneity, as was common in these ecosystems historically, is thought to increase ecosystem resistance and resilience (Larkin et al. 2006, O’Hara and Ramage 2013, Reynolds et al. 2013). These terms reflect the ability of ecosystems to experience disturbance with only minimal change to structure (resistance), or maintain similar functional attributes following disturbance (resilience; DeRose and Long 2014). Resistance and resilience are especially important in a rapidly changing environment in which fire occurrence and drought-related disturbance are increasing (Westerling et al. 2006, Allen et al. 2010, Garfin et al. 2013). Lower stand densities and a heterogeneous forest structure allow ecosystems to better persist in an uncertain future (Fulé 2008) by reducing fire hazard (Stephens et al. 2009), and decreasing drought stress (O'Hara and Nagel 2006, Dore et al. 2012). Heterogeneity may also increase genetic diversity at the population level (Li et al. 2001, Huang et al. 2002) due to the presence of a wider range of environmental conditions in the understory (Meyer et al. 2001). This genetic diversity may facilitate in-situ adaptation under uncertain future conditions (Hoffman and Sgrò 2011). Forest management partially informed by the NRV is still relevant in light of these climatic changes because these natural structural conditions and disturbance regimes reflect the evolutionary history under which many current tree populations and forest communities have developed (Fulé 2008).

Our study uses a combination of dendrochronological reconstruction and spatial analyses to quantify historical fine-scale heterogeneity in dry mixed-conifer forests of the Southwest, a recognized gap in scientific knowledge (Reynolds et al. 2013) that will help inform future land management strategies. The spatial and temporal relationships discussed in this study also help to describe inter and intraspecific competition and facilitation (e.g. Mast and Wolf 2004), ecological niche theory, and gap-partitioning in mixed-species forests (Canham 1989). The primary objectives for this study were to: 1) describe the spatial and temporal dynamics of dry mixed-conifer forests on the Mogollon Rim, AZ, USA and 2) provide new information concerning the spatial relationships of trees both within and between species.

Methods

Defining Dry Mixed-Conifer

In the context of this project, we define dry mixed-conifer as, historically, having a dominant component of *Pinus ponderosa* with at least one additional coniferous species in a dominant or co-dominant position in the overstory. The possible coniferous species included are commonly found at more mesic or higher-elevation sites (e.g. *Pseudotsuga menziesii, Abies* spp., *Picea* spp., and others) and do not typically include *Juniperus* spp. or *Pinus edulis*. Being "historically dry mixed-conifer" is an important distinction because many contemporary mixed-conifer forests were historically ponderosa pine, or pine-oak forests with the site potential to become mixed-conifer, limited by frequent low-severity fire (Johnson 1994). Our analysis focused on ecosystems that were historically dry mixed-conifer, and the results of this study are most applicable to these types of sites along the Mogollon Rim, AZ, USA.

Field Sites and Site Selection

In the summer of 2014, we collected data on field sites within the Mogollon Rim Ranger District of the Coconino National Forest in Arizona, USA (Figure 3.1). We selected these sites using several GIS layers, including the Southwest Regional Gap Analysis (SWReGAP) dataset of cover type classification (USGS 2004), an airborne LiDAR (Light detection and ranging)-derived digital elevation model (1x1m resolution), a layer of fire perimeters (for fires greater than 10 acres) between 1970 and 2013 (USDA 2014), and two layers with the locations of all roads and trails on Coconino National Forest (USDA 2014). We selected sites that could accommodate a 100m x 100m plot on relatively moderate and homogeneous slopes (< 30% slope). Additionally, we selected study sites that were all on south or west-facing aspects with vegetation identified as "Rocky Mountain Dry-Mesic Montane Mixed-Conifer Forest" in the SWReGAP layer (USGS 2004). We selected these south or west aspects because these are the areas that are likely to be targeted for future restoration treatments in dry mixed-conifer ecosystems on the Mogollon Rim.

We also avoided selection of study sites with intensive timber harvests and areas that overlapped the boundaries of recent fires (fires since 1970); loss of historical remnants due to decomposition and fire occurrence can decrease the accuracy of reconstructions (Fulé et al. 2002). Through visual analysis of overstory structure, we also rejected any sites that appeared to have been pine or pine-oak forests (historically) that had experienced recent mixed-conifer encroachment. Finally, we ensured that field sites were at least 100m from any roads or designated trails; this stratification reduces the likelihood of human tampering with sites during data collection and ensures that we were sampling from sites that received minimal levels of recent human disturbance. Finally, we selected sites non-randomly to ensure observation could be made in multiple canyons across the broader landscape.

Soils were derived from sedimentary parent materials at all sites (Table 3.1). Soil texture analysis revealed that all soils were loam or sandy loam. Soils were also well-drained and rocky. The Soldier soil series is the most common type, and is present on all sites; this soil series is composed of cherty limestone and sandstone from the Kaibab formation, and typically underlies forests with high timber value (Soil survey staff, NRCS 2015). The Palomino series (high productivity), Clover series (high productivity), and Rockland series (low-moderate productivity) were also present on our sites (Soil survey staff, NRCS 2015). Three of our four sites had site indices (for *Pseudotsuga menziesii,* following the methods of Edminster et al. 1991) exceeding 26m with a base age of 100 years. The least productive site (West Leonard) showed evidence of past insect and pathogen damage with overstory mortality for small proportions of larger *Pseudotsuga menziesii*, leading to few options for proper "site trees." Dils et al. (2015) report that mortality of *Pseudotsuga menziesii* from Douglas-fir beetle (*Dendroctonus pseudotsugae*) has been common on this part of the Mogollon Rim in recent years. For these reasons, the site index (of 18.2m) on the West Leonard site may be under-representing the actual growth potential on the site. However, this site also had a substantial component of the Rockland soil series, the least productive soil type on our sites. A more thorough description of site differences and soil conditions can be found in Table 3.1. All analyses of soil texture, structure, and macro and micronutrient composition were performed by the Environmental Analysis Laboratory at Brigham Young University, Provo, UT, USA, in the spring of 2015.

Mean elevation of the sites is approximately 2300m. Annual precipitation, averaging 84.5cm, is bi-modal, with the majority falling in the summer monsoon (July-September), or as winter snowfall (December-February; PRISM Climate Group, 2004). Annual temperatures range between 3.5 (avg. min) and 15.5 (avg. max) °C; temperatures are typically warmest in June and July, and coolest in January and February (PRISM Climate Group, 2004) with diurnal shifts of 15°C or more. Our sites had nine tree species present: *Abies concolor* var. *concolor* (Gordon) Lindley ex Hildebrand, *Acer grandidentatum* Nutt., *Pinus ponderosa* var. *scopulorum* (Engelm.), *Pinus strobiformis* Engelm., *Populus tremuloides* Michx., *Pseudotsuga menziesii* var. *glauca* (Mayr) Franco, *Quercus gambelii* Nutt., *Robinia neomexicana* A.Gray, and *Salix scouleriana* Barratt ex Hook. (Table 3.2). We also identified *Acer negundo* L., *Juniperus depeana* Steud., *Juniperus scopulorum* Sarg., and *Pinus edulis* Engelm. beyond the site boundaries but in the immediate area.

Timber harvests began in this portion of Coconino National Forest in the late 1950's and proceeded through the late 1980's, with more limited harvest occurring to current day (B. Greco, personal communication, November 15, 2014). Early harvests focused on the removal of large conifers, but later harvests attempted to create a two-aged structure by removing both large and small conifers and facilitating the growth of a new cohort in the understory (B. Greco, personal communication, November 15, 2014). Sanitation treatments to remove trees infected by dwarf mistletoe (*Arceuthobium* spp.) were also common (B. Greco, personal communication, November 15, 2014). For all analyses, we assumed a single harvest year of 1982 on the Hi Fuller, East Barbershop, and West Leonard sites, and two harvests (1960 and 1980) on the the East Bear site. These years were based on visual analysis of release years on increment cores adjacent to cut stumps. O'Reilly et al. (2015) later quantified harvest on the sites (see Results, Objective 2) using growth release data.

Field Data Collection and Laboratory Methods

Field methods were a slight variation of those used by Fulé et al. (1997) and adapted for spatial analysis by Moore et al. (2004) and Sánchez Meador et al. (2011). On each of four sites, we established a 100m x 100m square fixed-area plot. O'Neill et al. (1996) recommend that study extent should be at least 2-5 times the size of the patches being measured; group sizes reported in previous studies of dry mixed-conifer spatial pattern in the West rarely exceed 0.3 hectares (Larson et al. 2012, Churchill et al. 2013, Appendix-Table 1).

On each site, we collected data for all live trees taller than 1.37m (breast height), and for every historical remnant (stump, log, snag, or stump hole) greater than 20cm or 15cm in diameter (for conifers and hardwoods, respectively). Runs of the Bakker et al.

(2008) historical reconstruction model (see “Data Analysis - Objective 1…”) predicted that any historical remnants smaller than these sizes were not present prior to Euro-American settlement (based on dendrochronological data across many similar sites in the Southwest and an exponential decay model). We measured diameter at breast height (DBH, 1.37m above ground level) for all live trees and diameter at stump height (0.4m above ground level) for all historical remnants. For each live tree and historical remnant, we also identified species, and recorded condition class following Thomas et al. (1979) and Waddell (2002). Condition classes were as follows: live, declining, recent snag, loose-bark snag, clean snag (no bark), snag broken above breast height, snag broken below breast height, downed and dead (log), cut stump, and stump holes. For historical remnants, we identified tree species using a combination of bark characteristics, limb structure, wood density, wood scent, and adjacent overstory species composition.

For all “large trees” (live hardwoods greater than 20cm and live conifers greater than 40cm), and for a random sample of small live trees (smaller than above cutoffs; 10% of *Abies concolor* and 20% of all other species), we also measured diameter at stump height (40cm above ground level) and collected two crown radius measurements (long and short sides of the tree crown). Sampling rates were the same as those presented by Fulé et al. 1997, but *Abies concolor* was sampled at a lower rate because of its widespread abundance at each site. For large live trees and the sample of small live trees, we collected increment cores at 40cm above ground level. More accurate tree ages can be obtained by coring closer to ground level, but age data is used in conjunction with measured tree size to determine historical tree size (Bakker et al. 2008); tree size shows large variation below 40cm due to butt swell (Fulé et al. 1997). We used these data (of tree age) to develop species-specific growth rates for historical reconstructions. Finally, we determined the spatial location of all live trees and historical structures using an Impulse 400 surveying laser and Mapstar compass (Laser Technology Inc., U.S.A.), with accuracy within 0.1m and 0.1°, respectively.

We mounted, surfaced and cross-dated all increment cores in the laboratory according to standard dendrochronological techniques (Stokes and Smiley 1968). If increment cores were partially rotten or did not intersect pith (tree center), we estimated the number of rings to pith using a transparent estimator sheet (Applequist 1958). Cores that were not within 10 years of pith were excluded from the age analysis.

Data Analysis – Objective 1, Describe the spatial and temporal dynamics of dry mixed-conifer forests on the Mogollon Rim, AZ, USA

We reconstructed stand structure, species composition, and spatial pattern using the historical reconstruction model of Bakker et al. (2008). Huffman et al. (2001) demonstrated that an earlier version of this model has minimal bias in reconstructing historical forest structure in the Southwest. For all analyses, we reconstructed forest conditions in 1879, the year of widespread fire exclusion in the area (Huffman et al. 2015). We assumed that this was the time at which forest structure and processes began to deviate from the NRV. Additionally, we reconstructed forest conditions for 1910 (30 years after fire-exclusion) and for 1983 (immediately after most timber harvests) to quantify the relationships between tree recruitment, established overstory trees, and harvested areas.

The reconstruction model of Bakker et al. (2008) relies on a combination of dendrochronological data, species-specific size-age relationships calculated across many sites in the Southwest, and exponential models of wood decomposition. When the pith of increment cores predated 1879, we used the proportional reconstruction method described by Bakker (2005) to determine tree size in 1879. Any trees with establishment dates after 1879 were not considered to have been present in the 1879 reconstruction. For trees without age data, and for all historical remnants, historical tree size was predicted using species-specific backgrowth models. These predictive models "backgrow" trees beginning at the year of data collection (2014; for live trees), or at the estimated death year (based on exponential decay models; for historical remnants.) These methods of historical reconstruction are further described by Bakker et al. (2008).

We calculated the number of live trees ha^{-1}, the amount of live basal area ha^{-1}, percent canopy cover, quadratic mean diameter (QMD), and Reineke's stand density index (Reineke 1933) as measures of absolute and relative forest density for 1879 and 2014. All metrics provided are for trees > 5cm DBH. Stand density index (as provided) is the number of 25.4 cm trees ha^{-1} as a function of the total number of live trees ha^{-1} and the QMD. We also estimated canopy cover using the buffer and clip tools in ESRI ArcGIS 10.2. (ESRI 2011). We defined canopy cover as the proportion of the total plot area covered by measured or estimated tree crowns. When not measured (and for all historical trees) we estimated crown size using species-specific non-linear regressions of tree diameter to crown radius. We developed the fitted model for *Populus tremuloides* from data on the San Francisco Peaks, AZ, USA (n=32, Sánchez Meador et al. *unpublished data*), because of sample size limitations on the Mogollon Rim (n=6). Sample size used for model development ranged 27-363 for all species (Appendix-Table 4). Models of diameter to crown radius for all coniferous species had R^2 values of 0.76-0.89. Models for hardwood species had R^2 values of 0.19-0.34. Though model fits for hardwood species were poor, these equations were still used because residuals for the predictive models did not demonstrate heteroscedascity. Including nearest neighbor distance or height as additional variables in multiple regression models did not significantly improve model fit.

We examined changes in species composition using ecological importance value (EIV), a measure of relative species dominance on a site determined by combining the measurements of basal area and live trees (by species) into one standardized metric (Curtis and McIntosh 1951). Our method differs from the original EIV method of Curtis and McIntosh (1951) because it does not incorporate presence/absence across multiple sites as a third variable of species dominance. Our formula was as follows:

$$EIV(X) = \left[\frac{\#\ live\ trees\ of\ species\ X}{\#\ live\ trees\ of\ all\ species} * 100\right] + [\frac{live\ basal\ area\ for\ species\ x}{live\ basal\ area\ for\ all\ species} * 100]$$

where X is the target species of analysis, and EIV is the ecological importance value for species X on a given site.

We also created stem maps and diameter distributions for each site for both 1879 and 2014, and contemporary standing age distributions for each site. Because we did not collect age data for all live trees on all sites, age distributions were estimated by multiplying the number of trees sampled in each 10-year bin by an expansion factor (based on the number of trees dated out of the total sampled). We did not correct for the time needed to grow to 40cm in height, which probably varies by species and site.

To determine how historical conditions on our sites relate to the established NRV, we combined the results of all studies of reference conditions summarized in Reynolds et al. (2013), or completed more recently (Matonis et al. 2013), that reported both tree density (trees ha^{-1}) and basal area (m^2 ha^{-1}) for a given site. We developed 95% confidence intervals for historical and contemporary conditions of the previous studies meeting these qualifications, and compared the findings from our sites to these intervals.

We used a combination of spatial analyses to quantify mean patterns at the site extent and the range and variability of fine-scale structural elements for both 1879 and 2014 (individual trees, small groups, and large groups; Anselin 1995, Larson and Churchill 2012). We also examined spatial autocorrelation of size and species to gain further insight into the ecological function of these ecosystems. All spatial analyses for this project were completed in the R environment (R Core Team, 2014). Specifically, we used the “spatstat” package (Baddeley and Turner 2005) for point pattern analysis, and the “spdep” package (Bivand 2014) for tests of spatial autocorrelation.

1. Average Patterns at the Site Extent

To characterize global spatial patterns at the site extent, we calculated the Clark and Evans (1954) R index for all trees (>5cm) on each site for both 1879 and 2014. Clark and Evans R, a first-order point pattern statistic, is a ratio of the average nearest neighbor distance of a given pattern to the expected distance of a Poisson point process with the same density (Clark and Evans 1954). For each site, we also performed one-sided significance tests for the R index based on 999 Monte Carlo simulations of complete spatial randomness (CSR). For this test, H_a: R index less than under simulations of CSR, indicating significant aggregation of events. P-values for this test are given as the rank of the observed R index among the R indices for the 999 simulations of CSR divided by 1000 (number of simulations plus the observed pattern). We corrected for edge effects in this analysis using a guard correction (i.e., reduced sample; Baddeley and Turner 2005). The tested extent was the outer boundary of the plot minus the maximum observed nearest neighbor distance for the given dataset (on all sides).

As a further measure of spatial pattern that incorporates changes in scales at the site extent (second order), we performed univariate Ripley's K analyses (Ripley 1977) following the L transformation of Besag (1977). Though the paired correlation function (PCF; Stoyan and Stoyan 1994) has seen increased use recently because of its ease of interpretation (e.g. Fry et al. 2014), the Ripley's K analysis allows direct comparison to a greater number of published studies (Larson and Churchill 2012), and both tests are statistically valid if interpreted correctly (Baddeley et al. 2014). For each point pattern, we tested for homogeneity (trees equally likely to be present on majority of site; an assumption of the Ripley's K analysis) using the spatial scan test at a radius of 16.5m (Kulldorff 1997). This radius, derived from analysis of a 1x1m LiDAR-derived DEM, corresponds to the size of drainages or changes in slope on each site that might result greater densities in parts of a given site, and, therefore, an inhomogeneous pattern.

To develop confidence envelopes for each Ripley's K analysis, we performed 999

Monte Carlo simulations of complete spatial randomness. The upper and lower bounds of these pointwise envelopes are the 2.5th and 97.5th percentile values (of simulations and the observed pattern) at each distance in the test interval. We performed these tests at distances of 0-50m with 1m breaks. To determine if aggregation was statistically significant (for a given pattern) we used the Diggle, Cressie, Loosmore, and Ford (DCLF) goodness of fit test (described in Loosmore and Ford 2006). We used a one-tailed test between 0 and 30m, corresponding to the range of reported patch sizes in southwestern ponderosa pine forests (Reynolds et al. 2013) and the minimum and maximum observed patch sizes in dry mixed-conifer forests in the West (North et al. 2007, Matonis et al. 2013). Patterns were determined to be significantly different from random (rejecting the null hypothesis of complete spatial randomness) if p-values for the DCLF test were < 0.05. For any site-level patterns demonstrating significant aggregation, we also fit a model of a Matérn cluster process (using minimum contrast methods) to the given point pattern (Matérn 1960; as used in Baddeley et al. 2014). Fitting this model allows for the estimation of mean patch sizes in the given dataset (Baddeley et al. 2014). To correct for edge effects in the Ripley's K analyses, we used isotropic edge correction (Ripley 1988), which reduces the weight of points adjacent to the site boundary to the overall pattern.

We performed global and local Moran’s I analysis for all trees by diameter in both historical and contemporary datasets (Cliff and Ord 1981). These analyses determine if trees of similar size are growing in close proximity to one another (global), and the scale at which this occurs (local). We determined p-values for these analyses with 999 random permutations of the original observed pattern; p-values were one-sided, and were the rank of the observed pattern within the 999 simulations divided by 1000. Lower ranks showed greater relative autocorrelation. We also performed local Moran's I analyses (for both contemporary and historical diameter) for trees on each site, producing autocorrelograms. For each autocorrelogram, p-values (at each 2m lag distance of 2-50m) were adjusted for multiple comparisons using the Bonferroni method (Bonferroni 1938; p=observed p * number of comparisons).

2. Range and Variability of Fine-Scale Structural Elements

Many previous studies of tree spatial pattern have focused solely on stand-scale patterns and average patterns across study areas (Larson and Churchill 2012). Ripley's K analysis can help to infer the mean patch size if a pattern displays aggregation, but does not describe the range and distribution of group sizes (Larson and Churchill 2012, Reynolds et al. 2013). We used a group delineation method first employed by Larson and Churchill (2008) and developed from the continuum percolation method of Plotkin et al. (2002). With this method, trees must be within a given lag distance of another live tree to be considered part of a group. To determine group membership we used a 6m lag distance, following Sánchez Meador et al. (2011). In addition, we used measured and estimated crown radii to determine group membership. This “crown radius method” projects circular buffered polygons onto each tree based on measured or estimated crown radius and determines if overlap occurs between adjacent crowns. The crown radius method simply assumes that any trees with overlapping crowns are part of a given group. A combination of both patch delineation methods is useful for two reasons: 1) the biological definition of tree groups involves contiguous groups of trees with interlocking crowns, and is not solely based on distance between trees (Reynolds et al. 2013), and 2) models are inherently imperfect and exact reconstruction of tree size and crown radius is unlikely (Sánchez Meador et al. 2010), so point proximity (without weighting by tree size) can be a useful metric to identify biological interactions.

