DRIVERS OF VARIABILITY IN DRY MIXED-CONIFER FORESTS OF THE MOGOLLON RIM, ARIZONA

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ABSTRACT

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The structure and composition of southwestern dry mixed-conifer forests has changed significantly since Euro-American settlement and fire regime disruption in the late 1800s. This change in forest condition has decreased their resiliency to disturbance events, endangering the important ecosystem services these forests provide. Restoration of southwestern dry mixed-conifer forests is informed by a historic range of variability, however, managers and researchers still lack a full understanding of how environmental conditions drove historic forest conditions. My study investigates the variation of southwestern dry mixed-conifer forests on the Mogollon Rim in northern Arizona, and (1) compares the historical and contemporary ranges of variability, and (2) identifies important environmental drivers of historical and contemporary variation in these forests. I utilize forest inventory surveys from 2014 and dendrochronological reconstruction modelling to describe the distribution of historical forest structure in 1879. Additionally, I use Moran's I correlogram analysis to measure the degree of spatial autocorrelation in the forest at each time period. To further identify important drivers of forest variation, I use structural equation modeling techniques to describe the causal pathways between forest structure, forest composition, and a suite of environmental factors drawn from measures of climate, topography, and soil.

Forest structure on the Mogollon Rim has changed significantly from the historic (1879) to contemporary (2014) time periods. Density increased from an average of 174 (50 – 350) to 809 (200 – 2395) trees per ha, basal area increased from 18.3 (1.8 – 66.5) to 32.0 (11.5 – 58.2) m^2 per ha, and average tree diameter decreased from 29.4 (13.2 – 55.1) to 20.8 (8.5 -37.9) cm. These results are similar to the historic range of variability found in other dry mixed-conifer forests in the Southwest. I found that the historical forest structure was not significantly spatially autocorrelated, while contemporary density and diameter had significant autocorrelation at distances under 400m. This suggests that forests were historically heterogeneous at multiple spatial scales, and that contemporary forests may be forming more homogeneous stands. I found that contemporary measures of climate, topography, and soil tend to have stronger correlation with forest structure and composition than historically, and I describe the changes to the relative strengths of important environmental pathways. My findings suggest that fire regime disruption has altered the structure, composition, and environmental drivers of variation in dry mixed-conifer forests. Managers can utilize this increased understanding of variation to tailor restoration treatments to the environmental template of each site.

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Preface

The following thesis was written in the journal format described by the Northern Arizona University Graduate College. Chapter 3 has been written and formatted for submission to a peer reviewed journal yet to be determined, and is intended to stand on its own. For this reason, there is some redundancy between the following chapters.

Chapter 1: Introduction

Dry forests across the southwestern United States have changed significantly over the last century, posing a monumental challenge for forest managers. Land use practices following Euro-American settlement in the late nineteenth century led to these changes. Unregulated logging removed many large, fire-resistant trees, providing space for many small young trees to establish. Overgrazing decreased and broke the continuity of fine surface fuels that maintained a natural fire regime of frequent, low to mixed severity fires. This disruption of the fire regimes is evident in the fire record and was perpetuated by active fire suppression in the early twentieth century (Bahre, 1998; Cooper, 1960; Savage and Swetnam, 1990).

Disruption to the frequent fire regime has led to widespread increases in forest density, as well as changes to forest composition (Reynolds et al., 2013), decreasing their resilience to disturbances such as, insects, drought, and fire (Bryant et al., 2019), and possible conversion to non-forested ecosystems (Walker et al., 2018). This decreased resilience endangers the ecosystem services that they provide, such as watershed protection (O'Donnell et al., 2018) and wildlife habitat for endangered species (Margolis and Malevich et al,. 2016; Wan et al., 2017). With drought and severe wildfire expected to increase as climate change progresses (Westerling et al., 2006; Allen et al., 2010; Westerling 2016), restoring the resilience of these forests is an immediate concern for forest manager (Allen et al., 2019).

Ecological restoration of these forests has been advocated as a way for managers to address these changes (Allen et al., 2002). In its most general definition, ecological restoration is the "process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed," and seeks to set these ecosystems on an appropriate trajectory towards sustainable ecosystem functioning (SER, 2004). The concept of a historical range of variability is often used to guide reference conditions and evaluate the success or progress of restoration efforts (Keane et al., 2009). This concept describes the range of conditions that varied through time and space, that were present during the development of ecosystems or the evolution of species (Landres et al., 1999). Historically guided ecological restoration has proven effective at increasing understory abundance (Abella and Springer, 2015) and soil functioning (Sánchez Meador et al., 2017), and reducing the severity of modeled fire behavior (Fulé et al., 2012; Kalies and Yocom Kent, 2016) and the likelihood of post-disturbance conversion to non-forested ecosystems.

My study focuses on informing a better understanding of the historical variability in dry mixed-conifer forests in the Southwest. Like many dry forests in the west, this ecosystem type has experienced significant changes to forest structure and composition as a result of frequent fire regime disruption (Reynolds et al., 2013). These complex forests are generally found at intermediate elevations of 2270 to 3030m, and positioned higher than ponderosa pine (*Pinus ponderosa*) forests and lower than spruce-fir forests (Romme et al., 2009). Historically, these forests were open, relatively low density, and dominated by fire tolerant ponderosa pine, arranged as a individuals or groups of trees in a matrix of grassy openings (Larson and Churchill, 2012; Reynolds et al., 2013). With the absence of natural fire regimes for over one hundred years, shade-tolerant/fire-intolerant species have filled in these forests, making them denser, more closed, and forming larger, denser groups of trees, with fewer openings (Romme et al., 2009; Reynolds et al., 2013). These trends have been observed in mixed-conifer forests across the Southwest (Fulé et al., 2002, 2003, 2009; Cocke et al., 2005; Heinlein et al., 2005; Huffman et al., 2015; Strahan et al., 2016; Rodman et al., 2016, 2017). While the historical conditions of ponderosa pine forests have been extensively studied, mixed-conifer forests in the Southwest are not as well studied (Larson and Churchill, 2012; Reynolds et al., 2013; Wassermann et al., 2019).