To correct for edge effects, we used a “reduced sample” method for all patch delineation procedures (similar to Lydersen et al. 2013). To perform this correction, we created an interior buffer 10.6m within the site boundary. This distance corresponds to the maximum observed crown radius measurement on any tree on our study sites, and reduces the impact of tree crowns outside the plot perimeter. To be included in the final tally, an individual tree must be within the buffered plot area. Tree groups are removed from the analysis if they are entirely outside of the buffered area. Because very large tree groups may begin within the buffered area, continue through the buffer, and extend off the plot, it is possible that we are under-representing the size of some large tree groups (Lydersen et al. 2013).

We binned groups into three distinct size classes: single trees, small groups (2-4 trees), and large groups (5+ trees). These bin sizes were based on historical mean group sizes reported in Sánchez Meador et al. (2011) for southwestern ponderosa pine forests, and Lydersen et al. (2013) for mixed-conifer forests in the Sierra Nevada. Large groups were the same size or greater than the largest mean patch sizes reported in these two studies.

Data Analysis – Objective 2, Provide new information concerning the spatial relationships of trees both within and between species

For analysis of within-species patterns, we performed Univariate Ripley's K analysis for each of four different species groups: 1) hardwoods *(Acer grandidentatum*, *Quercus gambelii*, *Populus tremuloides*, and *Robinia neomexicana*), 2) conifer species with intermediate fire and shade tolerance (*Pinus strobiformis*, and *Pseudotsuga menziesii*), 3) *Abies concolor* only, and 4) *Pinus ponderosa*. Species were grouped because of relatively similar species silvics (Burns and Honkala 1990a, Burns and Honkala 1990b). For example, all hardwoods on our sites tend to re-sprout from shared root systems of other nearby individuals. These four analyses (for hardwoods, mid-tolerants, fire-intolerant/shade-tolerant *Abies concolor,* and fire-tolerant/shade intolerant *Pinus ponderosa*) provide information on four distinctly different functional groups that can be compared across multiple sites. We pooled results from each analysis (using the pool.envelope function in spatstat; Baddeley and Turner 2005) that had greater than 25 observations (for both 1879 and 2014 separately) to display the pattern for each species group; small sample sizes can produce abnormally large values of the test statistic at a given scale. This "pooling" of multiple samples produces a weighted mean envelope, where the weight for a given site is based on the number of points in each analysis divided by the total number of points in all analysis being pooled.

To analyze bivariate relationships between species groups, we performed a Monte Carlo permutation test (999 simulations) of the Join Count statistic (Cliff and Ord 1981). This analysis tests for spatial autocorrelation of binary variables (1=tree of a test species, 0=tree of any other species), and determines if members of a given species tend to intermix with other species or if they are spatially segregated (significant autocorrelation by species). We performed this analysis for each species in both historical and contemporary datasets, pooling the results of ranks within the simulations from each site with a weighted average. The weight for a given test was based on the number of individuals of species x on a given site, divided by the total number of species x across all sites. We then determined the p-value by dividing the weighted mean statistic by 1000 and subtracting the subsequent value from 1. For example, if weighted mean rank for all tests was 112, then *p*=0.888.

We also performed the Ripley's Bivariate K test (Lotwick and Silverman 1982) to understand the scales of attraction and inhibition between overstory trees and regeneration. We performed this test for the reconstructed 1879 overstory and first cohort after fire exclusion (1879-1910), and for the reconstructed 1983 overstory and the first cohort following timber harvests in the 1980's (1983-2014). For these analyses, we developed 95% confidence envelopes using 999 random shifts of regeneration relative to original overstory trees. These methods test the antecedent hypothesis of spatial dependence between overstory and regeneration (Goreaud and Pélissier 2003). We tested for significant interaction between the two types of points using the two-tailed variation of the Maximum Absolute Deviation test at all distances because we had no *a priori* estimate of interaction distance (Baddeley et al. 2014). We performed this analysis for recruitment of all species at each site, and performed separate analyses for individual tree species.

Finally, we used chi-square contingency analysis (Pearson 1900) to compare the distributions of different tree species across patch sizes. We used this analysis to determine the likelihood of individuals of a given species being isolated single trees, members of small groups (2-4 trees), and members of large groups (5+ trees). In this analysis, we combined results from both patch delineation methods (6m fixed distance and crown overlap) into one matrix and divided the matrix by two, thus giving each delineation method equal weight without artificially increasing sample sizes. We compared observed group membership to expected group membership for each species across all sites in 1879 and 2014 (H_a: interaction between species and group membership for a given tree). Following recommendations in Frankfort-Nachmias and Leon-Guerrero (2011), we only performed this analysis for species that had at least two observations per cell (single tree, small group, large group), and ensured that at least 80% of all cells had at least five observations. These restrictions satisfy assumptions of sample-size that can influence the analysis (Frankfort-Nachmias and Leon-Guerrero 2011). Species meeting these restrictions in the 1879 reconstruction are: *Abies concolor, Pinus ponderosa, Populus tremuloides, Pseudotsuga menziesii,* and *Quercus gambelii*. Only *Salix scouleriana* and *Populus tremuloides* were excluded in the analysis of contemporary (2014) group membership. We acknowledge that removing species from the analysis can have influences on subsequent results.

If chi-square analysis revealed statistically significant differences between observed and expected values ($\alpha=0.05$), we also performed post-hoc analysis by comparing standardized Pearson Residuals to the critical threshold of the distribution (also with $\alpha=0.05$), thereby determining if the deviation was significantly different than the expected value for a given cell (Agresti 2002). We performed this post-hoc analysis using the “polytomous” package (Arppe 2013) in R.

Our null hypothesis for all tests was “no relationship”, or “no difference from complete spatial randomness.” We hypothesized (H_{a1}) that *Abies concolor* would have a greater propensity to grow in mixed species groups and in larger groups because of its shade tolerance and intolerance of fire. We also hypothesized (H_{a2}) that *Pinus ponderosa* would grow in small groups and as isolated single trees, showing a greater propensity to grow in a spatially segregated manner, in openings and away from individuals of other species. Finally, due to vegetative reproduction strategies (Burns and Honkala 1990b), we hypothesized (H_{a3}) that hardwood species would be more likely to be members of groups and would show significant autocorrelation by species.

Case Studies vs. Replicates

Because of the variability in Southwestern dry mixed-conifer forests, and between our sites, we present many of the analyses for the sites independently and use standard deviation to describe the spread between sites rather than standard error. In this sense, our four sites are four independent case-studies within dry mixed-conifer ecosystems of the Southwest. For certain spatial analyses, for example in describing species-specific spatial patterns, the sites were pooled to combine all individuals of a given species. In these cases, the questions being asked relate to the overall pattern of a given species and sites are treated as replicated samples from a larger population.

Results

Objective 1 – Density and Structure

Overall tree density (for trees > 5cm dbh) increased markedly on each of our sites between 1879 and 2014 (Figure 3.2-West Leonard site only, Table 3.3-all sites). Estimated historical densities were between 80-159 live trees ha^{-1} (mean=129.5, standard deviation or sd=35.1) and 4.9-13.0 m^{2} of basal area ha^{-1} (mean=10.1, sd=3.5). Contemporary densities were between 427 and 1069 live trees ha^{-1} (mean=744.3, sd=295.3) and 36.9-44.6 m^{2} of basal area ha^{-1} (mean=41.9, sd=3.4). Canopy cover also changed drastically between 1879 and 2014. We estimate that historical canopy cover was between 8.7 and 17.5 percent (mean=14.8, sd=4.2). In 2014, canopy cover was consistently high across all sites, with a range of 51.0-56.7 percent (mean=54.7, sd=2.5). East Barbershop (159 trees ha^{-1}, 11 m^{2} of basal area ha^{-1}, 17.5 percent canopy cover), East Bear (149 trees ha^{-1}, 13 m^{2} of basal area ha^{-1}, 17.3 percent canopy cover), and Hi Fuller (130 trees ha^{-1}, 11.4 m^{2} of basal area ha^{-1}, 15.8 percent canopy cover) had higher historical densities, and West Leonard had the lowest historical density (80 trees ha^{-1}, 4.9 m^{2} of basal area ha^{-1}, 8.7 percent canopy cover).

Quadratic mean diameter did not change dramatically over this time period. In 1879, mean QMD (for all sites) was 31.1 cm (sd=2.7). In 2014, mean QMD was 28.2 cm (sd=6.6). Contemporary diameter distributions follow the a “reverse j” pattern with progressively fewer trees in larger size classes. Historically, the diameter distributions showed an irregular uneven-aged structure. The majority of live standing trees established in the decades following 1879 (e.g. Hi Fuller Site, Fig. 3.3e). Sampling rates to make these conclusions are relatively high. Of 1204 increment cores sampled, 862 were within 10 years of intersecting pith. We successfully dated 16.9% of all live trees and 63.2% of all large live trees (conifers greater than 40cm and hardwoods greater than 20cm) on the sites.

Objective 1 – Species Composition

Fire-intolerant and shade-tolerant species have increased in relative abundance when compared to historical levels (Figure 3.3). On the Hi Fuller, East Bear, and West Leonard sites, *Pinus ponderosa* was the most dominant species historically (EIV values: 105.5, 133.8, 108.2, respectively). Hi Fuller and East Bear also had relatively high levels of *Quercus gambelii* (EIV 38.4, 24.4), and only minor components of *Abies concolor* and *Pseudotsuga menziesii.* East Barbershop, a more mesic site, was dominated by a mixture of *Quercus gambelii* (EIV 65.2), *Abies concolor* (EIV 44.4), and *Pinus ponderosa* (EIV 38.9) in the 1879 reconstruction, with minor components of *Populus tremuloides*, *Pseudotsuga menziesii*, and *Acer grandidentatum*. Contemporarily, *Abies concolor* and *Pseudotsuga menziesii* are the dominant species on Hi Fuller, East Barbershop, and West Leonard. *Pinus ponderosa* is still the most prevalent species on the East Bear site.

Shortly after 1879, the assumed year of fire-exclusion, early-seral and shade-intolerant species (*Pinus ponderosa* especially) successfully regenerated, occupying growing space (e.g. Hi Fuller Site, Figure 3.2e). Between 1900 and 1920, all sites showed a shift in recruitment to mid-tolerant *Pseudotsuga menziesii* and shade-tolerant *Abies* *concolor*. Following timber harvests in the 1960's and 1980's, there was again a peak in shade-intolerant recruitment (e.g. Hi Fuller Site, Figure 3.2e).

Objective 1 - Average Patterns at the Site Extent

Based on Clark and Evans R analyses, only one of our sites, East Barbershop, demonstrated statistically significant aggregation historically (R=0.7732, p<0.0001). Patterns on the Hi Fuller (R=0.9655, p=0.315), East Bear (R=0.9541, p=0.219), and West Leonard (R=1.1, p=0.767) sites were not significantly different from CSR. Contemporary distributions of live trees showed statistically significant aggregation on East Barbershop (R=0.7934, p<0.0001), and West Leonard (R=0.91, p<0.001) sites, but were not different from random on Hi Fuller (R=1.00 p=0.566) or East Bear (R=1.05, p=0.939) sites.

Ripley's K analyses (Fig. 3.5) revealed multiple scales of aggregation historically and contemporarily, suggesting that trees grew in groups of varying sizes. Hi Fuller, East Bear, and East Barbershop showed statistically significant aggregation in the 1879 reconstruction, with mean patch sizes of 0.115, 0.052, and 0.002 hectares (respectively). West Leonard did not exhibit significant deviation from the confidence envelopes of CSR, but showed a trend towards aggregation at about 10m. All sites had patterns that exhibited aggregation in 2014, primarily with very small mean patch sizes. Hi Fuller, East Bear, East Barbershop and West Leonard all have contemporary mean patch sizes less than 0.05 ha (see Figure 3.4).

Global Moran's I analyses revealed that groups on the sites likely had a mix of tree sizes historically (no significant spatial autocorrelation by size; p-values: Hi Fuller=0.451, East Bear=0.294, East Barbershop=0.494, West Leonard=0.966). Contemporarily, three of four sites exhibit statistically significant autocorrelation by size (α=0.05; p-values=East Bear=0.002, East Barbershop=0.001, West Leonard=0.004). Hi Fuller was not autocorrelated by size. Local Moran's I analysis provided no substantial insight into the scale at which these relationships occur (Figure 3.5, Appendix-Figures 4-6). Only the East Barbershop site demonstrated statistically significant autocorrelation (α=0.05) at multiple lag distances (see Figure 3.5b). This site had even-sized patches (in 2014) that were 4-26m in radius.

Objective 1 - Range and Variability in Fine-Scale Structural Elements

We found considerable variability in the tree group sizes between methods used (6m fixed distances, and crown delineation) and between sites (see Table 3.4). The use of a fixed 6m distance tended to predict that a greater number of trees were members of groups than the method based on crown overlap. Based on the 6m fixed distance, the largest tree group (historically) was 18 trees (on East Barbershop). Based on crown overlap, the largest group on any of the sites (historically) was 9 trees (on East Bear).

Historically, mean group sizes ranged from 1.4-3.3 trees (Table 3.4). In 2014, the majority of trees were in large groups across all sites, and mean group sizes ranged from 5.5-311 trees (Table 3.5). The maximum group size in 2014 was 367 (for the crown overlap method) to 621 (for the 6m fixed distance method; Table 3.5). More productive sites and those with an important component of hardwoods had larger mean group sizes (e.g. East Barbershop). Our least productive site (West Leonard) was dominated by individual trees and small groups.

Objective 2 - Average Patterns at the Site Extent by Species/Functional Group

Species groups demonstrated differing spatial patterns at multiple scales, as is reflected in the results of Ripley's K analysis (Figure 3.6). *Abies concolor,* the most shade tolerant/fire-intolerant conifer on our sites, exhibited increasing aggregation to 3 meters historically and was random beyond this distance (Figure 3.6a). This species did not exhibit statistically significant aggregation in 1879 based on the goodness of fit test for the model of CSR ($p=0.32$). *Abies concolor* patterns were aggregated in 2014 ($p<0.01$), with the peak in aggregation at 10m (Figure 3.6e). Mid-tolerant species (*Pseudotsuga menziesii* and *Pinus strobiformis*) had a slightly different pattern (Figures 3.6b and 3.6f). Historically, individuals of these species (like *Abies concolor*) showed a trend toward aggregation at short distances but were random at most scales ($p=0.62$). Contemporarily, aggregation for these species was significant ($p=0.04$) and occurred at finer scales (than *Abies concolor*) suggesting small groups of two-three adjacent trees. *Pinus ponderosa* showed significant aggregation historically (p-value=0.01; Figure 3.6c). Peaks in aggregation for this species occurred at scales of 6-10 meters. *Pinus ponderosa* species had a random distribution in 2014 ($p=0.48$; Figure 3.6g). Hardwood species in the analysis showed little evidence of aggregation in 1879 ($p=0.26$; Figure 3.6d), but high levels of aggregation across all scales in 2014 ($p<0.01$; Figure 3.6h). Historical hardwood patterns were driven (primarily) by *Quercus gambelii* and *Populus tremuloides;* contemporary patterns were driven by a mixture of species including: *Quercus gambelii, Acer glabrum,* and *Robinia neomexicana.*

Join count analysis revealed that species groups also differed in respect to their level of spatial autocorrelation (tendency to grow in close proximity to individuals of the same species). *Abies concolor* individuals did not exhibit significant autocorrelation by species either historically (p=0.80) or contemporarily (p=0.82). Mid-tolerant species were intermixed with other species, and did not demonstrate substantial repulsion or attraction (p=0.55) historically. Though not significantly so, mid-tolerant individuals tended to grow in close proximity to one another and away from individuals of other species in 2014 (p=0.14). However, *Pinus strobiformis* and *Pseudotsuga menziesii* differed in their historical patterns of interspecific interaction. *Pinus strobiformis* showed statistically significant spatial autocorrelation by species in 1879 (p=0.02), while *Pseudotsuga menziesii* was not spatially autocorrelated (p=0.74). *Pinus ponderosa* demonstrated no spatial autocorrelation historically (p=0.47), but exhibited increased (albeit insignificant) spatial autocorrelation in 2014 (p=0.20). Historically, hardwoods showed insignificant spatial autocorrelation (p=0.24), and were more autocorrelated in 2014 (p=0.12).

Objective 2 - Patterns of Recruitment 1879-1910

As shown in Figure 3.7, tree recruitment between 1879 and 1910 was either attracted to, or randomly distributed around, existing overstory trees (from the 1879 reconstruction). Recruitment on Hi Fuller and East Barbershop, the two sites that have the highest proportion of shade-tolerant species, was attracted to the established overstory at most scales, though this trend was not statistically significant on the East Barbershop site (Hi Fuller: p=0.03, East Barbershop: p=0.12). East Bear and West Leonard showed no strong relationships between the 1879 overstory and the first cohort after fire exclusion.

Objective 2 - Patterns of Recruitment 1983-2014

There were 423 cut stumps on our sites, or 6.2% of all trees and remnants sampled. *Pinus ponderosa* (193 stumps), *Pseudotsuga menziesii* (120 stumps) and *Abies concolor* (96 stumps) were the most intensively harvested. There were also 12 *Quercus gambelii* and 2 *Pinus strobiformis* stumps on the sites. Average size of stumps (at 40cm above ground level) was highest for *Pinus ponderosa* (40.27 cm), Quercus gambelii (36.98 cm), and Abies concolor (33.47 cm), and was lower for *Pseudotsuga menziesii* (29.76 cm) and *Pinus strobiformis* (24.5 cm). Harvests were evenly distributed across sites, 76 stumps on East Barbershop, 141 stumps on West Leonard, 90 stumps on Hi Fuller, and 116 stumps on East Bear. Harvests appeared to be targeting ridges and flatter areas rather than steep slopes. O’Reilly et al. (2015) quantified growth releases for unharvested trees on our sites and found releases (that are likely attributed to timber harvests) in 1969 and 1988 and an earlier release in 1910. The 1910 release is likely due to a factor besides harvesting (B. Greco, personal communication, November 15, 2014). Harvests of large *Pinus ponderosa* may have also contributed to shifts in species composition on our sites between 1879 and 2014.

The relationship between stumps and successful regeneration following timber harvests shows a similar trend (Figure 3.8) to that displayed by recruitment between 1879 and 1910. Recruitment between 1983 and 2014 showed an attraction to the established overstory, especially at distances less than 10m (Figure 3.8, a-c), and regeneration occurred away from cut stumps (Figure 3.8, d-f). Figure 3.10 describes this relationship by species group. *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Quercus* gambelii, all either shade-intolerant or mid-tolerant species, were neither attracted to, nor repulsed by, stumps. Though *Pinus strobiformis* recruitment does show some statistically insignificant fine-scale attraction to stumps, this relationship is random at most scales. *Abies concolor* and *Acer grandidentatum*, two very shade tolerant species, tended to regenerate in areas that were not harvested. Perhaps most surprisingly, *Robinia neomexicana*, a known gap-invader, did not appear to regenerate near stumps.

Objective 2- Range and Variability in Fine-Scale Structural Elements, by Species

Species was an important factor in influencing the proportion of trees in different group sizes; proportions of trees as individuals, small groups, and large groups deviated significantly from expected values in the 1879 dataset (X^2=44.45, $p<0.0001$; Table 3.5). Individuals of the other species were excluded because of sample-size limitations. Post-hoc analysis revealed that *Pinus ponderosa* was significantly more likely to be found as isolated single trees than other species (standardized Pearson residual=2.42, $p<0.05$), and in large groups less frequently than other species (standardized Pearson residual=-3.12, $p<0.05$). *Quercus gambelii* were significantly less likely to be found as isolated individuals than other species (standardized Pearson residual=-3.16, $p<0.05$). No other species analyzed showed statistically significant deviations from expected values, but *Abies concolor, Populus tremuloides,* and *Quercus gambelii* trended towards membership in large groups historically (Table 3.5). *Pseudotsuga menziesii* showed no clear trends in group membership. In 2014, greater than 89% of all trees were present in large groups, and there did not appear to be any evidence of a relationship between species and group membership (X^2=2.5129, p=0.64; Table 3.6).

Discussion

Forest structural changes have occurred in many dry mixed-conifer forests of the Southwest since Euro-American settlement, leading to functional changes in these ecosystems (Fulé et al. 2002, Mast and Wolf 2004, Heinlein et al. 2005, Fulé et al. 2009, Huffman et al. 2015). These relationships can be partially exhibited through the spatial interactions between individual trees. With this project we had two primary objectives: 1) describe the spatial and temporal dynamics of dry mixed-conifer forests on the Mogollon Rim, AZ, USA, and 2) provide new information concerning the spatial relationships of trees both within and between species. Objective 1 is focused on overall trends and patterns, while objective 2 is focused on niche differentiation between species groups and its relationship with spatial pattern.

Objective 1 - Describe the spatial and temporal dynamics of dry mixed-conifer forests on the Mogollon Rim, AZ, USA

Our sites, as a whole, were not significantly different from previous studies of the NRV for dry mixed-conifer forests in the Southwest (Figure 3.10). The 95 percent confidence intervals for these previous studies of the NRV stretch between 7 and 23 m^2 of basal area ha^{-1}, and 25-200 live trees ha^{-1}. West Leonard, our least productive site, is the only site that deviates outside of these confidence intervals with 4.9 m^2 of basal area ha^{-1} (with 80 live trees ha^{-1}, the site does not deviate from the interval for live trees ha^{-1}). The West Leonard site has the lowest historical density of any reconstructed dry mixed-conifer site in the Southwest.

Management based on the NRV should reduce forest densities in many of these fire-prone ecosystems in the Southwest and focus on retaining species that were dominant historically such as *Pinus ponderosa* and *Quercus gambelii.* Less fire-tolerant species were present as well, though these species (notably *Abies concolor*) were less prevalent than they are today. Mean and maximum tree group size both increased between 1879 and 2014, aligning with the findings of other studies of mixed-conifer forests in the West (e.g. Churchill et al. 2013, Lydersen et al. 2013).

Based on Ripley's K analysis, three of four sites were significantly aggregated in 1879, suggesting that silvicultural treatments focusing on the retention of tree groups may best mimic the NRV in productive dry mixed-conifer forests on the Mogollon Rim, AZ. Tree spatial patterns might exhibit aggregation for any number of reasons. Past work has suggested that patch formation can occur in open areas of bare mineral soil after local disturbance (Stephens and Fry 2005, Sánchez Meador et al. 2009, Larson and Churchill 2012). However, competition between seedlings and understory communities (Puhlick et al. 2012), and local environmental and soil characteristics (Abella and Denton 2009) also be important factors in creating an aggregated/patchy structure. Random patterns, also common in frequent-fire forests (Schneider 2012), can occur on productive sites with no substantial barriers to tree regeneration, though these findings (in ponderosa pine forests) differ from our results in the mixed-conifer forest type. The research area of Schneider (2012) appears to have a similar soil type and climate to those of our sites; the primary difference is the overstory species composition. The added overstory species present in mixed-conifer ecosystems likely alter the relationship between individuals, resulting in different spatial patterns and increases in ecosystem complexity (relative to ponderosa pine and pine-oak forests).

Forest canopy continuity increased and total open space decreased on our sites between 1879 and 2014. Though we did not directly quantify opening structure, discrete openings probably had an important role in the function of frequent-fire forests (Larson and Churchill 2012, Reynolds et al. 2013, Dickinson 2014). Our results showed that canopy gaps may have inhibited initial tree recruitment following fire exclusion and following timber harvests. These results are consistent with findings in other mixed-conifer forests in the West (North et al. 2004), but contrast strongly with some ponderosa pine forests in the Southwest (Sánchez Meador et al. 2009). Differences in findings may reflect variations in livestock grazing intensities that would have altered the competition between seedlings and the understory (Larson and Churchill 2012; Puhlick et al. 2012). The study area of Sánchez Meador et al. (2009) was closer to urban centers than our sites on the Mogollon Rim, and experienced continued cattle grazing into the early 1900’s.

Understory community composition may have also differed between ponderosa pine and mixed-conifer ecosystems historically because of differing overstory composition (Korb et al. 2007), slightly different disturbance regimes (Swetnam and Baisan 1996, Brown et al. 2001), and changes in available moisture in the understory. Patterns of tree establishment vary between species (Bigelow et al. 2011). Shade-tolerant individuals, when present, could more easily establish in the understory of established groups. This is less likely in ponderosa pine forests (Sánchez Meador et al. 2009; Puhlick et al. 2012), where trees tend to establish in small even-aged patches, in canopy gaps, and on bare mineral soil (Cooper 1961, Mast and Veblen 1999, Sánchez Meador et al. 2009).

Temporal trends in species dynamics on our sites reflect colonization by early seral species (such as *Robinia neomexicana* and *Pinus ponderosa*) when stand densities are low and growing space is plentiful. As densities increased, the successful regeneration of shade-tolerant and mid-tolerant species (e.g. *Abies concolor,* and *Pseudotsuga menziesii*) increased. These species are now the most dominant components of many dry mixed-conifer forests on the Mogollon Rim (this study, Huffman et al. 2015). Heinlein et al. (2005) and Fulé et al. (2009) suggest that *Pinus ponderosa* and *Populus tremuloides* have declined in relative dominance on their sites on the San Francisco Peaks and in southwestern Colorado (respectively). This is true of *Pinus ponderosa* in forests on our sites, but our results also suggested that *Populus tremuloides* may have only been a minor component of dry mixed-conifer forests on the Mogollon Rim historically. The frequent fire intervals and relatively warm temperatures on the Mogollon Rim (Huffman et al. 2015) may have made establishment of *Populus tremuloides* less successful than on other mixed-conifer sites in the Southwest. Our results contrast with studies on the San Francisco Peaks, AZ (Heinlein et al. 2005), Kaibab Plateau, AZ (Binkley et al. 2006, Vankat 2011), and the San Juan Mountains, CO (Fulé et al. 2009). Many of these studies used similar methodologies (to our study) and found a greater number of *Populus tremuloides* than were present on our sites.

Objective 2 - Provide new information concerning the spatial relationships of trees both within and between species

We had three hypotheses relating to species groups and their spatial pattern. H_{a1}: *Abies concolor* would have a greater propensity to grow in larger groups intermixed with other species, because of its shade tolerance and fire intolerance. H_{a2}: *Pinus ponderosa* would grow in small groups and as isolated single trees, showing a greater propensity to grow in a spatially segregated manner away from individuals of other species. H_{a3}: hardwood species would be more likely to be members of groups and would show significant autocorrelation by species.

Spatial patterns of *Abies concolor* were not significantly different from CSR. Individuals of this species tended to grow intermixed with other species and were more likely to occur in larger groups; however, these results were not statistically significant so we could not accept $H_{a1.}$ Lydersen et al. (2013) also identified a weakly positive association between *Abies concolor* and large group membership in the Sierra Nevada. Mast and Wolf (2004) demonstrated positive spatial associations between *Abies concolor* trees and *Pinus ponderosa* trees (in larger size-classes), suggesting that *Abies concolor* recruitment might have been facilitated by established groups of *Pinus ponderosa*. Successful tree regeneration for this species showed a weakly negative relationship with stumps and a positive relationship with established overstory trees. Cool, mesic, closed canopy microclimates are beneficial to tree recruitment for *Abies concolor* (Burns and Honkala 1990a).

Pinus ponderosa was significantly aggregated at scales < 30m historically, but did not exhibit significant spatial autocorrelation, suggesting that the species was often intermixing with individuals of other species. Therefore we could not accept H_{a2}, that this species grew in a spatially segregated manner. *Pinus ponderosa* requires large amounts of light for successful regeneration (Bigelow et al. 2011), and it is possible that seedling- and sapling-sized *Pinus ponderosa* would demonstrate greater spatial autocorrelation. This species also did not appear successfully regenerate in openings following fire exclusion or timber harvests. However, *Pinus ponderosa* were significantly more likely to grow as isolated individual trees and significantly less likely to grow in large groups (than other species).

Surprisingly, deciduous hardwood species did not show significant aggregation at any scales historically. This may be due to some inaccuracy in historical reconstruction of hardwood species (because of relatively quick decomposition rates), as recognized by Matonis et al. (2013). In 1879, *Quercus gambelii* were significantly less likely to be found as individual trees than other species analyzed, and they trended towards membership in small groups and large groups (though these findings were not statistically significant). Because of sprouting capability and limitations to more mesic microsites (e.g. *Acer grandidentatum*), it makes sense that many hardwoods on our sites would demonstrate aggregation and spatial autocorrelation, and results from our sites (contemporarily) support these hypotheses. The effect of frequent fire on many of these hardwood species is unknown, and additional research is needed in to hardwood ecology in forests of the Southwest.

Forest spatial patterns are the complex result of interactions between established overstory trees, the understory environment (Puhlick et al. 2012), disturbance history (Stephens and Fry 2005, Sánchez Meador et al. 2009), and autecological traits of individual species (Lydersen et al. 2013). Many species appear to have an inherent spatial pattern, but these patterns are also impacted by variations in soil, climate, and other factors across their distribution (Abella and Denton 2009). The interactions between species groups (Mast and Wolf 2004) and interspecific variations in response to disturbance events (Sánchez Meador and Moore 2010, Reynolds et al. 2013) are also important determinants of spatial pattern.

Heterogeneity of Pattern and Process in Dry Mixed-Conifer Forests

Overstory groups and open areas create very different microenvironmental conditions (Meyer et al. 2001) and may create variations in processes such as fire behavior (Fry and Stephens 2010). In the Front Range of Colorado, proximity to grasslands is thought to be an important driver of historical fire frequency, because of the abundance and continuity of fine fuels in these areas (Gartner et al. 2012). This influence on fire behavior may also be an important contributor to fine-scale structural heterogeneity in dry mixed-conifer forests of the Southwest. Frequent surface fires probably limited successful tree regeneration because it takes several years for seedlings and saplings to be able to tolerate surface fire (Bailey and Covington 2002). If grassy openings were more prone to frequent burning, then closed canopy groups might have provided safe sites for successful regeneration of species that could tolerate the lower light availability in this microenvironment. From the perspective of a seedling or sapling, frequent fire forests were areas of high relative stress, and facilitation was probably an important factor in determining the locations of tree recruitment (see Bertness and Callaway 1994). Fry and Stephens (2010) identified a negative association between *Pinus jeffreyi* canopies and fine fuels in the understory, even in areas that had not experienced surface fire events for at least two decades. These fuel dynamics might lead to the inhibition of surface fire immediately beneath these tree canopies. However, fire intensity (and related tree mortality) is often highest with low moisture levels in the duff layer (Varner et al. 2007) and fuel moistures are typically lowest between the stem and the dripline of established overstory trees (Hille and Stephens 2005). In the absence of fire, regeneration on our sites was positively associated with the established overstory, and negatively associated with harvested openings, but determining if this relationship holds true under an active fire regime requires additional study.

Mortality due to pathogens, insects, and parasitic plants could provide an explanation for the negative relationship between tree recruitment and openings. *Armillaria solidipies* (a common root disease) is known to affect as many as 30 percent of live trees in some mixed-conifer forests of the Southwest (Dils et al. 2015). Sanitation treatments could remove some of the infected individuals, but the pathogen is still present in the harvested opening. The continued presence of root disease may then limit successful tree establishment in these openings. Similarly, western spruce budworm (*Choristoneura occidentalis*) and dwarf mistletoes (*Arceuthobium* spp.) spread top-down, and can cause rapid mortality of small trees (Brookes et al. 1987, Castello et al. 1995, Conklin and Fairweather 2010). Dwarf mistletoes also spread more quickly in relatively open-canopied areas (Castello et al. 1995, Conklin and Fairweather 2010), such as from tree groups to adjacent canopy gaps. Browse by ungulates can also have important effects on seedlings and saplings (Fairweather et al. 2008), and may have limited tree recruitment in some areas.

Fine-scale heterogeneity provided a positive feedback loop in many western forests that led to further heterogeneity in disturbance and recruitment (Stephens and Fry 2005, Sánchez Meador et al. 2009, Fry and Stephens 2010, Larson and Churchill 2012). It is possible, then, that restoration of these structural conditions and a natural disturbance regime may prevent the need for multiple timber harvests to maintain resistance and resilience to future disturbance. Given the high costs of mechanical thinning, low value of wood products removed (Huang et al. 2013), and the detrimental impacts of harvesting (Ampoorter et al. 2012), it makes sense to minimize re-entry whenever possible. However, the incorporation of an active fire regime (e.g. Lydersen and North 2012) is something that may not be feasible under current federal policy (Stephens and Ruth 2005), or in all locations in the Southwest because of proximity to established development. Fulé and Laughlin (2007) suggested that prescribed or managed fire may accomplish the goals of forest restoration, though under certain circumstances this management strategy could cause unacceptable mortality of large, older trees (Fulé et al. 2004). The results of managed or prescribed fire on creating or maintaining fine-scale spatial structure of forests is a poorly understood concept. This is an important area for future work because mechanical thinning may be infeasible in many situations.

Stand-scale and fine-scale spatial patterns are important to incorporate into silvicultural treatments (Reynolds et al. 2013). Stand-scale patterns, or the average pattern at the extent of the management area, can be included as an overarching goal in silvicultural prescriptions; the fine-scale range and distribution of group sizes can then be used to develop marking guides, and as evaluation criteria for the success of these treatments. It also appears that individual species have unique roles in these patterns in mixed-species forests, an additional consideration for forest managers. Shade-tolerant conifers are more likely to be found in large groups than other species, and shade-intolerant conifers are less likely to be found in groups. Sprouting hardwoods also tend to grow in groups. We found no evidence to suggest that groups of trees had similar diameters, or consisted of individual species. Therefore, targeting a range of group sizes (1-18 trees or more), often with multiple species and with a range of tree diameters may most closely align with the natural ecology of these dry mixed-conifer ecosystems on the Mogollon Rim.

Study Limitations and Future Work

Our study has several limitations. We did not reconstruct every tree (specifically logs, snags, and stumps) using dendrochronological methods; snags, stumps, stump holes, and downed logs (from 2014) made up over half of the trees that were estimated to have been alive on our sites in 1879. Estimation of decomposition rates and models of tree size also provide compounding errors that may cause our results to deviate from actual historical conditions. Dendrochronological sampling of some snags, logs, or stumps may allow for model verification and validation in future studies (see Mast et al. 1999). Hardwoods may decompose more quickly than conifers (Matonis et al. 2013), and certain conifers may decompose more quickly than others (*Abies concolor*; North et al. 2007). Other studies have recognized these issues, and acknowledged that variations in decomposition rates may lead to bias in reconstruction (Fulé et al. 1997, Huffman et al. 2001, North et al. 2007, Matonis et al. 2013). Lastly, species identification for historical structures can be difficult in the field, especially without the presence of bark. These difficulties could lead to possible misidentification of some individuals.

Mortality of trees in the late 1800’s and early 1900’s might result in the loss of some historical remnants. Huffman et al. (2001) reported that approximately 6 percent of historical trees could not be located with dendrochronological reconstruction of ponderosa pine forests in the Southwest, and this could be due to decomposition, fire, or other factors that result in the loss of historical remnants. The loss of these historical remnants could be a larger concern in mixed-conifer forests, though little research has been done on this topic. In mixed-conifer forests on the north rim of the Grand Canyon, Vankat (2011) found that forest densities increased between the late 1800’s and 1935, but decreased between 1935 and 2014, primarily because of declines in densities of *Populus* *tremuloides*. These declines could be attributed to increasing ungulate browse, drought, and the exclusion of fire, and may have happened in other parts of the Southwest as well (Binkley et al. 2006, Fairweather et al. 2008). Given the relatively rapid decomposition of *Populus tremuloides* after ground contact (Hogg and Michaelian 2014), historical densities of this species are probably higher than predicted in many historical reconstructions of mixed-conifer forests (because of loss of remnants). These factors should be equivalent across most studies however, and our results showed lower densities of *Populus tremuloides* than were reported in other areas (Heinlein et al. 2005, Fulé et al. 2009). Loss of remnants due to management actions could also be a concern (Fulé et al. 1997), but harvesting began relatively late in this portion of Coconino National Forest (B. Greco, personal communication, November 15, 2014) and was probably not earlier than the late 1960's on any of our sites (O'Reilly et al. 2015). Many stumps present on our sites showed very little evidence of decay.

Early mortality (late 1800's, early 1900's) due to insects, pathogens, and parasitic plants could also lead to fewer historical remnants present in contemporary forests. Many of these factors, notably western spruce budworm (*Choristoneura occidentalis*) and dwarf mistletoes (*Arceuthobium* spp.) can cause rapid mortality in smaller trees (Brookes et al. 1987, Castello et al. 1995, Conklin and Fairweather 2010) that might decompose more quickly (than larger trees). Multiple outbreaks of *Choristoneura occidentalis* have occurred in the Southwest between the late 1800's and current day (Swetnam and Lynch 1993). This insect preferentially targets *Pseudotsuga menziesii* and *Abies concolor* (Swetnam and Lynch 1993), and mortality could have led to underestimates of historical densities of these species in reconstructions (specifically in smaller size classes). Douglas-fir beetle (*Dendroctonus pseudotsugae*) may have caused recent mortality of some trees on the West Leonard site. This beetle is causing widespread mortality of *Pseudotsuga menziesii* in mixed-conifer forests in Arizona (Dils et al. 2015) and preferentially targets large trees (Hadley and Veblen 1993). Past tree mortality due to *Dendroctonus pseudotsugae* could also lead to some inaccuracy in reconstructions, though there was little evidence of large snags or coarse woody debris from Douglas-fir individuals, and little is known about past outbreaks of this insect species in this area.

Our results did not deviate substantially from the results reported in previous studies (Figure 3.10) and other work suggests that the methods used in this study are well-founded, at least for coniferous species and *Quercus gambelii* (Huffman et al. 2001, Moore et al. 2004). A greater knowledge of the effectiveness of these methods in mixed-species forests may prove useful, especially because dendrochronological reconstructions have become prevalent in mixed-species forests in other regions in the western United States (Larson and Churchill 2012).

One-hectare areas may be too small to understand some aspects of structure and spatial pattern in these forests historically (e.g. larger groups and gaps), and the analysis of only four sites on sedimentary soils limits our ability to make broad conclusions across forests in the Southwest. Larger plot sizes, and the use of remote sensing techniques to quantify reference conditions in areas with active fire regimes may provide useful avenues for future work.

Further research is needed in different geographic areas within the Southwest, specifically southern Utah, the Kaibab Plateau and Madrean Sky Islands in Arizona, and forests in northern and western New Mexico. Studies at different elevations and across multiple soil types will help to develop a greater understanding of the factors driving the spatial patterns of dry mixed-conifer forests in the Southwest. Studies along climatic gradients or using climate analog sites (similar to Churchill et al. 2013) may be especially useful given the magnitude of expected climatic changes in the Southwest (Garfin et al. 2013).

Conclusions

Dry mixed-conifer forests in the Southwest have undergone considerable changes since Euro-American settlement in the late 1800's (Fulé et al. 2002, Mast and Wolf 2004, Heinlein et al. 2005, Fulé et al. 2009). Densities have increased and species composition has shifted, primarily as a result of the exclusion of low-moderate severity fires across much of the landscape. Some researchers suggest that many forests in the western United States (with a dominant component of *Pinus ponderosa*) have a history of mixed or high-severity fire, and that management for open forest conditions and frequent, low-severity fire may not fit within the natural range of variability (Williams and Baker 2012, Odion et al. 2014, Sheriff et al. 2014). These conclusions are certainly valid in some forests in the West, but restoration treatments are particularly appropriate in southwestern forests (Schoennagel et al. 2004), where historical structural conditions were primarily the result of frequent disturbances of low-severity (Covington and Moore 1994, Allen et al. 2002), even in the dry mixed-conifer forest type (Swetnam and Baisan 1996, Heinlein et al.

2005, O'Connor et al. 2014, Huffman et al. 2015).