My study seeks to improve the understanding of variability in southwestern mixed conifer forests by addressing the following research questions: (1) What was the historical range of variability in warm/dry mixed-conifer forests on the Mogollon Rim? (2) How did forest conditions vary spatially across mid-scales, and has spatial variation changed since fire exclusion? and (3) What were the drivers of variability in historical warm/dry mixed-conifer forests of the Southwest, and how have they changed? My findings advance the understanding of the historical range of variability in dry mixed-conifer forests, guide restoration goals, and comment on the relevance of historical conditions to contemporary ecosystems.

The chapters of the following thesis explore these research questions. Chapter two is a comprehensive literature review covering ecological restoration, current knowledge of the historical range of variability in southwestern mixed-conifer forests, the drivers of variability in these forests. Chapter three is an empirical study evaluating the historical conditions and drivers of variability in a dry mixed-conifer forest on the Mogollon Rim, in northern Arizona. Chapter four describes the implications this research has for the ecological restoration of these forests.

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Chapter 2: Literature Review

Introduction

Mixed-conifer forests are an important ecosystem covering 1 million hectares in the Southwest (Dieterich, 1983). These forests provide important ecosystem services such as watershed protection (O'Donnell et al., 2018), carbon sequestration, and nutrient cycling (Kalies and Yocom Kent, 2016; Sánchez Meador et al., 2017). They also provide critical wildlife habitat for multiple protected species, such as the Mexican spotted owl (*Strix occidentalis* lucida) (Wan et al., 2017) and the Jemez Mountains salamander (*Plethedon neomexicanus*) (Margolis and Malevich, 2016).

The community and composition of mixed-conifer forests in the Southwest have changed because of land management practices. These land management practices disrupted the natural fire disturbance regime that maintains these forests. Euro-American settlement varies through the region, and most settlement was complete by the end of the 1800s in northern Arizona (Bahre, 1998; Cooper, 1960). Sheep and cattle grazed in significant numbers almost immediately following settlement. This intense, unregulated, grazing disrupted the fine fuels in the understory that carry fire and maintain a frequent fire regime. Overharvesting of timber, focused on removing larger trees, also changed the structure of mixed-conifer forests in the Southwest by opening the overstory and allowing regeneration (Bahre, 1998; Cooper, 1960; Savage and Swetnam, 1990). Grazing, logging, and eventually active fire suppression combined to cause widespread fire regime disruption across the Southwest.

The changes to these forests caused by fire regime disruption have made them vulnerable to disturbances such as severe wildfire, drought, insects, disease, and climate change (Reynolds et al., 2013; Bryant et al., 2019). Ecological restoration of these forests has been suggested as a way to address these changes (Allen et al., 2002). Ecological restoration is broadly defined as the "process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed," and seeks to set these ecosystems on a trajectory towards sustainable ecosystem functioning (SER, 2004). Effective ecological restoration is guided by a reference ecosystem that serves as a model for setting restoration goals as well as evaluating progress towards those goals (SER, 2004). Using an existing, unaltered ecosystems as a reference is often preferable, however, due to the widespread nature of fire regime disruption few mixed-conifer forests remain unaffected.

When extant examples of reference conditions are not available locally, managers may use the conditions that were present prior to disruption as the reference. The concept of a historical range of variability (HRV) describes the range of conditions that were present during the development or evolution of ecosystems or species (Landres et al., 1999; Keane et al., 2009). It is important that HRV provides more than just a snapshot of the past, and that it describes a range of conditions that vary over time and space. Use of HRV to guide restoration is based on two key concepts: "(1) that past conditions and processes provide context and guidance for managing ecological systems today, and (2) that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems" (Landres et al., 1999). The application of HRV restoration reasons that it by approximating a range of conditions that were present during a species evolutionary history, conditions that will continue to sustain that species will likely be present. These historical conditions also are assumed to be sustainable over time and resilient to disturbances, and by approximating these conditions managers hope to set the ecosystem on a sustainable trajectory (Landres et al., 1999; SER, 2004). The use of HRV to guide restoration is not without limitations; limited data, spatial and temporal autocorrelation, and scale effects are just some of the considerations managers need to assess (Keane et al., 2009). There is also concern that historical conditions may no longer be appropriate guides for contemporary ecosystems. As climate change progresses, future climate conditions are expected to differ significantly from the conditions that were present during ecosystem development and species evolution and invasive species are often unfeasible to remove, with the latter permanently altering community composition. (Millar et al., 2007, 2014).

However, there is significant research indicating that restoring dry forests such as ponderosa pine and dry mixed-conifer can be beneficial. Restoration treatments in these forests typically involve mechanical thinning, prescribed fire, or a combination of both (Fulé et al., 2012; Abella and Springer, 2015; Sánchez Meador et al., 2017). Restoration treatments that combine both thinning and prescribed burning are more effective at maintaining target conditions (Stoddard et al., 2015), increase long-term understory vegetation abundance (Abella and Springer, 2015), increase soil function and nutrient cycling (Sánchez Meador et al., 2017), and decrease the severity of modeled fire behavior (Fulé et al., 2012; Kalies and Yocom Kent, 2016). Restoring forests guided by historical conditions can increase resilience to disturbance (Reynolds et al., 2013; Bryant et al., 2018), reduce the likelihood of conversion to non-forested ecosystems (Walker et al., 2018), and protect water resources (O'Donnell et al., 2018). Restoration treatments can also create spatial patterns that are consistent with historical conditions (Churchill et al., 2013; Larson et al., 2012; Cannon et al., 2019), and these restored forests also have a reduced risk of severe wildfire (Ziegler et al., 2017). Land managers in the Southwest are incorporating HRV into their management objectives and planning documents (Reynolds et al., 2013; Addington et al., 2018; Evans et al., 2011).