A knowledge of the natural range of variability, and an improved knowledge of historical processes in these ecosystems provide very important input into the development of a management framework that targets ecosystem resilience (Reynolds et al. 2013, DeRose and Long 2014). Beyond targets of tree density and species composition, a greater knowledge of forest spatial structure, the role of individual species within it, and positive or negative associations between species groups all provide important information that can be utilized by managers in future treatments. The natural range of variability is an important consideration for management in frequent-fire forests in the West (Fulé 2008, Reynolds et al. 2013), but contemporary issues such as climate change (Millar et al. 2007, Garfin et al. 2013), predicted increases in fire size and severity (Westerling et al. 2006), shifts in species dominance due to drought (McIntyre et al. 2015), and the introduction of invasive species (Keeley 2006, Geils et al. 2010), provide additional considerations for forest managers.

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Table 3.1: Characteristics of study sites on the Mogollon Rim, AZ, USA, including physiographic variables, vegetation type, soil characteristics, and various measures of site productivity.

	Site			
Metric	**Hi Fuller**	**East Bear**	**East Barbershop**	**West Leonard**
USFS Plant Association[a]	White fir/sprucefir fleabane	White fir/Oregongrape: RONE phase	White fir/bigtooth maple	White fir/Oregongrape: typic phase
Soil Parent Material[b]	Mixed Sedimentary	Mixed Sedimentary	Mixed Sedimentary	Mixed Sedimentary
NRCS Soil Series[b]	Clover Springs (ClB), Soldier (SlC & SlE)	Soldier (SlC & SlE)	Soldier (SlE)	Soldier (SlE), Palomino (PaC), L.S. Rockland (Ls)
NRCS Timber Group[b]	1 (High Quality)	1 (High Quality)	1 (High Quality)	1 (High Quality), 2b (Low-Moderate)
SW ReGAP Landcover Type[c]	S032: Dry-Mesic Montane Mixed Conifer Forest…	S032: Dry-Mesic Montane Mixed Conifer Forest…	S032: Dry-Mesic Montane Mixed Conifer Forest…	S032: Dry-Mesic Montane Mixed Conifer Forest…
***Pseudotsuga menziesii* Site Index**[d]	30.1 (3.7) n = 8	26.8 (2.0) n = 9	30.7 (7.3) n = 7	18.2 (3.2) n = 7
Soil pH[e]	5.1	5	5	4.9
% Organic Matter[e]	6.7	9.5	8	7.3
% Sand[e]	38.9	59.8	30.9	44.9
% Silt[e]	40.7	23.8	44.7	34.7
% Clay[e]	20.4	16.4	24.4	20.4
Texture[e]	Loam	Sandy Loam	Loam	Loam
Cation Exchange Capacity (meq/100g)[e]	41.8	30.9	84.2	51.4
Nitrate (ppm of N)[e]	8	17	11	7
Phosphorous (ppm of P)[e]	51	8.4	10	4.7
Potassium (ppm of K)[e]	746	242	294	368
Elevation (m)[f]	2240	2283	2340	2377
Mean Annual Precip (cm)[g]	76.3	80.3	87.1	94.4
Aspect[f]	285	257	269	258
% Slope[f]	24.0	26.8	14.3	22.8

[a]: Understory plant associations keyed in the field following Stuever and Hayden (1997)

[b]: Soil series and timber group determined using web soil survey data (Soil survey staff, NRCS 2015)

[c] : Land cover type of site in SWReGAP dataset (USGS 2004)

[d] : Site index expressed in meters with a base year of 100. First number is the mean, second number is the standard deviation of all samples at a given site. “n” is the number of site trees in the anaysis. Methods following Edminster et al. (1991).

[e] : Soil analyses performed in spring 2015 by the Environmental Analytical Lab at Brigham Young University, Provo, UT, USA.

[f] : Metrics derived from 1x1m LiDAR (Light detection and ranging)-derived digital elevation model

[g] : Mean annual precipitation from the PRISM raster of 30-year normals (PRISM Climate Group, 2004)

Table 3.2: Scientific names, common names, species code, and overviews of species silvics for all species present on study sites on the Mogollon Rim, AZ, USA. Bark thickness:tree diameter ratio provides a useful measure of relative fire-resistance.

Binomial Name	**Common Name**	**Code**	**Shade Tolerance**[a]	**Fire Resistance**[a]	**Bark Thickness/ Tree Diameter**	**Resprouter?**	**Citations**
Abies concolor var. *concolor* (Gordon) Lindley ex Hildebrand	White fir	ABCO	High	Low	0.036	n	2,3
Acer grandidentatum Nutt	Bigtooth maple	ACGR	High	Moderate[b]	0.039	y	1
Pinus ponderosa var. *scopulorum* (Engelm.)	Ponderosa pine	PIPO	Low	High	0.041	n	2,3
Pinus strobiformis Engelm.	Southwestern white pine	PIST	Moderate	Moderate	0.014	n	2,3
Populus tremuloides Michx.	Quaking aspen	POTR	Low	Low	0.02	y	2,3
Pseudotsuga menziesii var. *glauca* (Mayr) Franco	Douglas-fir	PSME	Moderate	Moderate	0.03	n	1,2
Quercus gambelii Nutt	Gambel oak	QUGA	Moderate	High	0.039	y	1,2
Robinia neomexicana A.Gray	New Mexico locust	RONE	Moderate	Moderate	0.043	y	1,2
Salix scouleriana Barratt ex Hook.	Scouler's willow	SASC	Low	Low[b]	Unk	y	1,2

[a] Shade tolerance and fire tolerance ranked based on information from Reynolds et al. (2013; Figure 2, pp. 4), or by information in Fire Effects Information System (FEIS) database (US Forest Service 2014).

[b] Indicates that little is known about the relative fire resistance of this species.

ices for Table 5.2

DA Forest Service. 2015. Fire Effects Information System (FEIS). Available online at: http://www.feis-crs.org/. Accessed [2/5/2015]

ghlin, D.C., P.Z. Fulé, D.W. Huffman, J.E. Crouse, and E. Laliberte. 2011. Climatic constraints on trait-based forest assembly. Ecology, 99(6):1489-1499.

nolds, R.T., A.J. Sánchez Meador, J.A. Youtz, T. Nicolet, M.S. Matonis, P.L. Jackson, D.G. DeLorenzo, and A.D. Graves. 2013. Restoring composition and structure in southwestern frequent-fire forests: a science-based framework for improving ecosystem resiliency. General Technical Report RMRS-GTR-310. Fort Collins, CO.

Table 3.3: Summaries of tree density and size metrics for study sites on the Mogollon Rim, AZ, USA following dendrochronological reconstruction of 1879 and in 2014. All metrics are provided for trees > 5cm diameter at breast height (DBH, 1.37m). Canopy cover is given as the percent of the total site covered by the vertical projection of tree crown. Reineke's stand density index (SDI; Reineke 1933) is a commonly-used measure of stand density that gives the number of 25.4 cm (DBH) trees ha^{-1} that would be present on a site of equivalent density. SDI is given in metric values. Maximum SDI values (metric) for *Pinus ponderosa*-,*Pseudotsuga menziesii*-, and *Populus trumuloides*-dominated stands are approximately 1100, 1450, and 1600 respectively (Shaw and Long 2010).

Metric	**Year**	**Site**				**Mean (SD)**
		Hi Fuller	**East Bear**	**East Barbershop**	**West Leonard**	
Live Trees ha^{-1}	1879	130	149	159	80	129.5 (35.1)
	2014	427	574	907	1069	744.3 (295.3)
Basal Area (m^2 ha^{-1})	1879	11.4	13.0	11.0	4.9	10.1 (3.5)
	2014	42.8	44.6	43.4	36.9	41.9 (3.4)
Canopy Cover (%)	1879	15.8	17.3	17.5	8.7	14.8 (4.2)
	2014	51.0	55.8	55.5	56.7	54.7 (2.5)
Quadratic Mean Diameter (cm)	1879	33.4	33.3	29.7	28.0	31.1 (2.7)
	2014	35.7	31.4	24.7	21.0	28.2 (6.6)
Reineke's SDI (metric)	1879	201.9	230.4	204.2	93.8	182.6 (60.6)
	2014	737.8	808.5	865.6	786.3	799.6 (53.0)

Site	Year	Method	Single Trees		Small Groups (2-4)		Large Groups (5+)		Summary		
			Live Trees ha^{-1}	Basal Area m^2 ha^{-1}	Live Trees ha^{-1}	Basal Area m^2 ha^{-1}	Live Trees ha^{-1}	Basal Area m^2 ha^{-1}	Mean Group[a] Size (SD)	Number of Groups[a]	Max Group[a] Size
Hi Fuller	*1879*	*6m Fixed*	21	2.00	29	1.84	30	2.69	2.1 (1.9)	39	10
		Crown	40	2.96	40	3.57	0	0	1.4 (0.7)	58	4
	2014	*6m Fixed*	1	0.12	4	0.63	260	27.77	37.9 (83.3)	7	226
		Crown	20	1.33	19	2.19	226	25.00	5.5 (8.4)	48	49
East Bear	*1879*	*6m Fixed*	19	1.86	43	3.87	30	1.67	2.04 (1.7)	45	9
		Crown	41	2.88	45	4.15	6	0.36	1.4 (0.8)	64	9
	2014	*6m Fixed*	2	0.21	0	0	318	27.85	79.8 (147.6)	4	301
		Crown	17	1.07	31	2.27	272	24.72	6.2 (10.5)	52	54
East Barbershop	*1879*	*6m Fixed*	10	1.07	43	3.74	48	2.81	3.3 (3.5)	31	18
		Crown	25	2.23	51	3.86	25	1.52	2.0 (1.6)	50	8
	2014	*6m Fixed*	1	0.03	0	0	562	28.48	112.6 (226.1)	5	516
		Crown	17	0.40	28	1.30	518	26.81	13.7 (57.0)	41	367
West Leonard	*1879*	*6m Fixed*	20	1.33	20	0.74	9	0.73	1.6 (1.1)	31	6
		Crown	36	2.08	13	0.72	0	0	1.1 (0.4)	43	3
	2014	*6m Fixed*	1	0.14	0	0	621	23	311 (438.4)	2	621
		Crown	16	0.41	49	2.14	557	20.43	11.5 (28.8)	54	193

[a] Group summary metrics are given in number of trees. We also included single trees in the calculation of these values.

1879	**Single Trees**		**Small Groups (2-4)**		**Large Groups (5+)**	
Species	**Percent of Live Stems**	**Percent of Basal Area**	**Percent of Live Stems**	**Percent of Basal Area**	**Percent of Live Stems**	**Percent of Basal Area**
Abies concolor	32.4 *(0.17)*	37.4	34.3 *(-1.72)*	35.5	33.3 *(1.83)*	27.1
Acer grandidentatum	-	-	-	-	-	-
Pinus ponderosa	38.4 *(2.42)**	35.7	46.1 *(0.41)*	49.8	15.5 *(-3.12)**	14.5
Pinus strobiformis	83.3	77.0	16.7	23.0	0	0
Populus tremuloides	25 *(-0.44)*	8.6	25 *(1.28)*	29.1	50 *(1.99)*	62.2
Pseudotsuga menziesii	35.5 *(0.52)*	32.2	46.8 *(0.22)*	49.0	17.7 *(-0.83)*	18.9
Quercus gambelii	16.7 *(-3.16)**	16.0	52 *(1.43)*	53.0	31.3 *(1.77)*	31.0
Robinia neomexicana	50	50	50	50	-	-
ALL	32.9	33.7	44.1	46.2	23.0	20.1

* Indicates statistically significant difference (α=0.05) between observed and expected values for a given cell

\- Indicates no trees present in a given cell

2014	**Single Trees**		**Small Groups (2-4)**		**Large Groups (5+)**	
Species Code	**Percent of Live Stems**	**Percent of Basal Area**	**Percent of Live Stems**	**Percent of Basal Area**	**Percent of Live Stems**	**Percent of Basal Area**
Abies concolor	2.2	1.4	3.5	3.6	94.3	95.0
Acer grandidentatum	0.6	0.1	2.9	2.4	96.6	97.5
Pinus ponderosa	2.5	1.6	5.7	4.8	91.8	93.7
Pinus strobiformis	5.7	5.2	2.5	3.0	91.8	91.7
Populus tremuloides	0	0	0	0	100	100
Pseudotsuga menziesii	2.1	2.0	3.7	4.3	94.3	93.7
Quercus gambelii	0.6	0.6	2.2	2.1	97.2	97.3
Robinia neomexicana	4.7	5.3	6.3	5.6	89.1	89.1
ALL	2.1	1.7	3.7	3.9	94.2	94.3

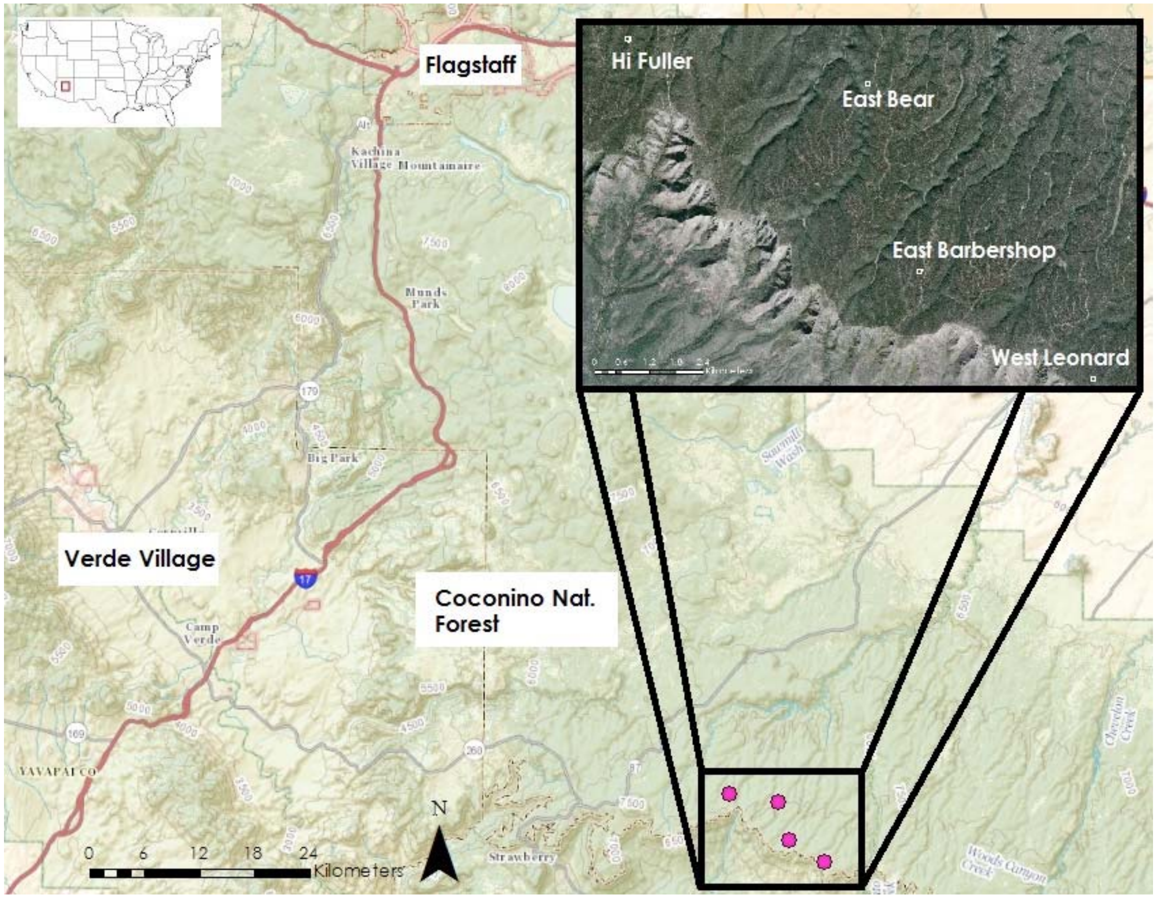
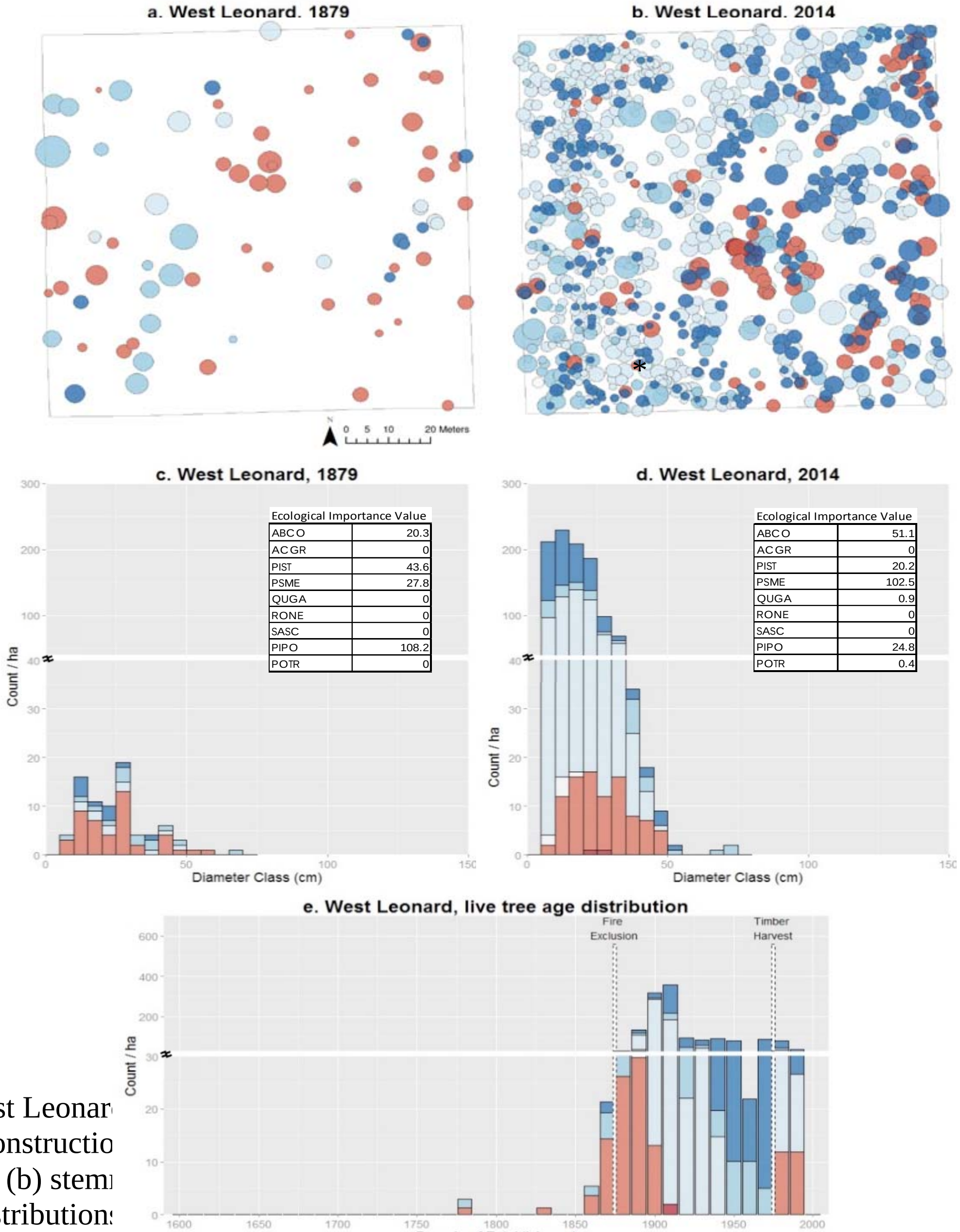


Figure 3.1: Overview of site locations in dry mixed-conifer forests on the Mogollon Rim, AZ, USA. The Hi Fuller, East Bear, East Barbershop, and West Leonard sites are all named after adjacent springs or canyons.



Ecological Importance Value	
ABCO	20.3
ACGR	0
PIST	43.6
PSME	27.8
QUGA	0
RONE	0
SASC	0
PIPO	108.2
POTR	0

Ecological Importance Value	
ABCO	51.1
ACGR	0
PIST	20.2
PSME	102.5
QUGA	0.9
RONE	0
SASC	0
PIPO	24.8
POTR	0.4

2: Changes on the West Leonar
ndrochronological reconstructio
(a) and contemporary (b) stem
prarily (d) diameter distribution
.37m above ground level), and live standing age distribution (e). Note that the
panels c-e are broken with differing scales below and above the break. Colors
species are scaled by relative shade tolerance ranging from blue (most shade
to red (least shade tolerant).

Species codes are as follows: ABCO-*Abies concolor*, ACGR-*Acer andidentatum*, PIST-*Pinus strobiformis*, PSME-*Pseudotsuga menziesii*, UGA-*Quercus gambelii*, RONE-*Robinia neomexicana*, SASC-*Salix ouleriana*, PIPO-*Pinus ponderosa*, and POTR-*Populus tremuloides*

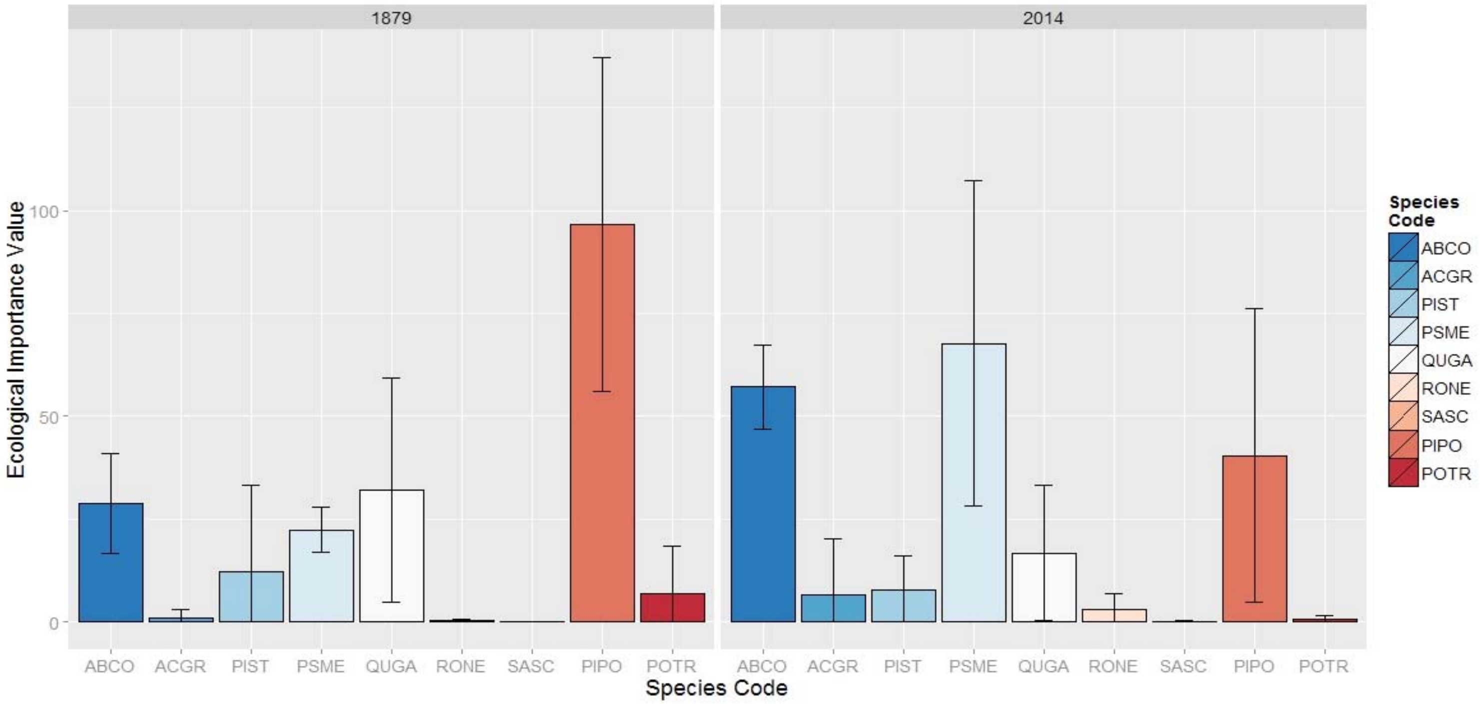


Figure 3.3: Changes in species composition on study sites on the Mogollon Rim, AZ, between 1879 (dendrochronological reconstruction) and 2014 (observed) as indicated by ecological importance value (EIV; Curtis and McIntosh 1951). Maximum value of EIV is 200 and indicates total site occupancy by a given species. The minimum value of EIV is 0 and indicates the absence of a species on a site. EIV values are the mean EIV for our four field sites (n=4), error bars are one standard deviation and data are for trees ≥ 5 cm in diameter at breast height (1.37m above ground level).

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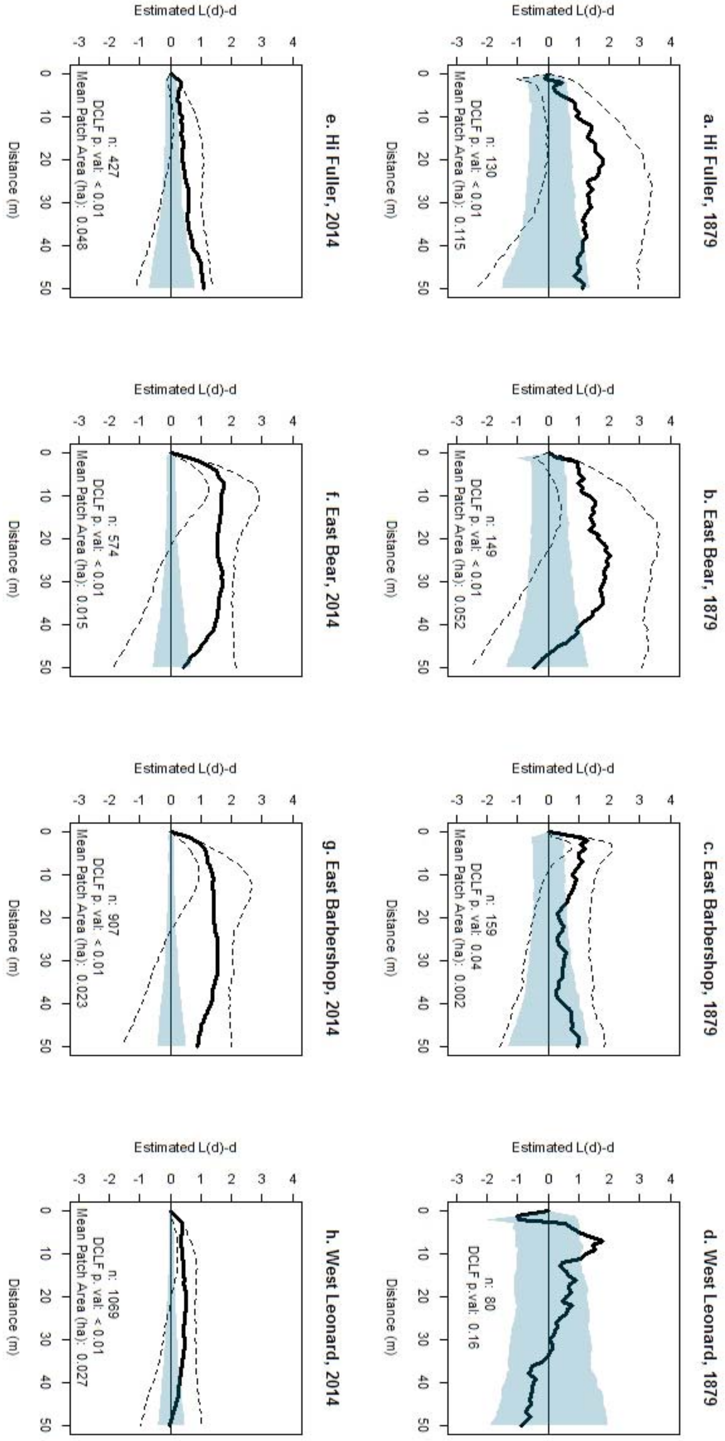
a. Hi Fuller, 1879
n: 130
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.115
b. East Bear, 1879
n: 149
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.052
c. East Barbershop, 1879
n: 159
DCLF p. val: 0.04
Mean Patch Area (ha): 0.002
d. West Leonard, 1879
n: 80
DCLF p.val: 0.16
e. Hi Fuller, 2014
n: 427
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.048
f. East Bear, 2014
n: 574
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.015
g. East Barbershop, 2014
n: 907
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.023
h. West Leonard, 2014
n: 1069
DCLF p. val: < 0.01
Mean Patch Area (ha): 0.027
Estimated L(d)-d
-3
-2
-1
0
1
2
3
4
Distance (m)
0
10
20
30
40
50

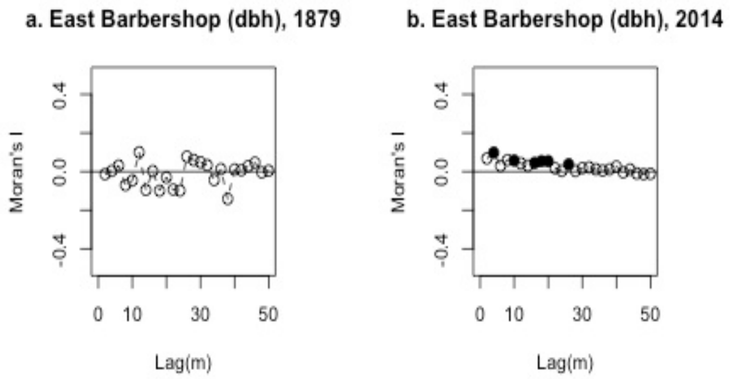

Figure 3.5: Correlograms for the East Barbershop site on the Mogollon Rim, AZ, USA based on (a) reconstructed (1879) diameter, and (b) contemporary (2014) diameter. Black points indicate statistical significance (α=0.05) at a given lag distance after Bonferroni correction for multiple comparisons. White points are not significantly different from the expected value at a given lag distance. Significance at a small-scales indicates the presence of tree groups (where patch radius = lag distance) with relatively similar diameters.

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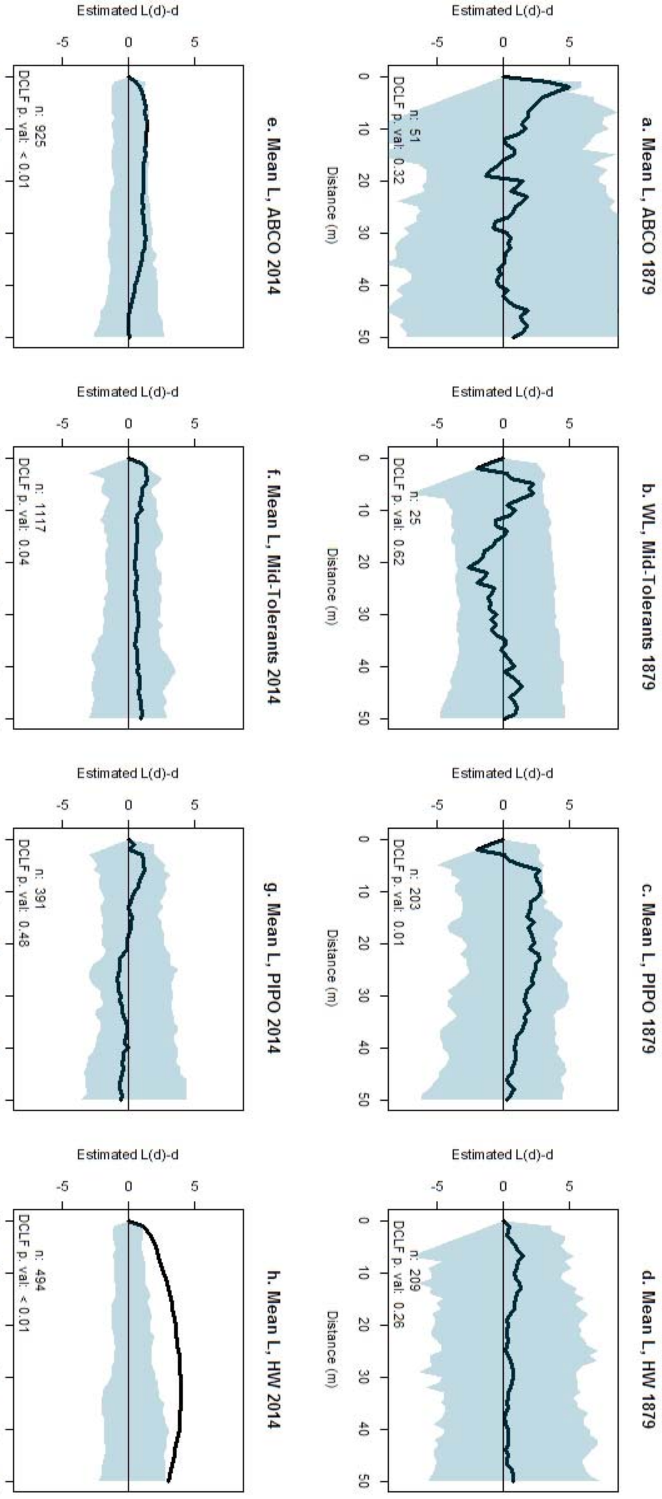
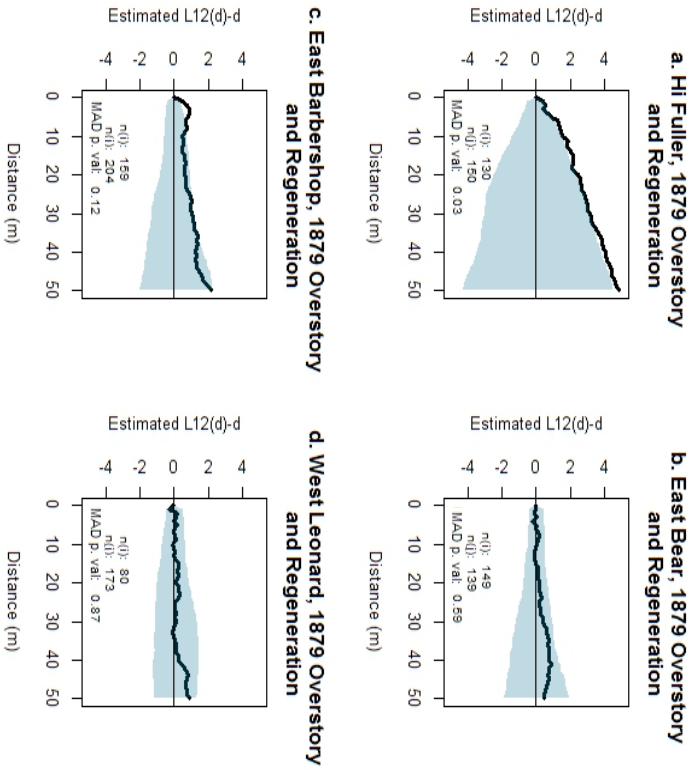
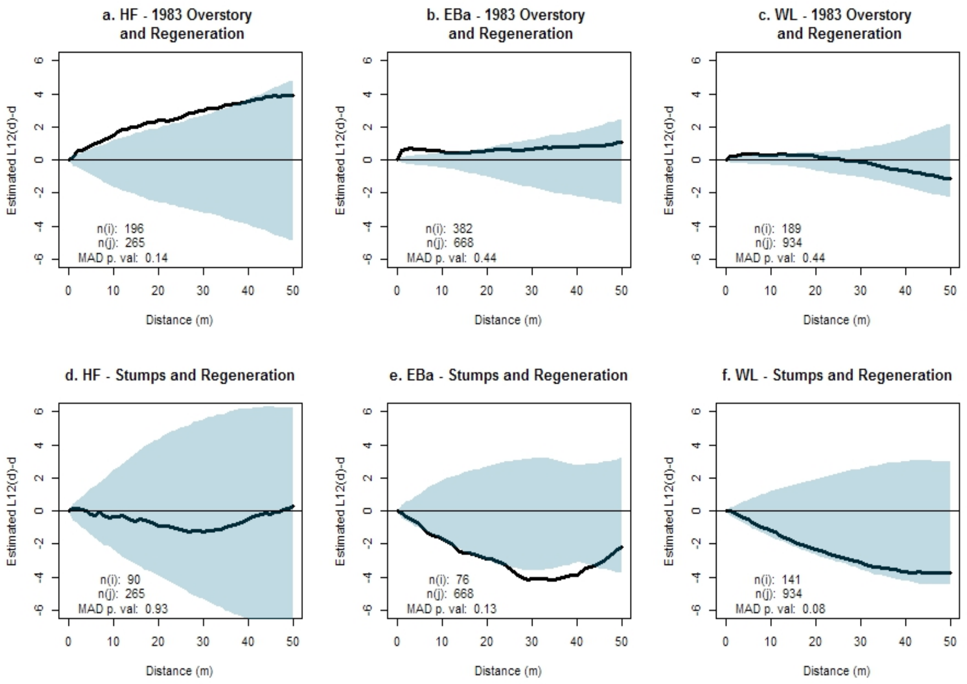
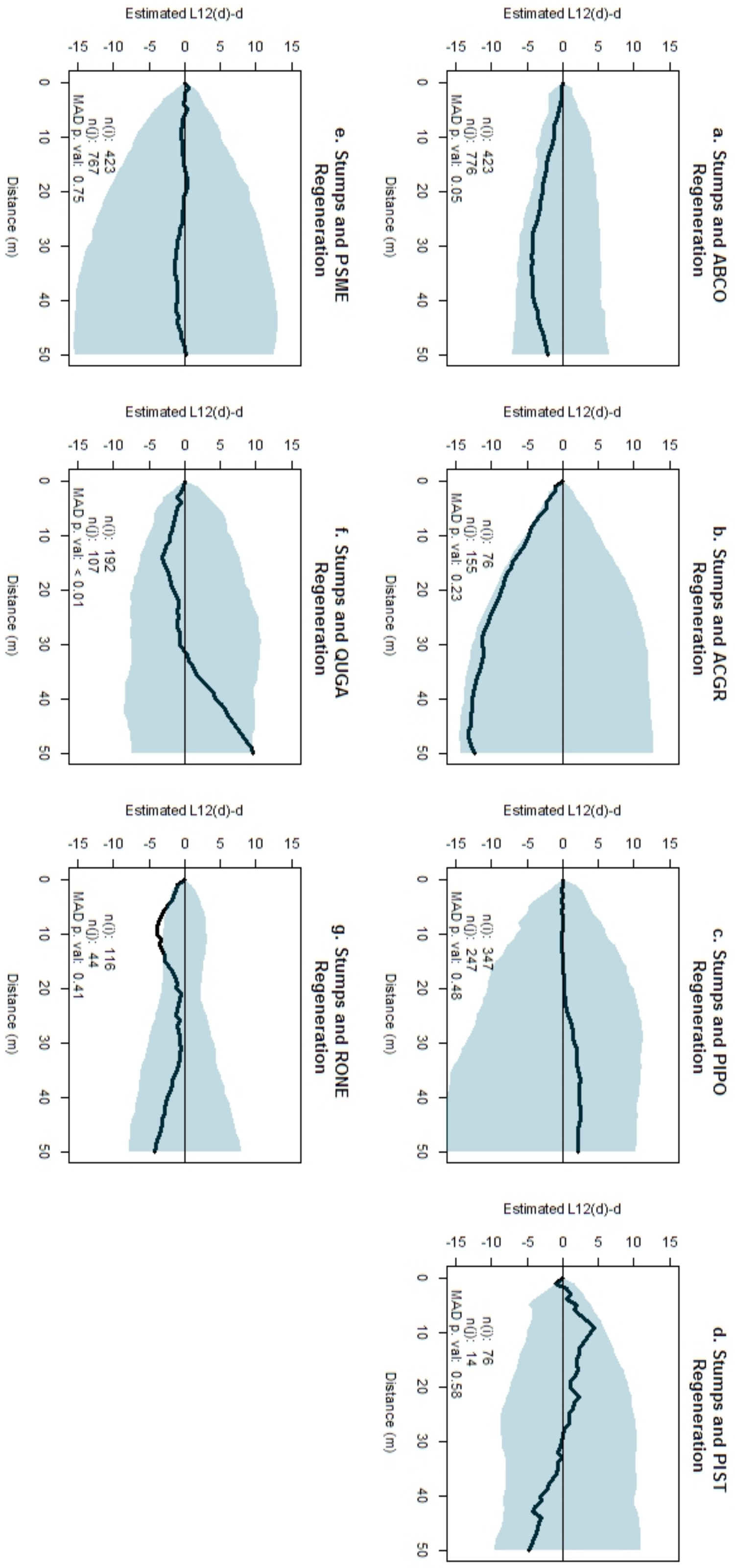
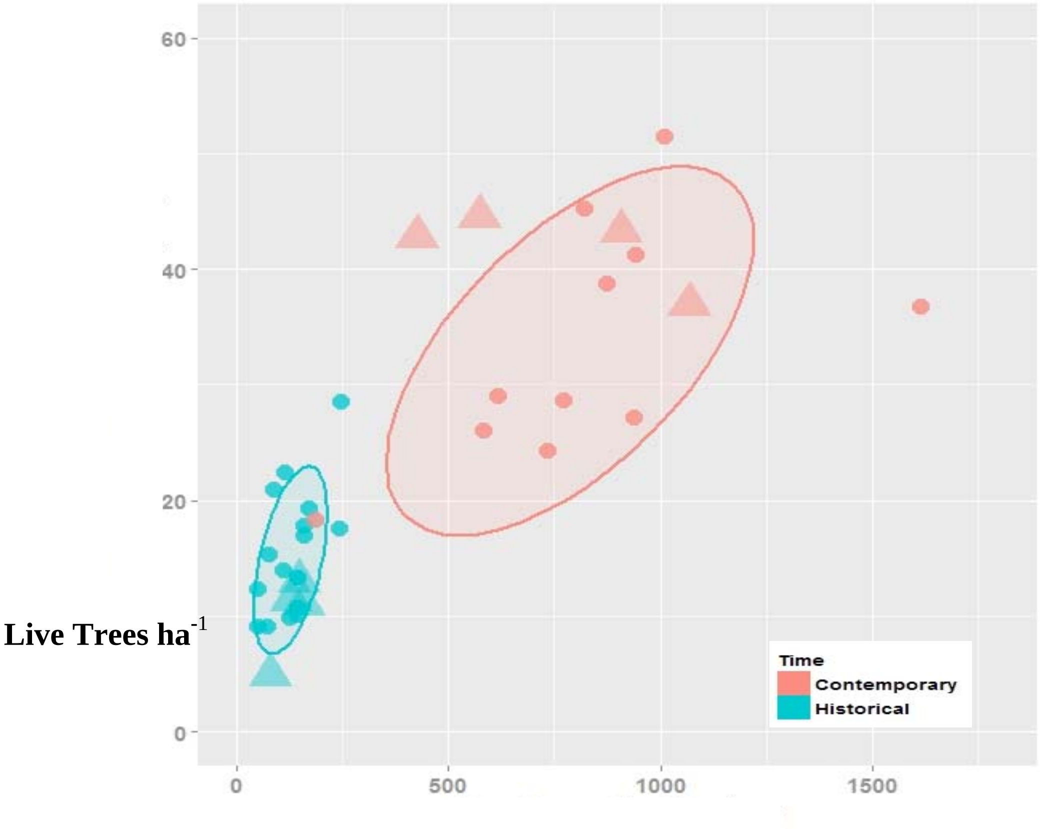