While there has been extensive research on the historic range of variability in southwestern ponderosa pine forests, there is still a need for more research on mixed-conifer forests in this region (Reynolds et al., 2013) A recent review of HRV in southwestern forests found more than twice as many studies in ponderosa pine than in dry mixed-conifer forests (Wassermann et al. 2019). Additional research is needed to understand the drivers of variability in these highly variable forests. In this review, I will discuss the methods used to determine HRV in dry mixed-conifer forests, the current state of knowledge of HRV in southwestern dry mixed-conifer forests, and the current state of knowledge concerning the drivers of variability in dry mixed-conifer forests.

Determining the historical range of variability in western forests

Researchers use a variety of methods to determine HRV in western dry forests, including historical accounts, historical surveys, and reconstruction techniques. While historical accounts may be qualitative, they can be useful ways of describing HRV and corroborating other lines of evidence. Woolsey's (1911) description of ponderosa pine stands as "a pure park-like stand made up of scattered groups of 2 to 20 trees" is often cited as to describe historical conditions in ponderosa pine forests. Cooper's (1960) consolidation of historical accounts give similar descriptions of open, park-like forests of ponderosa pine. Unfortunately, these accounts do not describe conditions in mixed-conifer forests

Historical forest surveys are another line of evidence used to determine the historical conditions of forests in across the west. Detailed surveys from experimental forests that mapped trees out have been vital to understanding historical conditions in southwestern ponderosa pine forests (Sánchez Meador and Moore, 2008). These types of surveys have been used to understand fine scale patterns in ponderosa pine forests, and to validate reconstruction models (Huffman et al., 2001; Moore et al., 2004; Sánchez Meador et al., 2010). Stephens et al. (2018) used historical timber surveys to evaluate historical cool/moist mixed-conifer conditions in the Sierras. There is a wide variety in the availability and quality of these surveys and unfortunately, detailed historical surveys are typically small in extent, limiting their ability to make inferences to the wider landscape. In the Southwest, detailed historical surveys are confined to ponderosa pine forests, limiting forest managers' ability to understand historical conditions in mixed-conifer forests.

General Land Office surveys have also been used to determine historical conditions. GLO studies from the early 1900s, while spatially extensive, have a very low sampling density, only 1 point per 800m, with only 2 to 4 trees per point (Levine et al., 2017). To account for the sparse survey design, researchers use plotless density estimators to determine historical conditions (Williams and Baker, 2011). These surveys have also been used to determine historical conditions in dry forests in the Southwest (Williams and Baker, 2012), however there are concerns about the reliability of these estimates (Levine et al. 2017). These concerns suggest that previous density estimates from calculated from GLO surveys (Williams and Baker, 2011, 2012) tend to overestimate forest densities.

When the availability of historical surveys is not adequate, an alternative strategy is to reconstruct the historical forest conditions from contemporary forest surveys. The historical forest conditions can be reconstructed from contemporary surveys using reconstruction methods developed by Huffman et al. (2001), Bakker et al. (2008), Sánchez Meador et al. (2010), and recently updated by Rodman et al. (2016). This reconstruction model uses dendrochronological data and “back-growth” regression equations to estimate the diameter of each tree in a plot during a set reconstruction year. Historic diameters for live trees are based on dendrochronological increment data collected on site and adjusted using bark thickness equations developed by Myers (1963) and Laughlin et al. (2011), and locally developed dbh-dsh relationship equations. For trees without increment data, species-specific “back-growth” equations are used to estimate the historical diameter. These equations calculate the historic inside-bark diameter using log-log regression, and inputs for the inventory and targeted reconstruction years, inside-bark diameter at the inventory year, and species-specific coefficients. Historic diameters for currently dead trees are estimated by using current diameter and decomposition equations based on snag/log class to determine death date, and then input into the “back-growth” equations to estimate the diameter during the reconstruction year.

Dendrochronological reconstruction techniques are appropriate where slow decomposition and an absence of fire mean that evidence of pre-settlement forest structure is still apparent, such as in the Southwest (Huffman et al., 2001; Moore et al., 2004) or the Colorado Front Range (Battaglia et al., 2018). Evidence of small trees that were present historically may be missed by the model, but historical accounts and the frequency of fires suggests that these small trees did not contribute significantly to the overall historic forest structure. Additionally, sensitivity analysis has shown the model to be robust, and comparisons to historical surveys indicate that 91 to 94 percent of pre-settlement trees can be identified by contemporary surveys (Huffman et al., 2001; Moore et al., 2004). The model was originally developed for use in ponderosa pine forests near Flagstaff, AZ, and most research using this model is constrained to ponderosa pine forests. Recently, Rodman et al. (2016) expanded the model for use in southwestern dry mixed-conifer forests by incorporating 'back-growth' equations for additional species. These methods continue to be used to determine historical conditions in both ponderosa pine and dry mixed-conifer forests of the Southwest (Cocke et al., 2005; Fulé et al., 2009; Rodman et al., 2016)

Fire regimes are an important part of HRV, and there are also a variety of tools that researchers use to make study historical fire regimes. One of the most common is the use of fire scars. Fire scars can give a good estimate of the frequency of fire regimes, because a single tree can record multiple fires as the 'cat face' reburns and the tree heals over subsequent scars. (Swetnam and Baisan, 1996). However, not all fires scar all trees, so while a scar is definitive evidence of a fire, absence of a scar does not necessarily mean a fire did not occur (Swetnam and Baisan, 1996). Fire scars also have a long inference period, recording fires as early as the 1500s (Dieterich, 1983). Researchers take a probabilistic, opportunistic, or targeted approaches to sampling fire scars, and with targeted sampling being both efficient and accurate (Van Horne and Fulé, 2006; Farris et al., 2013). It is harder to use fire scar records to make inferences about severe fire regimes because these more intense fires will kill and/or consume a tree and any evidence it had recorded.