a. Mean L, ABCO 1879
n: 51
DCLF p. val: 0.32
b. WL, Mid-Tolerants 1879
n: 25
DCLF p. val: 0.62
c. Mean L, PIPO 1879
n: 203
DCLF p. val: 0.01
d. Mean L, HW 1879
n: 209
DCLF p. val: 0.26
e. Mean L, ABCO 2014
n: 925
DCLF p. val: < 0.01
f. Mean L, Mid-Tolerants 2014
n: 1117
DCLF p. val: 0.04
g. Mean L, PIPO 2014
n: 391
DCLF p. val: 0.48
h. Mean L, HW 2014
n: 494
DCLF p. val: < 0.01
Estimated L(d)-d
-5
0
5
Distance (m)
0
10
20
30
40
50


a. Hi Fuller, 1879 Overstory and Regeneration
n(i): 130
n(j): 150
MAD p. val: 0.03
b. East Bear, 1879 Overstory and Regeneration
n(i): 149
n(j): 139
MAD p. val: 0.59
c. East Barbershop, 1879 Overstory and Regeneration
n(i): 159
n(j): 204
MAD p. val: 0.12
d. West Leonard, 1879 Overstory and Regeneration
n(i): 80
n(j): 173
MAD p. val: 0.87
Estimated L12(d)-d
-4
-2
0
2
4
Distance (m)
0
10
20
30
40
50


a. HF - 1983 Overstory and Regeneration
b. EBa - 1983 Overstory and Regeneration
c. WL - 1983 Overstory and Regeneration
d. HF - Stumps and Regeneration
e. EBa - Stumps and Regeneration
f. WL - Stumps and Regeneration
Estimated L12(d)-d
-6
-4
-2
0
2
4
6
Distance (m)
0
10
20
30
40
50
n(i): 196
n(j): 265
MAD p. val: 0.14
n(i): 382
n(j): 668
MAD p. val: 0.44
n(i): 189
n(j): 934
MAD p. val: 0.44
n(i): 90
n(j): 265
MAD p. val: 0.93
n(i): 76
n(j): 668
MAD p. val: 0.13
n(i): 141
n(j): 934
MAD p. val: 0.08

.9: Besag’s L mations of bivariate K12 analyses for four study sites on ollon Rim, AZ, USA. ar was excluded due nce of multiple . Panels show the ship between the ucted overstory (cut and tree recruitment 1984 and 2014 for a ecies across all sites. areas are 95% nce envelopes for dence, based on 999 shifts of successfully ating trees. Deviations lack line) above the nce envelope indicate n at a given scale. ons below the e indicate repulsion. he number of stumps alysis, n(j) is the of trees that fully regenerated 1984 and 2014. We ned if deviations from idence envelope were ally significant using a m Absolute on (MAD; Baddeley ner 2005) goodness of MAD p-values less 5 indicate stastically ant differences for a ttern.





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Chapter 4

Implications to Management

Increases in forest density, changes in tree size- and age-structure, and shifts in species composition have occurred in many southwestern forests following Euro-American settlement in the late 1800’s (Covington and Moore 1994, Mast et al. 1999, Fulé et al. 2002). The effects of these structural changes, in combination with current and future climatic change (Westerling et al. 2006, Garfin et al. 2013), bring up difficult questions that must be addressed by forest managers in the Southwestern region in upcoming years. Increases in fire size and severity (Westerling et al. 2006) are only one symptom of other problems facing forests; drought-related mortality (Allen et al. 2010), and other alterations to ecosystem function are also major concerns (Reynolds et al. 2013).

Active management and a laissez-faire style of no interference offer two distinctly different approaches in response to these problems. Some researchers question the importance of active management, stating instead that contemporary forest structure and patterns of disturbance are not outside of the natural range of variability (Williams and Baker 2012, Odion et al. 2014). While these conclusions are valid in some areas in the western United States, restoration treatments and active forest management are particularly appropriate in many southwestern forests (Schoennagel et al. 2004), where historical forest conditions were influenced by frequent, low-severity fire (Covington and Moore 1994, Allen et al. 2002), even in the dry mixed-conifer forest type (Swetnam and

Baisan 1996, Heinlein et al. 2005, Huffman et al. 2015). Many of these forests had much lower densities than are present today (Reynolds et al. 2013, Chapter 3-Figure 3.10). Active management in dry mixed-conifer forests in the Southwest is both prudent and valuable.

Management partially based on the natural range of variability (NRV) of frequent-fire forests is likely to increase ecosystem resistance and resilience in the face of climate change (Fulé 2008). These terms reflect the ability of ecosystems to experience disturbance with only minimal change to structure (resistance), or maintain similar functional attributes following disturbance (resilience; DeRose and Long 2014). Site-specific restoration treatments of these forests may not be feasible (or even advisable) under the projections of future environmental conditions, but a knowledge of the NRV can provide important input into the development of a management framework that targets long-term resilience (Millar et al. 2007, Reynolds et al. 2013, DeRose and Long 2014). Metrics quantifying tree density, species composition, spatial pattern and the role of individual species within it, and positive or negative associations between species groups, all provide important information that can be utilized by managers in future treatments.

Current Management Strategies

Dry mixed-conifer forests are present on tribal lands, privately owned properties, Department of Interior lands, and USDA Forest Service lands in the Southwest (USGS 2004). Management differs based on ownership, between land management agencies, and even within a given parcel. For this reason, summaries of current management strategies in this forest type are general and may not apply in all places. Currently, many dry mixed-conifer forests on US Forest Service lands in the Southwest are managed with uneven-aged techniques (small group selection, individual tree selection, free thins) when not already identified as restricted-use habitat for the Northern Goshawk (*Accipter gentilis*), Mexican Spotted Owl (*Strix occidentalis*), or other species of special consideration (J. Youtz, personal communication, Nov. 20, 2014); occasional deviations into even-aged management techniques (shelterwood, clear cut, seed tree) are made when insect mortality, pathogens, or other tree diseases reach epidemic levels (Reynolds et al. 2013). Uneven-aged techniques in these forests typically have a planned 30-year re-entry period, and silviculturists attempt to maintain densities between 14 and 23 m^2 of basal area ha^{-1} (60-100 ft^2 of basal area ac^{-1}). Based on an estimate of tree lifespans (of about 210 years) in the forest type, silviculturists plan on approximately 6-7 age classes (J. Youtz, personal communication, Nov. 20, 2014). Typically, group selection methods (or "modified individual-tree selection with group retention") are utilized, with the goal of encouraging the recruitment of shade-intolerant and fire-tolerant species (especially *Pinus ponderosa* and *Populus tremuloides*, but also *Pinus strobiformis, Pinus flexilis* and *Pseudotsuga menziesii*). Marking crews are often told to preferentially leave individuals of the more shade-intolerant and fire-tolerant coniferous species, especially in the larger size classes. Greater proportions of *Abies concolor* (all size classes) and *Pseudotsuga menziesii* (small size classes) are often removed (J. Youtz, personal communication, Nov. 20, 2014).

Forest managers often attempt to encourage the regrowth of *Populus tremuloides* through fencing, “jackstrawing”, and other techniques meant to reduce the impacts of ungulate browsing (Fairweather et al. 2008). For other hardwood species such as *Quercus gambelii* and *Acer grandidentatum*, most groups are left unharvested to provide thermal cover and habitat for wildlife (J. Youtz, personal communication, Nov. 20, 2014). Because of its tendency to invade openings, group selection treatments are often avoided in close proximity to established populations of *Robinia neomexicana* (Reynolds et al. 2013).

Multi-scaled heterogeneity has become an important goal for managers working US Forest Service lands in the Southwest (Reynolds et al. 2013), and this was an important structural characteristic of many frequent-fire frests in the West historically (Larson and Churchill 2012). At the fine-scale (< 4ha extent), forests had a mix of individual trees and groups of trees with interlocking crowns, discrete openings, and grassy interspaces (Larson and Churchill 2012, Reynolds et al. 2013). At the intermediate-scale (4-400 ha extent; hereafter referred to as “stand-scale”), trees could be arranged in an aggregated spatial distribution (trees tending to grow in groups), a random spatial distribution, or, less commonly, in a uniform spatial distribution (evenly spaced) (Abella and Denton 2009, Reynolds et al. 2013). At a coarse-scale (> 400 ha extent; hereafter referred to as the “landscape-scale”), forests probably had a variety of densities, seral stages, and species compositions. These differences were based on disturbance history, aspect, slope position, soils, and many other factors (Evans et al. 2011, Reynolds et al. 2013).

Management Considerations and Research Findings

Density

Current management of dry-mixed conifer forests in the Southwest aligns relatively well with previous studies of the natural range of variability (NRV) in these ecosystems. The 95 percent confidence interval of these previous studies stretches between 7 and 23 m^2 of basal area ha^{-1} (about 30-100 ft^2 ac^{-1}), and 25-200 trees ha^{-1} (10-80 trees ac^{-1}), and includes the range of 14-23 m^2 currently targeted by Forest Service silviculturists (Chapter 3-Figure 3.10). The majority of dry mixed-conifer forests in the Southwest are currently denser than the established NRV (Chapter 3-Figure 3.10), and our results in Chapter 3 do not substantially expand these estimates. With the exception of the West Leonard site, which has the lowest density observed in any study of reference conditions in southwestern dry mixed-conifer ecosystems, all of our sites were within the established natural range of variability (NRV) in the 1879 reconstructions. There is considerable variability in dry mixed-conifer forests, and incorporating this variability into silvicultural practice is a difficult, yet crucial, endeavor. Prescriptions should account for local variability in tree density and species composition based on site index values, understory plant associations, and the pattern and density of historical remnants when determining leave-tree density and regeneration treatments for a given stand (Reynolds et al. 2013).

Managers should consider lower residual tree densities (than the current range of management) in some dry mixed-conifer forests in the Southwest. Several studies of reference conditions in these ecosystems suggest that forests had lower densities than the current range of 14-23 m^2 of basal area (Chapter 3, Heinlein et al. 2005). Areas with the lowest observed densities are on southwest facing slopes with relatively poor soils (see Heinlein et al. 2005, and “West Leonard” site in Appendix-Tables 2-3). The sites with the highest densities are typically on more mesic sites with a lower proportion of *Pinus ponderosa* (historically), a higher number of shade-tolerant conifers (historically), or on more productive soils (e.g. “Swamp Ridge” site in Fulé et al. 2002, and “East Barbershop” site in Chapter 3).

Species Composition

Our study corroborates the findings of many others (Fulé et al. 2002, Mast and Wolf 2004, Heinlein et al. 2005, Fulé et al. 2009) that have documented shifts in species composition in southwestern mixed-conifer forests since Euro-American settlement in the Southwest. On our sites on the Mogollon Rim, AZ, *Pinus ponderosa* was the most dominant species historically, averaging 56.5 trees ha^{-1}, and 5.21 m^2 of basal area (Appendix-Tables 2 and 3). In 1879, *Pinus ponderosa* made up about half of the trees and total basal area across all sites. Contemporary data show that *Pinus ponderosa* now averages 102.5 trees ha^{-1} and 10.16 m^2 of basal area on our sites (Appendix-Tables 2 and 3). The majority of the density increases occurred on the East Bear site, with comparatively smaller increases on the rest of the sites. Individuals of this species should be thinned where it is still a dominant or co-dominant overstory component, but at a lower rate than other more shade-tolerant species.

Abies concolor and *Pseudotsuga menziesii* were both important historically as well, each making up 10-20% of the total trees and basal area on our sites (20-40% total). *Abies concolor* tended to show slightly higher population numbers than *Pseudotsuga menziesii*, but this relationship varied between sites. Increases in tree density for these species are drastic. They should be heavily thinned (either through mechanical treatment, prescribed fire, or managed wildfire) in most dry mixed-conifer forests on the Mogollon Rim. Retention preference could be given to larger, more fire-resistant individuals. *Pinus strobiformis* was especially dominant on our most rocky and unproductive site (West Leonard), but was not widespread historically or contemporarily. Given the current consideration of white pine blister rust (a tree disease caused by the invasive pathogen *Cronartium ribicola*), maintaining a vigorous population of *Pinus strobiformis* across the landscape may help to develop genetic resistance (to this tree disease) in the future (Conklin et al. 2009, Geils et al. 2010).

Populus tremuloides was also not a major component on our sites, with the exception of a small drainage in East Barbershop (currently dominated by *Acer grandidentatum*); however, reconstruction of historical *Populus tremuloides* populations is somewhat uncertain (Vankat 2011, Matonis et al. 2013). *Populus tremuloides* densities were lower than those reported in previous studies using similar methods (e.g Heinlein et al. 2005), and reestablishment may be a lower priority across this portion of the Mogollon Rim than on other sites in northern Arizona. Browsing by elk was readily apparent on our sites, and changes in wildlife policy might help to reestablish *Populus tremuloides* populations without active forest management (Fairweather et al. 2008).

Quercus gambelii was the second most prevalent species on our sites historically, averaging 30.5 trees ha^{-1} and 1.32 m^{2} of basal area ha^{-1}. In a review of changes in *Quercus gambelii* density and size structure, Abella and Fulé (2008) suggest that densities have increased and average size of individuals of this species has decreased (relative to historical levels) in pine-oak forests in the Southwest. These changes are said to be the result of fire exclusion increasing the number of small stems and firewood harvesting removing large live (and standing dead) individuals (Abella and Fulé 2008). Though there was evidence of oak harvesting on our sites, quadratic mean diameter did not change substantially between 1879 and 2014 (23.2 cm and 23.6cm respectively), and we estimate that density of *Quercus gambelii* has more than doubled (both in live trees ha^{-1} and basal area^{-1}) since Euro-American settlement. Increases in the recruitment of *Quercus gambelii* were apparent on the East Barbershop site after 1879, but were not readily apparent on the rest of the sites. Abella and Fulé (2008) argue that passive management of *Quercus gambelii* may not restore stand structural conditions to those consistent with the NRV. On our sites on the Mogollon Rim, there is no evidence to suggest a need to promote the growth of large *Quercus gambelii*, but removal of smaller, less fire-tolerant individuals is an appropriate management strategy. Similar to *Pinus ponderosa*, *Quercus gambelii* should be retained at higher rate than other species. Oaks are likely to increase in abundance under climate change in many places in the West (McIntyre et al. 2015), so the drought and fire tolerance of this genus is an important consideration for silviculturists.

Our samples of *Acer grandidentatum* and *Robinia neomexicana* are too limited to make strong inferences, but limited research suggests that these species might be able to tolerate the historical fire regimes on the Mogollon Rim, and probably existed in these areas historically (Stephens and Fulé 2005, Corbin and Page 2011). Stephens and Fulé (2005) report densities of about 60 *Robinia neomexicana* stems ha^{-1} on the Powell Plateau, a site with an active and frequent fire regime in the Grand Canyon, AZ. Similarly, Corbin and Page (2011) found that *Acer grandidentatum* re-sprouted well following topkill in two prescribed fires and a wildfire in northern Utah. On our study sites, few *Robinia neomexicana* individuals pre-dated Euro-American settlement, but these findings must be approached cautiously. Given the short-lived nature of the above-ground portion of the plant, and (probably) rapid decomposition, we can not conclude that *Robinia neomexicana* has shown substantial increases in density between 1879 and 2014. Fulé et al. (1997) also recognized these issues, and removed *Robinia neomexicana* from their analysis. *Robinia neomexicana* has value in these ecosystems, and increases the presence of available nitrogen and calcium in the soil (Klemmedson 1994). This species should, therefore, not be fully removed from forests. Greater research into hardwood ecology in this region is needed to determine historical prevalence of these species, and their relationship to frequent, low-severity fire regimes. Treatments of *Acer grandidentatum* with prescribed fire are likely to re-establish natural population levels of this species, and provide a useful avenue for adaptive management. Silvicultural treatments that do not create large canopy gaps adjacent to established *Robinia neomexicana* may prevent the expansion of this species beyond acceptable levels (Reynolds et al. 2013). The retention of approximately 60 stems ha^{-1} is an appropriate goal for *Robinia neomexicana* where the species is already well-established (following Stephens and Fulé 2005). These treatment options are not drastic, and preserve options for a time when greater knowledge can be developed regarding the ecology of these species.

Age and Size Structure

Our results suggest that dry mixed-conifer forests on the Mogollon Rim were uneven-sized and probably uneven-aged. Trees did not show significant autocorrelation by size, so any groups of trees likely had a variety of tree sizes within them; groups of trees with similar diameters were probably not common historically. Diameter distributions suggest that shade-intolerant species were normally distributed at about 25cm with fewer large and small trees. Shade-tolerants and hardwoods were more evenly spread across the distribution. Overall, trees tended to demonstrate an irregular uneven-aged structure in our 1879 reconstructions. The largest trees on each site were *Pinus ponderosa*, *Pseudotsuga menziesii*, *Pinus strobiformis,* and *Quercus gambelii,* though the East Barbershop site also had several large *Abies concolor*.

The different species present have a variety of regeneration strategies and periodicities, so evidence of clear cohorts of regeneration may not be as obvious as in southwestern ponderosa pine forests (Mast et al. 1999, Brown and Wu 2005). Strong inferences as to the number of cohorts and recommended cutting cycle/number of entries for uneven-aged management could be made with a thorough dendrochronological reconstruction of live and dead trees in this forest type. Studies similar to Mast et al.

(1999) would prove useful in the mixed-conifer forest type to determine target age structures for restoration treatments.

Spatial Pattern

Stand-scale and fine-scale heterogeneity may have provided a positive feedback loop in many western forests, facilitating future heterogeneity (Stephens and Fry 2005, Fry and Stephens 2010, Larson and Churchill 2012). For this reason, it is possible that management for structural heterogeneity and the reintroduction of a natural disturbance regime may prevent the need for multiple timber harvests to maintain resistance and resilience to future disturbance. Given the high costs of mechanical thinning, low value of wood products removed in the Southwest (Huang et al. 2013), and the detrimental impacts of harvesting (Ampoorter et al. 2012), it makes sense to minimize re-entry whenever possible. However, the incorporation of an active fire regime (e.g. Lydersen and North 2012) is something that may not be feasible under current federal policy (Stephens and Ruth 2005), or in all locations in the Southwest because of proximity to established development.

A primary goal of our study was to develop a greater knowledge of historical tree spatial patterns in dry mixed-conifer forests of the Southwest. These findings can be explicitly incorporated into silvicultural strategies in the region. Overall spatial patterns, often described with first-order and second-order point pattern statistics, can help to inform land managers on their overarching goals for stand-scale heterogeneity in a given treatment area. These statistical methods, such as the Clark and Evans' R Index (Clark and Evans 1954) or the Ripley's Univariate K analysis (Ripley 1977), quantify the average pattern across a given study area, and describe the pattern as aggregated, random, or uniform. Forests with aggregated patterns show a tendency to grow in explicit groups. In an aggregated pattern, individuals are closer to one another than could be expected due to random chance, usually based on site variability or an underlying biological process. Random patterns might show some grouping (primarily just due to chance), but also have many isolated single trees. Uniform patterns of trees are realtively uncommon in natural systems, but could result from minimum spacing-based thins (Larson and Churchill 2008) or a plantation environment.

Pinus ponderosa and pine-oak forests show a gradient of pattern that appears to be related to site productivity. Forests with low site index values and having soils derived from cinder or basalt, tend to show very strong aggregation (Dyer et al. 2008, Abella and Denton 2009, Sánchez Meador et al. 2009, 2011). More productive sites underlain by limestone-derived soils are more likely to be randomly distributed, with only fine-scale aggregation (Schneider 2012). These changes could result from variations in rates of structural development (Larson et al. 2008) or, perhaps, differences in disturbance history or drought stress.

Dry mixed-conifer forests show slightly different spatial patterns (than ponderosa pine forests) because of the added complexity of the overstory species composition. Less-productive dry mixed-conifer forests tend to have smaller group sizes (Reynolds et al. 2013), and are more likely to have been randomly distributed (Sánchez Meador et al. unpublished data), though only limited research has been done on this topic. More productive dry mixed-conifer forests may have been more likely to have exhibited aggregation historically (see Chapter 3). At the fine-scale, incorporating group-retention strategies into silviculture becomes more important when patterns demonstrated statistically significant aggregation historically (Sánchez Meador 2011). This is because these patterns are driven by ecological processes inherent to local populations or site conditions. Managers can target aggregated or random tree distributions at the stand-scale in their goals and objectives, but a more explicit understanding of fine-scale variability in group structure and the distribution of open space helps to develop concrete targets that can be evaluated to determine treatment success (Larson and Churchill 2012, Churchill et al. 2013, Reynolds et al. 2013).

Fine-scale variability in group structure (on our sites) differed based on the local site characteristics and species present. More mesic sites with substantial components of hardwoods showed a greater number of trees in groups with fewer individual trees (e.g. East Barbershop; see Chapter 3 – Table 4). Less productive sites were more-commonly dominated by isolated single trees and small groups (e.g. West Leonard site, Chapter 3). *Abies concolor* showed a tendency to grow in larger groups, while *Pinus ponderosa* tended to grow as isolated single trees, with fewer individuals as parts of large groups. *Abies concolor* also tended to grow intermixed with other species, while *Pinus ponderosa* was neither repulsed by nor attracted to other species. Hardwoods tended to grow in small or large tree groups, primarily with other hardwoods, and were less likely to grow as isolated individuals. *Pseudotsuga menziesii* showed no clear trends. This species was present across all group-sizes, but may intermix with other species.

Opening sizes probably showed substantial variation, as suggested by studies in other regions (Lydersen et al. 2013, Dickinson 2014, Fry et al. 2014), but quantifying openings was not a major goal of this study. Total open space was substantially higher than current levels on the Mogollon Rim; estimated mean canopy cover on our sites averaged 14.8% historically, and exceeded 50% on all sites contemporarily. Explicitly including opening sizes into treatment may be a valuable goal for managers, but openings can be difficult to quantify. Other studies have suggested that open areas were really the background matrix in the historical frequent-fire environment (Laughlin et al. 2006, Reynolds et al. 2013), rather than being discrete patches.

Methods of Including Spatially Explicit Reference Conditions into Silviculture

There are multiple strategies with which managers can target spatial heterogeneity at the fine-scale and stand-scale. One method is evidence-based restoration (Moore et al. 1999). To implement this method, marking crews identify old trees, logs, snags, etc. and leave live trees in close proximity to these structures. This method is very site-specific, which is important if the primary goal of a treatment is restoration. This method is known to effectively re-create historical fine-scale spatial structure in ponderosa pine forests (Tuten et al. 2015), but no studies have tested the effectiveness of this method in dry mixed-conifer forests. Another common marking technique, the ICO (individuals, clumps, and openings) method described by Churchill et al. (2013, 2014) relies on bins of group sizes when developing prescriptions. After prescription development, marking crews attempt to retain the suggested number of groups of given sizes. This ICO method is easily evaluated for success and is widely accepted in other regions in the West, but hasn't been previously used in the Southwest. Given the variability of spatial patterns demonstrated by previous studies, this method would need to be tailored based on local site characteristics to be used an effective restoration tool.

A key difference between the ICO method and the evidence-based mark is an underlying assumption about the location of tree groups. Evidence-based marking attempts to return a grouped structure in which tree groups are located in close proximity to their historical location. ICO guidelines do not consider the location of groups as explicitly. Managers must determine which marking methods best meet their objectives based on project goals, site conditions, and available resources.

Specific Management Recommendations

Mimicking natural patterns of stand dynamics and disturbance is of great importance in modern silviculture (O'Hara 2002, O'Hara and Ramage 2013). Through the reconstruction of historical forest structure and tree species composition, we are able to present specific management recommendations regarding these aspects of forests for use in future silvicultural treatments on the Mogollon Rim, AZ. Tree density, species composition, and spatial pattern are interacting factors in mixed-species stands, and must be considered simultaneously when planning management actions.

First, we recommend the retention of 5-16 m^2 of basal area ha^{-1} (25-70 ft^2 ac^{-1}), and 75-200 trees ha^{-1} (35-80 trees ac^{-1}) in dry mixed-conifer forests on the Mogollon Rim (trees > 5 cm/2 in diameter at breast height). These recommendations are made with the assumption that some mortality may occur post-treatment. Secondly, we recommend the use of uneven-aged management techniques to retain individuals across a range of diameter classes in dry mixed-conifer forests on the Mogollon Rim. Chapter 3-Figure 3.2, and Figures 1-3 in the Appendix can provide general guidelines for a desirable diameter distribution. Multiple cohorts should be present on each site, and these cohorts should be spatially intermixed. Retention of larger trees is an important goal on sites that show evidence of early logging. Reconstruction of historical size and age structure were not primary goals of our study, and further research is needed in these areas.

In regards to species composition, we recommend preferential retention of healthy and vigorous *Pinus ponderosa* and *Quercus gambelii* on many dry mixed-conifer sites. Components of *Pseudotsuga menziesii*, *Abies concolor*, *Populus tremuloides*, and *Pinus strobiformis* were also important in these ecosystems historically. Our preference list for retention (high to low) is as follows: *Pinus ponderosa*, *Quercus gambelii, Pinus strobiformis, Populus tremuloides, Pseudotsuga menziesii, Abies concolor*. Across the landscape (in dry mixed-conifer forests), approximately 50 percent of basal area and live trees should be *Pinus ponderosa,* 15 percent should be *Quercus gambelii,* with 10-15 percent each of *Abies concolor* and *Pseudotsuga menziesii.* We also recommend the retention of 10 percent or less of *Pinus strobiformis*, and *Populus tremuloides* in this forest type. These species likely had important roles in certain places, but do not appear to have been widespread historically. Harvests to *Robinia neomexicana* and *Acer grandidentatum* can be made when necessary, but we provide no specific recommendations for these species.

In dry mixed-conifer forests on the Mogollon Rim, managers should treat for an aggregated or grouped spatial structure at the stand-scale, with a wide range of group sizes (1-18 trees or more). Our findings suggest that approximately 30 percent of trees and basal area were isolated individuals, 45 percent of trees and basal area were in small groups (2-4 trees), and 25 percent of trees and basal area were in large groups (5 or more trees). Variation within these targets is an important consideration. Sites with more hardwoods and *Abies concolor* appear to have had larger group sizes historically. *Pinus ponderosa* should be retained more commonly as individual trees than other species, and hardwoods should be kept in groups more often than other species. Groups often had a mixture of tree diameters within them, and had multiple species as well. There is, however, some evidence for single-species groups, especially for *Pinus ponderosa* and *Quercus gambelii*. *Abies concolor* appears to have been a part of many mixed-species groups, often with *Pinus ponderosa* and *Quercus gambelii.* Established groups may facilitate the growth of this species. See Table 4.1 and Figure 4.1 for a more thorough description of recommendations regarding spatial structure, density, and species composition in dry mixed-conifer forests on the Mogollon Rim, AZ.

The use of the ICO method of marking (Churchill et al. 2013, 2014) may be most intuitive for managers, because it is analogous to marking based on a target diameter distribution. This method of marking may also be most useful for incorporating our results into silvicultural prescriptions and marking guides in the Southwest. Incorporating “rapid assessments” meant to quickly characterize historical forest structure and species composition (see Sensibaugh et al. 2013) might help to further explain site variability and help to better-inform these ICO methods. Our results help to quantify characteristics of historical forest structure, but are not meant to be representative of all dry mixed-conifer forests in the Southwest. Rather, our recommendations are a starting point for managers that can be adjusted based on local site-conditions and contemporary considerations of forest health (Reynolds et al. 2013).

Conclusions

Dry mixed-conifer forests in the Southwest have undergone considerable changes since Euro-American settlement. Tree densities have increased, and species composition has shifted, primarily as a result of the exclusion of low/moderate-severity fires across much of the landscape. Silvicultural treatments focusing on the reduction of forest densities and targeting multi-scaled heterogeneity, may improve ecosystem function and increase the resistance and resilience of forested ecosystems to disturbance (Reynolds et al. 2013). Density, species composition, and spatial pattern all varied substantially across the landscape, and the factors affecting this variability are beginning to become understood. The NRV is an important consideration for management in frequent-fire forests in the West, but contemporary issues such as climate change (Garfin et al. 2013), predicted increases in fire size and severity (Westerling et al. 2006), shifts in species dominance due to drought (McIntyre et al. 2015), and the introduction of invasive species (Keeley 2006, Geils et al. 2010), provide many important considerations for forest managers in the future.

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observed
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Plot means (in
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are also
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Species	**Single Trees**		**Small Groups (2-4)**		**Large Groups (5+)**		**Total**		**Notes**
	Trees ac^{-1}	**Basal Area $ft^2\ ac^{-1}$**	**Trees ac^{-1}**	**Basal Area $ft^2\ ac^{-1}$**	**Trees ac^{-1}**	**Basal Area $ft^2\ ac^{-1}$**	**Trees ac^{-1}**	**Basal Area $ft^2\ ac^{-1}$**	
Abies concolor	1 to 4	1 to 6	1 to 4	1 to 6	0 to 3	0 to 4	4 to 10 (7.5)	2 to 14 (7)	Often growing in mixed-species groups, often a component of larger grou
Acer grandidentatum	-	-	-	-	-	-	-	-	No specific recommendations for this species. Limited evidence suggests that it may be occupying some sites previously occupied by *P. tremuloid*
Pinus ponderosa	4 to 20	4 to 13	5 to 20	5 to 20	0 to 10	0 to 8	10 to 40 (23)	11 to 40 (23)	Occasionally grew in groups with only *P. ponderosa,* but also grew in mixed-species groups. Less likely to be in large groups and more likely to single trees than other species.
Pinus strobiformis	0 to 6	0 to 5	0 to 2	0 to 2	-	-	0 to 8 (2)	0 to 6 (2)	Appeared to dominate in certain habitat types (rocky slopes and harsher sites), but was not widespread. Contemporary patterns suggest this speci can tolerate large groups, but this was not the case on our sites historically
Populus tremuloides	0 to 2	0 to 1	0 to 3	0 to 2	0 to 5	0 to 3	0 to 10 (3)	0 to 5 (1)	Tended to grow in groups more often than other species. Concerns of historical grazing impact and rapid decay may mean we are underpredicti densities for this species. Probably not a major component though.
Pseudotsuga menziesii	1 to 2	1 to 3	2 to 4	2 to 5	0 to 2	0 to 2	3 to 6 (5)	3 to 9 (6)	Found commonly as single trees, in small groups, and in large groups. Oft in mixed-species groups.
Quercus gambelii	0 to 4	0 to 2	0 to 13	0 to 6	0 to 8	0 to 4	0 to 25 (12)	0 to 12 (6)	Less likely to be found as isolated as single trees and more likely to be fou in groups than other trees. Often in single-species groups, but sometimes mixed with conifers, specifically *A. concolor*.
Robinia neomexicana	-	-	-	-	-	-	-	-	No specific recommendations for this species.Stephens and Fulé (2005) report densities of 24 tree ac^{-1} on the Powell Plateau, AZ, a site with continuous fire since the late 1800's.
ALL	4 to 15 (11)	5 to 15 (9)	5 to 20 (14)	5 to 20 (12)	0 to 20 (8)	0 to 15 (6)	35 to 65 (52)	25 to 60 (44)	Tree groups often had a mix of tree sizes and multiple species within them Single-species groups were also present for *P. ponderosa*, *P. strobiformis* , and *Q. gambelii*.

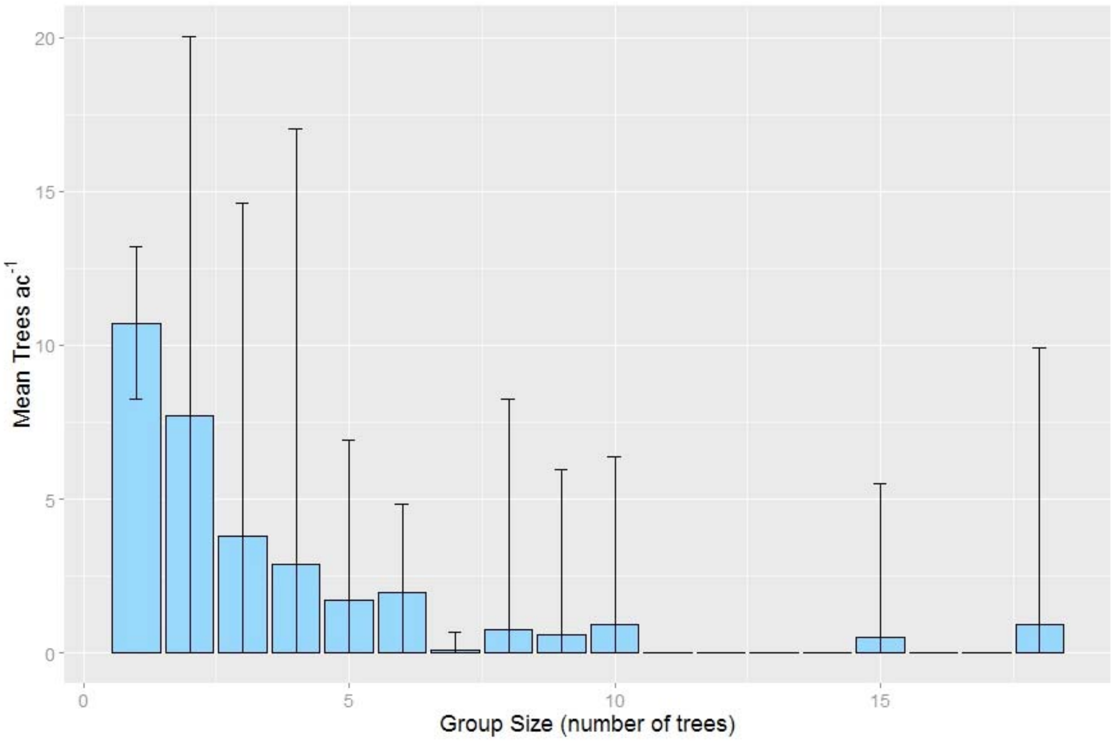

Figure 4.1: Distribution of historical (1879) tree group sizes for our sites on the Mogollon Rim, AZ, USA. Trees were assigned to groups based on two cluster algorithms on four different study sites. Bars are the mean number of trees ac^{-1} in a given group size. Error bars are one standard deviation.