Analyzing the age structure of a stand can give good information about the severity of a fire regime. Odion et al. (2016) used the average stand age from Forest Inventory Analysis plots to make inferences about historical fire regimes. While this extensive network can be used to assess contemporary forest conditions (Stephens et al., 2018), researchers should use caution when using average stand age to make inferences about cohort establishment. Average stand age is not appropriate when applied to ponderosa pine and dry mixed-conifer forests, because stand initiation is not necessarily due to high-severity fire (Brown and Wu, 2005; Fulé et al., 2009). Additionally, stands that contain residuals older would be mischaracterized by the use of average stand age (Stevens et al., 2016).

Rather than relying only on average stand age, many studies utilize a more detailed analysis that groups trees in a stand into cohorts, alongside fire scar analysis (Fulé et al., 2003; Tepley and Veblen, 2005; Fulé et al., 2009; Margolis and Balmat, 2009; O'Connor et al., 2014; Huffman et al., 2015; Margolis and Malevich, 2016). Heyerdahl et al. (2012, 2014) documents a method for categorizing fire severity from tree age data and available fire scars: high severity fire regimes leave no fire scars and one cohort with no residual trees established prior to cohort; mixed severity fire regimes leave fire scars and have one or more cohorts, or one cohort with older residual trees. Low severity leaves fire scars but no distinct cohorts (Heyerdahl et al., 2012, 2014).

Historical range of variability in southwestern dry mixed-conifer forests

Structure

An increasing number of studies in southwestern dry mixed-conifer forests has begun to define HRV in terms structure. Historically tree density ranged from 89 to 247 trees ha^{-1}, and basal area ranged from 7.8 to 28.5 m^2 ha^{-1} (Reynolds et al., 2013). Another more recent review describes a similar, but slightly smaller range of 109 to 180 trees ha^{-1} and 11.6 to19.1 m^2 ha^{-1} for basal area (Wasserman et al., 2019). Rodman et al. (2016) found the historical tree density on the Mogollon Rim to be within the expected range for dry mixed-conifer (140 trees ha^{-1} and 10.3 m^2 ha^{-1}), however, contemporary conditions (1117 trees ha^{-1} and 42.3 m^2 ha^{-1}) are well outside the historical ranges. Similar trends of significant increases in density have also been observed in mixed-conifer forests on the San Francisco Peaks (Cocke et al., 2005; Heinlein et al., 2005), at the North Rim of the Grand Canyon (Fulé et al., 2003), at Black Mesa (Strahan et al., 2016), and in southwest Colorado (Fulé et al., 2009).

Historical conditions in dry mixed-conifer forests outside the Southwest are generally similar to those in the Southwest. Reference conditions on the Front Range of Colorado and southern Wyoming are fairly similar to those in the Southwest and have also experienced significant increases in basal area and tree density (Brown et al., 2015; Battaglia et al., 2018). Mixed-conifer in the Sierra Nevada in California (Collins 2011, 2015; Lydersen et al., 2013; Stephens et al., 2015, 2018) and the Cascades and central mountains in Oregon (Hagmann 2013, 2014, 2017, Merschel 2014) had wider historical ranges that included denser forests than typically found in the Southwest. While basal area and tree density have increased significantly in Oregon forests, some Sierra mixed-conifer only saw significant increases in tree density (Stephens et al., 2015, 2018).

Dry mixed-conifer forests were historically relatively open, similar to conditions reported for ponderosa pine forests (Romme et al., 2009). Reference canopy cover has been reported at 13 to 21%, however Reynolds et al. (2013) acknowledge that there is little data for reference openness (which they defined as the inverse of canopy cover) in dry mixed-conifer forests in the Southwest. Mixed-conifer in the Sierra Nevada also had low canopy cover, ranging from 20 to 30%, though contemporary forests have significantly higher cover (Collins et al., 2011; Stephens et al., 2015). Mixed-conifer forests on the San Francisco Peaks also have a high contemporary canopy cover of 66% (Cocke et al., 2005).

The spatial arrangement of these conditions is another important aspect of forest structure. Fine-scale patterns in ponderosa pine forests are characterized by groups of trees and scattered individual trees arranged in a matrix of grass-forb-shrub openings (Larson and Churchill, 2012; Reynolds et al., 2013), and dry mixed-conifer forests were hypothesized to have similar historical patterns (Reynolds et al., 2013). However, recent research has found fine scale patterns to be highly variable, finding both aggregated and random tree patterns in historical conditions (Binkley et al., 2008; Lydersen et al., 2013; Rodman et al., 2016, 2017). The high variability in the level of aggregation found in mixed conifer is linked to the variability in species composition found in these forests; spatial patterns are known to differ between species (Rodman et al. 2016; Clyatt et al. 2016). Larson and Churchill's (2012) review that much of the previous research has been focused on the fine-scale patterns, and that ponderosa pine forests in northern Arizona and mixed-conifer forests in the Sierra Nevada. The spatial patterns of mixed-conifer forests largely un-analyzed (Larson and Churchill, 2012; Reynolds et al. 2013), and only recently have studies addressed this knowledge gap (Rodman et al., 2016, 2017).

Composition

These forests are diverse and can be difficult to define precisely. In the Southwest, these forests are typically found at elevation of 2270 m to 3030 m and are generally positioned between lower elevation ponderosa pine forests and higher elevation spruce-fir forests, and will intergrade with these forests at the boundaries (Romme et al., 2009). Species composition in mixed-conifer forests vary along a continuum that is often broken into two categories, 'warm' or 'dry' and 'cool' or 'wet.' The overstory community in dry mixed-conifer are defined by low shade tolerance, higher drought tolerance, and frequent-fire adapted traits. They are dominated by ponderosa pine (*Pinus ponderosa*), and includes minor components of Gambel oak (*Quercus gambelii*), Douglas-fir (*Pseudotsuga menziesii*), and may include southwestern white pine (*Pinus strobiformis*). Additional species found in dry mixed-conifer stands on the Mogollon Rim include New Mexico locust (*Robinia neomexicana*) and bigtooth maple (*Acer grandidentatum*) (Rodman et al. 2016).The understory community in dry mixed-conifer forests includes the shrubs *Amelanchier alnifolia*, *Arctostaphylos uva-ursi, Chimaphila umbellatum, Mahonia repens, Symphoricarpos rotundifolius,* and the herbs and grasses *Achillea lanulosa, Antennaria rosea, Carex geyeri, Delphinium nelson, Elymus elymoides, Erigeron formosissimus, Geranium caespitosum*, *Koeleria macrantha, Lathyrus leucanthus, Mertensia fusiformis*, *Poa fendleriana*, *Poa pratensis*, *Potentilla hippiana*, *Pseudocymopterus montanus,* and *Solidago simplex.* (Romme et al., 2009).

The overstory story community in wet mixed-conifer forests are defined by higher shade tolerance, lower drought tolerance, and lower fire adaptedness. These forests typically do not contain ponderosa pine, and instead contain greater numbers of Quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), Subalpine fir (*Abies lasiocarpa*) and white fir (*Abies concolor*). The understory community in wet mixed-conifer forests includes the shrubs *Lonicera involucrata, Rubus parviflorus, Sambucus microbotrys,* and *Vaccinium myrtillis,* and the herbs and grasses *Actaea rubra, Aquilegia elegantula, Arnica cordifolia, Artemisia franserioides, Bromopsis canadensis, Carex geyeri, Erigeron eximius, Erythronium grandiflorum, Fragaria vesca, Geranium richardsonii, Goodyera oblongifolia, Lathyrus leucanthus, Ligusticum porteri, Luzula parviflora, Maianthemum stellatum, Mertensia ciliata, Oreochrysum parryi, Orthilia secunda, Osmorhiza depauperata, Pedicularis racemosa*, *Pyrola minor,* and *Viola canadensis* (Romme et al., 2009).

Researchers have also described the changes to the composition of dry mixed-conifer forests in the Southwest. While these forests were historically dominated by ponderosa pine, species composition has shifted towards more shade-tolerant and fire-intolerant species (Reynolds et al., 2013). In southwestern Colorado, Fulé et al. (2003) found that ponderosa pine decreased by about half of its pre-settlement basal area by 2003, while white fir increased by six times and became the numerically dominant tree species in the study area. A similar trend has been found on the Mogollon Rim, where white pine, white fir, and Douglass-fir all increased in relative abundance (Huffman et al. 2015; Rodman et al. 2016). These changes in composition represent a decrease in community resilience to drought and fire (Strahan et al., 2016). While dry mixed-conifer forests occur at sites that can support cooler species such as white fir, these species have a lower fire tolerance, and the frequency of historical fire regimes likely kept these species restricted to cooler microsites and north facing slopes (Reynolds et al. 2013; Huffman et al. 2015)

Disturbance regimes

The characteristics of disturbances greatly influence the structure and composition of forests. In southwestern dry mixed-conifer forests, a fire regime consisting of frequent, low- to mixed-severity fires is understood to be important to maintaining forest conditions (Reynolds et al., 2013). On the more frequent end of the spectrum, researchers have estimated mean fire intervals (MFI) of 2 to 8.5 years on the Mogollon Rim (Huffman et al., 2015) and 4 to 14 years in the Sacramento Mountains (Brown et al., 2001); and 3 to 21 years on the San Francisco Peaks (Heinlein et al., 2005). Other researchers have found longer and more variable fire intervals that suggest a more mixed-severity fire regime – 12.4 to 31.6 years in northern New Mexico (Margolis and Balmat, 2009); 10 to 42 years in the Jemez Mountains (Margolis and Malevich, 2016); and 9 to 30 years in southwestern Colorado (Korb et al. 2013). Fire regimes can vary significantly over relatively short distances, emphasizing the need for managers to understand the site-specific characteristics of the fire regime in their area. (Korb et al., 2013).

There is debate about the role high-severity fire plays in the natural fire regime of southwestern dry mixed-conifer forests. While there is agreement that high-severity fires were historically present in these forests, there is disagreement about how ecologically significant these fires were (Odion et al., 2016). Some research suggests that dry mixed-conifer forests historically experienced mixed- to high-severity fires (Williams and Baker, 2012; Odion et al., 2014). Other research indicates that high-severity fires only affected 4 to 6% of the landscape (Stephens et al., 2015). Yocom-Kent et al. (2015) found high-severity fire to vary widely, with patch sizes ranging from 0.1 to 100 hectares.

After approximately one hundred years of fire suppression, the contemporary fire regime differs significantly from historical patterns. Across the western united states, there has been an increase in the size and number of large and severe forest fires since the 1980s (Westerling et al. 2016). In the sky islands of southern Arizona, the recent fire regime diverges significantly from the historical range of variability, with the proportion of high severity fire increasing four times since approximately 1880 (O'Connor et al. 2014).

Drivers of Variability

Dry mixed-conifer forests are highly variable, and while it is useful for forest managers to use a range of conditions to guide restoration activities, it is important to understand the processes that drive this variation. Such knowledge could help to further guide restoration within HRV and tailor prescriptions to site conditions. Fire, climate, soil, and topography are all important factors that drive forest condition.