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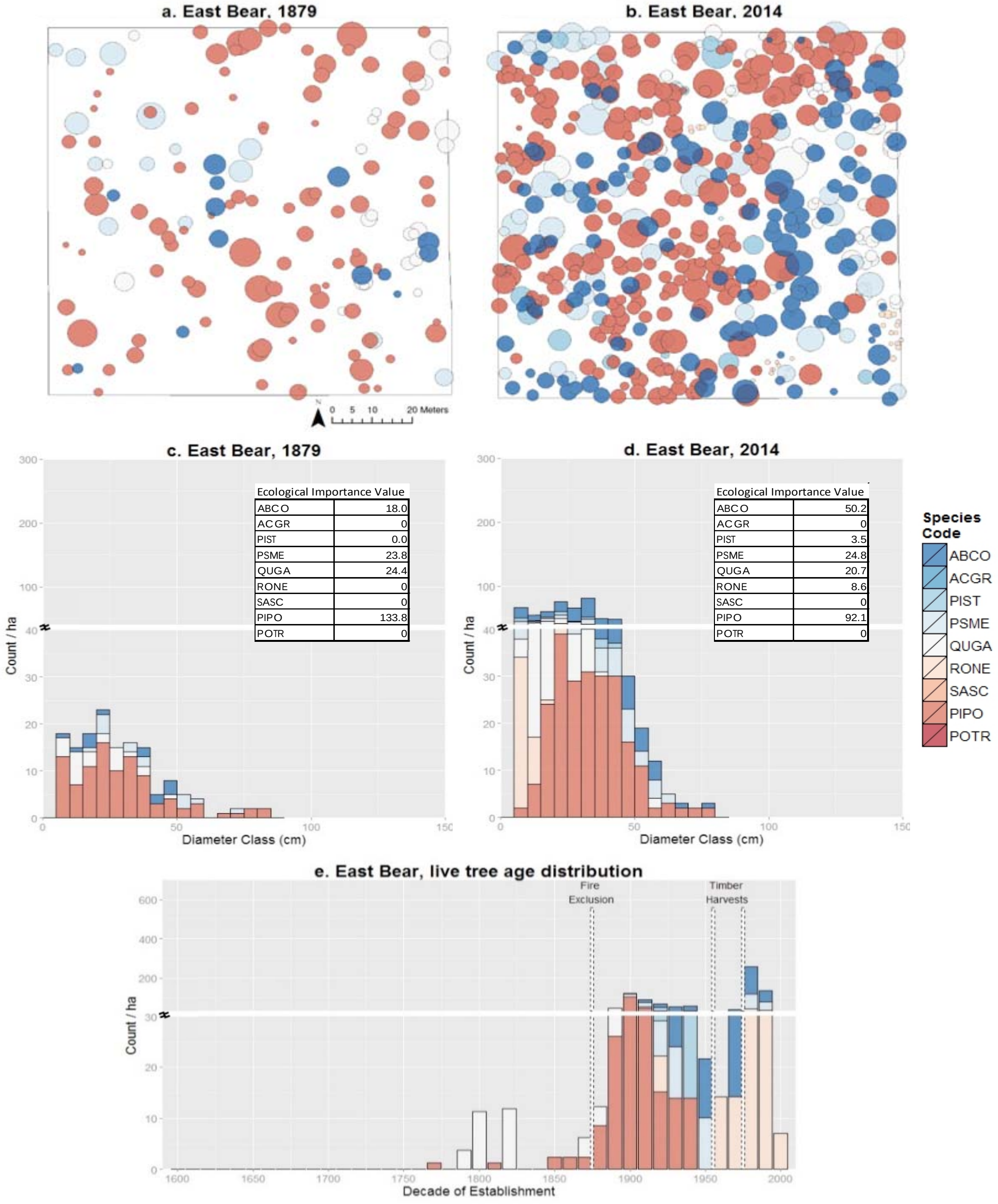
Appendix



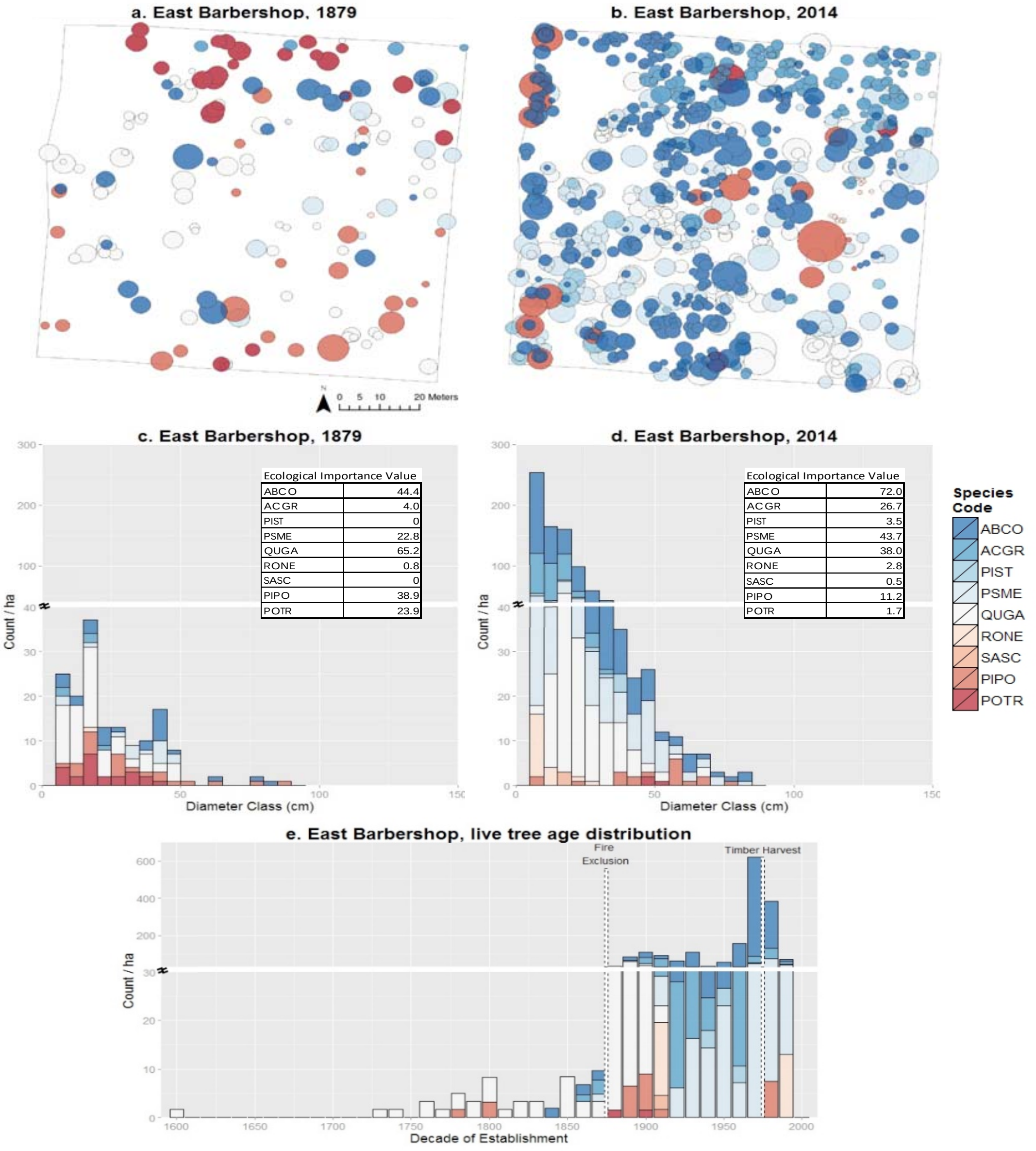
Ecological Importance Value

ABCO	18.0
ACGR	0
PIST	0.0
PSME	23.8
QUGA	24.4
RONE	0
SASC	0
PIPO	133.8
POTR	0

Ecological Importance Value

ABCO	50.2
ACGR	0
PIST	3.5
PSME	24.8
QUGA	20.7
RONE	8.6
SASC	0
PIPO	92.1
POTR	0

Figure 1: Changes on the East Bear site on the Mogollon Rim, AZ, USA between 1879 (dendrochronological reconstruction) and 2014 (observed). Panels include historical (a) and contemporary (b) stemmaps scaled by canopy area, historical (c) and contemporarily (d) diameter distributions for all live trees ≥ 5cm diameter at breast height (1.37m above ground level), and live standing age distribution (e). Note that the y-axes on panels c-e are broken with differing scales below and above the break. Colors for each species are scaled by relative shade tolerance ranging from blue (most shade tolerant) to red (least shade tolerant).



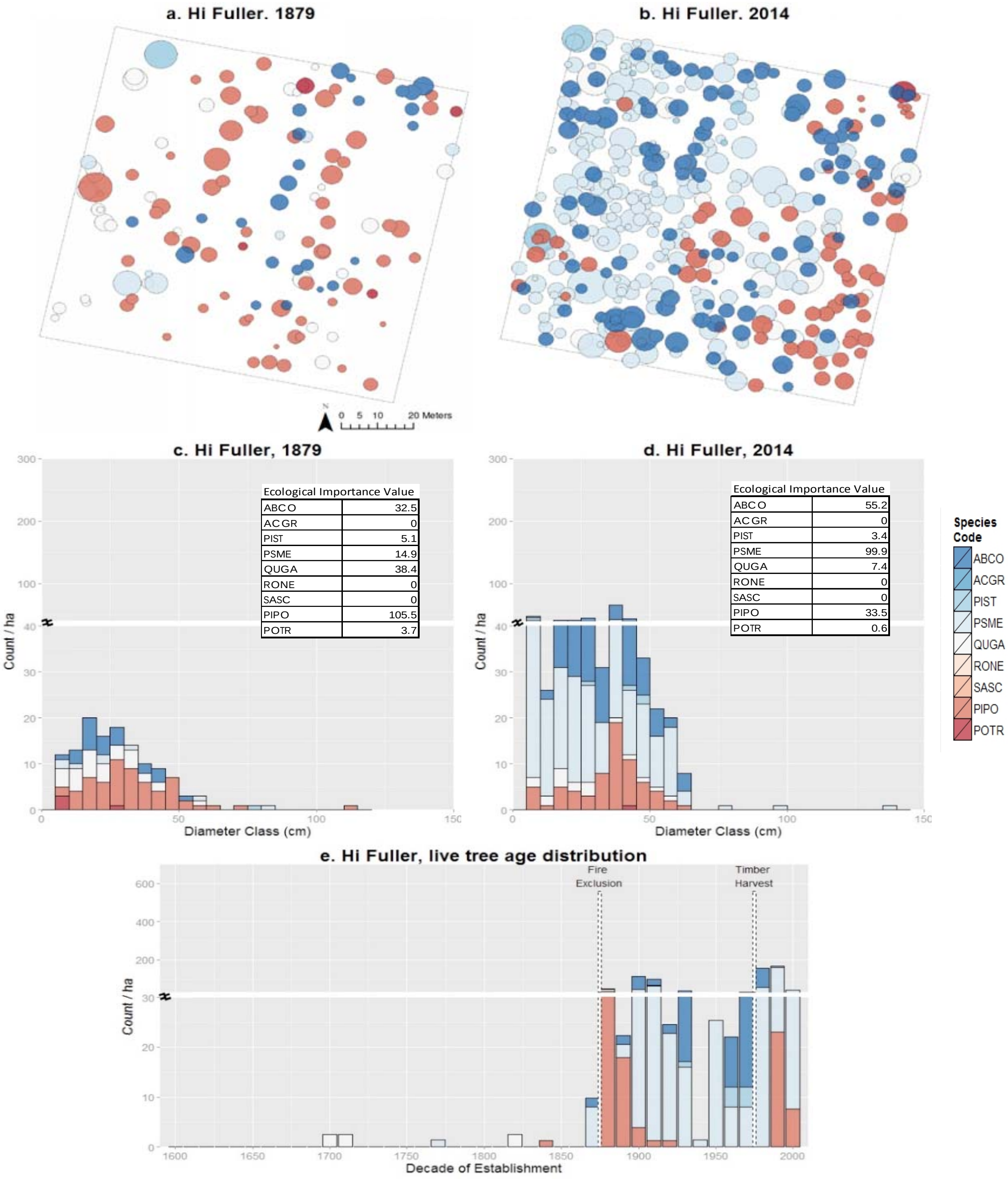
c. East Barbershop, 1879

Ecological Importance Value	
ABCO	44.4
ACGR	4.0
PIST	0
PSME	22.8
QUGA	65.2
RONE	0.8
SASC	0
PIPO	38.9
POTR	23.9

d. East Barbershop, 2014

Ecological Importance Value	
ABCO	72.0
ACGR	26.7
PIST	3.5
PSME	43.7
QUGA	38.0
RONE	2.8
SASC	0.5
PIPO	11.2
POTR	1.7

Figure 2: Changes on the East Barbershop site on the Mogollon Rim, AZ, USA between 1879 (dendrochronological reconstruction) and 2014 (observed). Panels include historical (a) and contemporary (b) stemmaps scaled by canopy area, historical (c) and contemporarily (d) diameter distributions for all live trees ≥ 5cm diameter at breast height (1.37m above ground level), and live standing age distribution (e). Note that the y-axes on panels c-e are broken with differing scales below and above the break. Colors for each species are scaled by relative shade tolerance ranging from blue* (most shade tolerant) to red (least shade tolerant).



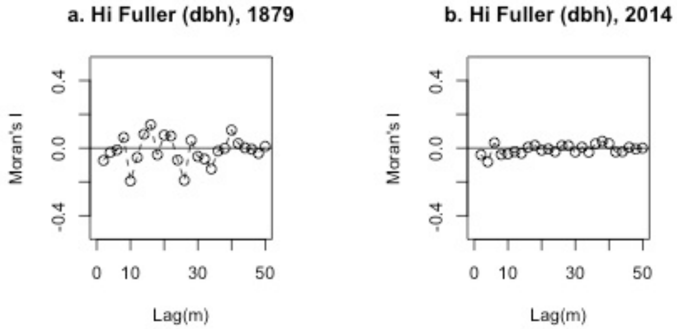
c. Hi Fuller, 1879 — Ecological Importance Value

ABCO	32.5
ACGR	0
PIST	5.1
PSME	14.9
QUGA	38.4
RONE	0
SASC	0
PIPO	105.5
POTR	3.7

d. Hi Fuller, 2014 — Ecological Importance Value

ABCO	55.2
ACGR	0
PIST	3.4
PSME	99.9
QUGA	7.4
RONE	0
SASC	0
PIPO	33.5
POTR	0.6

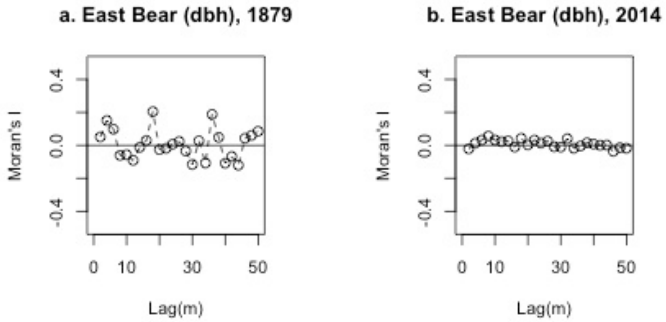
Figure 3: Changes on the Hi Fuller site on the Mogollon Rim, AZ, USA between 1879 (dendrochronological reconstruction) and 2014 (observed). Panels include historical (a) and contemporary (b) stemmaps scaled by canopy area, historical (c) and contemporarily (d) diameter distributions for all live trees ≥ 5cm diameter at breast height (1.37m above ground level), and live standing age distribution (e). Note that the y-axes on panels c-e are broken with differing scales below and above the break. Colors for each species are scaled by relative shade tolerance ranging from blue (most shade tolerant) to red (least shade tolerant).



a. Hi Fuller (dbh), 1879

b. Hi Fuller (dbh), 2014

Figure 4: Correlograms for the Hi Fuller site on the Mogollon Rim, AZ, USA based on (a) reconstructed (1879) diameter, and (b) contemporary (2014) diameter. Black points indicate statistical significance (α=0.05) at a given lag distance after Bonferroni correction for multiple comparisons. White points are not significantly different from the expected value at a given lag distance. Significance at small-scales indicates the presence of tree groups (where patch radius = lag distance) with relatively similar diameters.



a. East Bear (dbh), 1879

b. East Bear (dbh), 2014

Figure 5: Correlograms for the East Bear site on the Mogollon Rim, AZ, USA based on (a) reconstructed (1879) diameter, and (b) contemporary (2014) diameter. Black points indicate statistical significance (α=0.05) at a given lag distance after Bonferroni

correction for multiple comparisons. White points are not significantly different from the expected value at a given lag distance. Significance at small-scales indicates the presence of tree groups (where patch radius = lag distance) with relatively similar diameters.

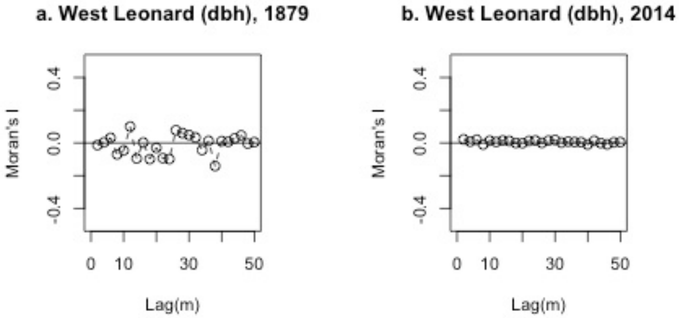


Figure 6: Correlograms for the West Leonard site on the Mogollon Rim, AZ, USA based on (a) reconstructed (1879) diameter, and (b) contemporary (2014) diameter. Black points indicate statistical significance (α=0.05) at a given lag distance after Bonferroni correction for multiple comparisons. White points are not significantly different from the expected value at a given lag distance. Significance at a small-scales indicates the presence of tree groups (where patch radius = lag distance) with relatively similar diameters.

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Study Location	Method of Reconstruction	Number of Mixed Conifer Plots	Plot Size (Hectares)	Est. Patch Size (Acres)
Uncompahgre Plateau, CO [1, 2]	Diameter/Tree Morphology	24	0.2 – 0.4	0.003 - 0.5
Grand Canyon, N. Rim, AZ [3]	Diameter/Dendrochronology	5	0.1	0.01-0.08
Grand Canyon, N. Rim, AZ [4]	Diameter/Dendrochronology	10	0.1	0.001-0.08
Baja California, Mexico [5]	None, fire regime is undisturbed	65	0.1	N/A
Baja California, Mexico [6]	None, fire regime is undisturbed	2	1	0.004-0.03
Sierra National Forest, CA [7]	Diameter/Dendrochronology	18	4	0.06-0.72
Yosemite National Park, CA [8]	Diameter/Tree Morphology	1	25.6	0.05-0.30
Stanislaus-Tuolumne Experimental Forest, CA [9]	Historical survey in 1929	3	4	0.02-0.30
Okanogan-Wenatchee National Forest, WA. [10]	Diameter/Dendrochronology	1	1	0.02-0.25
Swan Valley, MT [11]	Diameter/Dendrochronology	2	1	0.02-0.25
Boulder, CO [12]	Diameter/Dendrochronology	1	0.5	0.05
Front Range, CO [13]	Diameter/Dendrochronology	20	1	0.09

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Table 2: Total live trees ha^{-1}, historically (1879) and contemporarily (2014), for study sites on the Mogollon Rim, AZ, USA. Results are reported by species, site, and total.

Site	Year	ABCO	ACGR	PIPO	PIST	POTR	PSME	QUGA	RONE	SASC	Total
Hi Fuller	1879	25	0	61	1	4	8	31	0	0	130
	2014	115	0	68	9	1	216	18	0	0	427
East Bear	1879	13	0	97	0	0	14	25	0	0	149
	2014	140	0	230	20	0	60	79	45	0	574
East Barbershop	1879	26	5	23	0	23	15	66	1	0	159
	2014	353	186	19	16	3	146	161	20	3	907
West Leonard	1879	10	0	45	14	0	11	0	0	0	80
	2014	317	0	93	92	2	558	7	0	0	1069
Mean (sd) 1879		18.5 (8.19)	1.25 (2.5)	56.5 (31.17)	3.75 (6.85)	6.75 (11)	12 (3.16)	30.5 (27.21)	0.25 (0.5)	0	129.5 (35.12)
Mean (sd) 2014		231.25 (121.13)	46.5 (96)	102.5 (90.39)	34.25 (38.77)	1.5 (1.29)	245 (218.2)	66.25 (70.66)	16.25 (21.36)	0.75 (1.5)	744.25

Table 3: Basal area m^2 ha^{-1}, historically (1879) and contemporarily (2014), for study sites on the Mogollon Rim, AZ, USA. Results are reported by species, site, and total.

Site	Year	ABCO	ACGR	PIPO	PIST	POTR	PSME	QUGA	RONE	SASC	Total
Hi Fuller	1879	1.51	0	6.68	0.49	0.07	1.00	1.66	0	0	11.40
	2014	12.10	0	7.52	0.56	0.15	21.09	1.36	0	0	42.77
East Bear	1879	1.20	0	8.92	0	0	1.88	0.99	0	0	12.99
	2014	11.52	0	23.21	0	0	6.39	3.10	0.36	0	44.57
East Barbershop	1879	3.08	0.09	2.69	0	1.04	1.47	2.61	0.02	0	11.01
	2014	14.36	2.70	3.94	0.75	0.57	11.97	8.76	0.24	0.07	43.36
West Leonard	1879	0.39	0	2.57	1.29	0	0.70	0	0	0	4.94
	2014	7.91	0	5.96	4.30	0.09	18.59	0.10	0	0	36.94
Mean (sd) 1879		1.54 (1.13)	0.02 (0.05)	5.21 (3.12)	0.45 (0.61)	0.28 (0.51)	1.26 (0.52)	1.32 (1.1)	<0.01	0.00	10.09 (3.54)
Mean (sd) 2014		11.47 (2.68)	0.67 (1.35)	10.16 (8.83)	1.4 (1.96)	0.2 (0.25)	14.51 (6.64)	3.33 (3.82)	0.15 (0.18)	0.02 (0.03)	41.91 (3.4)

Table 4: Summaries of fitted models used to predict crown radius from diameter at stump height.

Species Code	Formula[y]	N	R^2 Value
ABCO	C.R.=0.2448*DSH^0.6058	336	0.8792
ACGR	C.R.=0.296*DSH^0.6026	60	0.3424
PIPO	C.R.=0.1791*DSH^0.6833	170	0.7629
PIST	C.R.=0.2354*DSH^0.6611	57	0.8837
POTR[z]	C.R.=0.6024*DSH^0.4209	51	0.29
PSME	C.R.=0.2586*DSH^0.5999	363	0.8627
QUGA	C.R.=0.2528*DSH^0.6247	150	0.1916
RONE	C.R.=0.2024*DSH^0.5171	27	0.318

[y] Formulas are all power functions and predict crown radius (in meters) from diameter at stump height (in centimeters)

[z] Formula for POTR (*Populus tremuloides*) developed from data on the San Francisco Peaks, AZ, USA, because of sample-size limitations on the Mogollon Rim (n=4)