Fire and other disturbances

In frequent fire forests such as dry mixed-conifer, fire is the primary disturbance agent that shapes forest conditions. Fire impacts species composition: shorter fire return intervals favor fire adapted species like ponderosa pine while longer fire return intervals allow fire-intolerant species such as white fir to establish and persist (Reynolds et al., 2013). Different species have varying recruitment responses after a fire. Fulé et al. (2009) found that the majority of aspen and spruce-fir stands were fire initiated, but half of ponderosa pine stands and the majority of dry mixed-conifer stands were not fire initiated. Tepley and Veblen (2015) found ponderosa pine, aspen, and Douglas-fir to be dependent on post-fire recruitment, while white fir recruits independently of fire timing. However, ponderosa pine regenerates in lower density in the interior of large, high-severity burn patches (Owen et al., 2017).

Dense forests with closed canopies can carry active crown fires which are severe and have high mortality, while more open forests support less severe surface fires (Reynolds et al., 2013). Mixed severity fire leads to heterogeneous and clumpy forest structure (Malone et al. 2018). Perhaps the best evidence demonstrating the importance that fire has in shaping the conditions of dry mixed-conifer forests are the numerous studies that have found changes to forest composition and structure after fire has been removed from the landscape (ex: Fulé et al., 2009; Huffman et al., 2015; Rodman et al. 2016; Strahan et al., 2016).

Aside from fire, pests and pathogens are disturbances that cause mortality in dry mixed-conifer forests. Bark beetles affect ponderosa pines, which can form a major component of dry-mixed conifer stands (Reynolds et al., 2013). Douglas-fir and Fir engraver beetles caused approximately 36,000 hectares of mortality in mixed-conifer forests in the Southwest in both 2013 and 2014 (USDA Forest Service, 2019). Defoliating insects such as spruce budworm and Douglass-fir tussock moth will also impact dry mixed-conifer species (Reynolds et al., 2013). Aspen is host to several defoliators and parasites, which contribute to the decline in aspen health and regeneration in the Southwest (USDA Forest Service, 2019). Parasites such as southwestern (ponderosa pine) dwarf mistletoe and Douglas-fir mistletoe infect about half of mixed-conifer forest acreage in the Southwest (Conklin and Fairweather, 2010). Soil fungi cause root diseases (such as Armillaria and Heterobasidion root diseases) and can cause changes to forest composition (Reynolds et al., 2013). White pine blister rust affects southwestern white pine, and has caused severe damage in the Sacramento Mountains, NM (USDA Forest Service, 2019).

Climate

Climate is also an important driver of forest conditions in southwestern dry mixed-conifer. Fire, which is an important driver of variation, is dependent on weather, so fire-climate interactions are one way that climate impacts forests. Superposed epoch analysis – a comparison of the climatic conditions before, during, and after multiple fire years – is frequently used to investigate this fire-climate relationship. Research suggests that widespread fire typically occurs during drought years, a similar relationship to lower elevation ponderosa pine forests (Swetnam and Baisan, 1996). However, unlike in ponderosa pine forests where fires are typically preceded by wet years, this relationship is generally not found in mixed-conifer forests (Swetnam and Baisan, 1996; Fulé et al., 2009; Margolis and Malevich, 2016). In ponderosa forests wet years are needed to grow sufficient surface fuels to carry a surface fire, and dry years are then needed to make the fuels available to burn, this relationship is due to the importance of surface fuels limiting fires. The absence of this relationship to preceding wet years suggests that mixed-conifer forests are limited only by the availability of fuel, not its quantity (Swetnam and Baisan, 1996). Where this relationship appears in mixed-conifer forests, it might be explained by fire spreading from ponderosa pine forests into mixed-conifer (Margolis and Balmat, 2009).

Interestingly, fire-climate relationships have changed since Euro-American settlement into the Southwest. Meunier et al. (2014) found that historically, widespread fire occurred during drought years preceded by wet years, but that after the 19th century, only preceding wet years were important to this relationship. Swetnam et al. (2016) found an opposite change – historically, only preceding wet years were significant to the timing of fire years, while after Euro-American settlement only drought was significant. Mueller et al. (2020) has found that increasingly warm and dry conditions are driving the increase in forested area burned at high-severity, and the strength of this relationship has only gotten stronger over time. This disagreement further emphasizes the complexity of fire-climate and forest relationships and the large variability in mixed-conifer forests.

Aside from fire-climate relations, climatic wetness has important influences on mixed-conifer structure and composition. Vegetation has a strong relationship with climate, and climate has been used to explain up to half of the variability in overstorey species abundance in the Southwest (Laughlin et al., 2011). Wetter sites have the potential to support higher densities of trees than drier sites do. Stephens et al. (2018) found that historic density in fir-dominated mixed-conifer forests in the Sierras was driven by climatic factors associated with water availability, and after a history of logging and fire-exclusion these sites experienced large increases in small to medium trees. Similarly, wet sites on the Mogollon Rim have experienced greater increases in density than have dry sites (Rodman et al. 2017). In drier forests such as ponderosa pine, precipitation drives the number of seedlings (Puhlick et al. 2012), and episodic years of higher precipitation drives the timing of seedling recruitment, and contributes to the even-aged structure of these forests (Brown and Wu 2005; League and Veblen 2006). Drought has the capacity to rapidly change the boundary between lower elevation forest types (Allen and Breshears 1998). If this trend holds true in higher elevational forests, mixed-conifer (which is essentially a large, heterogeneous ecotone) forests may experience drastic changes as climate change continues.

Soil and topography

The effects that soils have on forest conditions has also been repeatedly studied in the Southwest. Multiple studies have found that soil parent material, and the soil characteristics that are associated with these differences are important drivers of forest structure and composition. Soil parent material drives differences in understory vegetation communities (Abella and Covington, 2006; Laughlin et al., 2007); differences in overstory growth and regeneration (Abella and Covington, 2006; Puhlick et al., 2012); overstory structure and pattern (Rodman et al., 2017; Abella and Denton, 2009); and stand density index (Kimsey et al., 2019). The differences in soil parent material are associated with and often measured by soil characteristics such as pH, organic Carbon, total Nitrogen, water capacity, and percent silt, clay. The availability of high-resolution soil data (Ramcharan et al. 2017) now makes it possible to evaluate the relationship between soil and forest conditions at a finer scale.

The importance of topography as a driver of forest variation is less clear than the other factors discussed above. Urban et al. (2000) modeled mixed-conifer forests in the sierras based on topographic variables (slope facets, elevation, drainages). In their model, these topographic variables drive the availability of water and the water demand of stands, which thus influence forest structure, and define the extent of mixed-conifer forest types. Similarly, Laughlin et al.

(2011) successfully used solar radiation along with soil and climate data to predict plant community composition. However, Abella and Covington (2006) suggest that the effects of soil and climate are more important than topography, but admit their study area was topographically simple. When evaluating the relative importance that abiotic factors have on dry mixed-conifer historical conditions, Rodman et al. (2017) similarly found that soil, climate and TEU were more important than the topographic factors evaluated. It can be difficult to distinguish the individual effects of abiotic factors that are tightly intertwined, and Korb et al. (2013) suggested that microsite variability in topography, climate, and soil account for the variability in forest conditions and fire regimes found across a relatively small extent in south western mixed conifer forests in Colorado.

Determining the relative importance of drivers

Structural equation models (SEM) provide an analytical framework that can help ecologists and restoration managers understand the complex relationships between multiple environmental drivers of variability and forest structure and composition. SEM describes "the use of two or more structural [cause-effect] equations to model multivariate relationships" (Grace, 2006). This modeling approach developed from path analysis (Wright, 1960), and modern SEM largely uses maximum likelihood procedures (Grace et al., 2010; Eisenhauer et al., 2015). SEM allows researchers to model multivariate relationships and feedback loops, explicitly evaluate direct and indirect causal relationships in ecological systems, and include unmeasured concepts as latent or composite variables (Grace and Bollen, 2008; Grace et al., 2010).

These qualities make SEM approaches ideal for analyzing complex ecological systems, and SEM has been used to evaluate the relative importance of environmental drivers in a variety of ecosystem processes. SEM has been used to understand nutrient cycling and ecosystem function (Bowker et al., 2013; Laughlin et al., 2015; Wallace et al., 2018), tree mortality (Youngblood et al., 2009), and seed dispersal (Johnstone et al., 2009). In southwestern forests, researchers have used SEM to understand relationships between environmental conditions, fire history, understory species richness and abundance (Laughlin and Grace, 2006; Laughlin et al., 2007), and ponderosa pine regeneration (Puhlick et al., 2012).

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Chapter 3: Environmental drivers of variability in dry mixed-conifer forests on the Mogollon Rim, Arizona

Introduction

Mixed-conifer forests cover approximately 1 million hectares in the Southwest (Dieterich 1983) and provide critical ecosystem services such as wildlife habitat (Wan et al., 2017), watershed protection (O'Donnell et al., 2018), carbon sequestration, and nutrient cycling (Kalies and Yocom Kent, 2016; Sánchez Meador et al., 2017). However, the resilience of these forests decreased as a result of fire regime disruption caused by 20th century forest management practices, specifically logging, grazing and active fire-suppression (Covington et al., 1994, Romme et al., 2009). Disrupting the frequent, low-severity fire regime characteristic of these forests has altered the structure and composition of dry mixed-conifer forests in the Southwest (Fulé et al 2009, Huffman et al., 2015, Strahan et al., 2016). This has decreased these forest's resilience to disturbances such as severe wildfire, insects, disease, and climate change (Reynolds et al., 2013, Bryant et al., 2019). Restoring the structure and composition of these forests can increase forest resilience, however all restoration efforts require a benchmark for reference conditions (SER 2004).

A historical range of variability (HRV) describes the spatial and temporal range of conditions that historically were characteristic for an ecosystem minimally affected by people and is often used as an indicator of reference conditions (Keane et al., 2009). Reliance on HRV in ecological restoration assumes that historical conditions provide context for managing contemporary ecosystems, and its application is based on the premise that by approximating the range of conditions that were present during a species evolutionary history, conditions that will sustain these species are likely present (Landres et al., 1999). While there has been criticism that historical conditions will become irrelevant under the novel climate conditions anticipated in the future (Millar et al., 2007), restoring these forests to a more fire-adapted composition and structure would increase ecosystem resiliency (O'Donnell et al., 2018; Reynolds et al., 2013). An increased resiliency may allow these ecosystems to resist transitioning to non-forested landscapes due to severe wildfires under unprecedented climate change (Reynolds et al., 2013; Bryant et al., 2019; Walker et al., 2018).

In mixed-conifer forests the historic range of variability has been measured in terms of both composition and density. Species composition varies along a temperature-moisture gradient. At one end of the spectrum, 'warm-dry' mixed-conifer is dominated by ponderosa pine (*Pinus ponderosa*) and can include other fire-tolerant/shade intolerant species such as Gambel oak (*Quercus gambelii*), Douglas-fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*). 'Cool-moist' mixed-conifer generally lacks ponderosa pine, and has a greater composition of fire-intolerant/shade-tolerant species such as Quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), and white fir (*Abies concolor*) (Romme et al., 2009). Species composition has shifted towards more shade tolerant species over the last 100+ years; ponderosa pine has decreased in dominance and the proportion of southwestern white pine and white fir have increased (Fulé et al., 2009; Huffman et al., 2015; Rodman et al., 2016; Strahan et al., 2016).

Forest structure has also changed from undisturbed conditions. Historically, dry mixed-conifer forests in the Southwest had densities ranging from 51.6 to 245.6 trees per hectare and basal areas of 7.9 to 28.5 m^2 per hectare (Reynolds et al., 2013), however, contemporary forest conditions across the southwest are much denser (Fulé et al., 2003, 2009; Cocke et al., 2005; Heinlein et al., 2005; Strahan et al., 2016; Rodman et al., 2016, 2017). These overly dense forests are at an increased risk of burning at high severity in an increasing number of large, high-severity fires across the Southwest (Westerling et al., 2006; Westerling 2016). This contemporary fire regime differs from the natural historical fire regime of frequent, low- to mixed- severity fires (Reynolds et al., 2013). Mean fire intervals were generally longer and more variable than in ponderosa pine forests, from as short at 2 to 8.5 years on the Mogollon Rim (Huffman et al., 2015) to multiple decades in northern New Mexico (Margolis and Balmat, 2009; Margolis and Malevich, 2016) and southwestern Colorado (Fulé et al., 2009).

While previous studies have described the natural range of variability, researchers still lack a full understanding of the relationships that drive forest conditions. Topography, climate and soil factors are known to influence forest condition. Topographic models and measures of solar radiation have been used to understand variation in forest structure and composition (Urban et al., 2000; Laughlin et al., 2011). Climate has strong interactions with fire frequency (Swetnam and Baisan, 1996; Fulé et al., 2009; Margolis and Malevich, 2016); and precipitation and climatic water availability drive variation in seedling establishment (Brown and Wu 2005; League and Veblen 2006; Puhlick et al., 2012) and overall tree density (Rodman et al., 2017; Stephens et al. 2018). Soil properties, especially parent material, also influence forest structure and composition (Abella et al. 2006; Abella and Denton, 2009; Rodman et al., 2017; Kimsey et al., 2019). However, forest managers still lack an empirical, biogeographic understanding of how these environmental factors drive variability.

Additionally, managers are lacking a complete understanding of spatial heterogeneity in dry mixed-conifer forests. Variability in forests is spatially structured, and this spatial heterogeneity is hierarchically organized. Fine-scale (<4 ha) patterns typically describe the arrangement of individual trees within a stand and are nested within mid-scale (4-400 ha) patterns, which describe the variation of stands within a landscape. These mid-scale patterns are further nested within landscape-scale (400+ ha) patterns. A review of spatial analyses in fire-frequent forests found that the majority of spatial analyses of reference conditions focus on fine-scale tree patterns of clusters of trees, single trees, and openings, that manifest at scales 0.4 to 4 ha (Reynolds et al. 2013), however these results might be difficult for forest managers to implement in their stand level treatments (Larson and Churchill 2012). Landscape restoration projects that implement fine scale patterns without incorporating higher-order heterogeneity risk creating a landscape that is heterogeneous at fine-scales, but homogeneous over mid- to landscape-scales (Larson et al., 2012). Rodman et al. (2016, 2017) describe random fine-scale tree patterns on the southwestern dry mixed-conifer forests. Williams and Baker (2012) found high variability in a landscape-scale analysis of dry mixed-conifer reference conditions, however the resolution of their analysis is too coarse to be useful at mid-scales. The lack of mid-scale analyses of heterogeneity in southwestern dry mixed-conifer forest limits managers from designing appropriate restoration projects.

My study addresses these knowledge gaps by investigating historical variability and drivers of variability in dry mixed-conifer forests on the Mogollon Rim in northern Arizona. Specifically, I focus on answering the following research questions: (1) What was the historic range of variability in warm/dry mixed-conifer forests on the Mogollon Rim? (2) How did forest conditions vary spatially across mid-scales, and has spatial variation changed since fire exclusion? and (3) What were the drivers of variability in historical dry mixed-conifer forests of the Southwest, and how have they changed contemporarily? Answers to these questions can help managers incorporate an appropriate level of spatial and structural variability in restoration treatments and adjust the restoration objectives to better reflect the environmental template of a site. By analyzing how forest variability has changed between historical and contemporary time periods, I can better elucidate how fire-exclusion has impacted these forests.

Methods

Study Design

The site on the Mogollon Rim ranges from 2223 to 2399m in elevation, has a mean annual temperature of 9.3 degrees Celsius, and receives 9.2 cm of mean annual precipitation. The forests fall into the warm/dry classification of mixed-conifer forest (Romme et al., 2009), with a major component of ponderosa pine, and a mixture of southwestern white pine, Douglas-fir, white fir, Gambel oak, and quaking aspen. Additional species found on the Mogollon Rim include New Mexico locust (*Robinia neomexicana*) and bigtooth maple (*Acer grandidentatum*) (Rodman et al. 2016). Low-severity fires burned frequently on the Mogollon Rim with a mean fire interval of 2 to 8.5 years, up until 1879 (Huffman et al., 2015). The forests on the Mogollon Rim are currently the target of restoration efforts to increase forest resilience (Four Forest Restoration Initiative) and protect important municipal water supplies (Cragin Watershed Protection Project), and results from this study can be used to improve the restoration treatments across this landscape.

This study utilizes existing pre-treatment data collected from the Ecological Restoration Institute's long-term ecological assessment and research network (LEARN). In 2014, the Ecological Restoration Institute, with cooperation from the U.S. Forest Service, established a randomized, replicated experiment on the Mogollon Rim Ranger District of the Coconino National Forest (see Figure 1) to compare restoration treatments. The experimental area consists of six experimental blocks, each consisting of three treatment units. Field crews established 15 forest survey plots on a 60m grid within each treatment unit, for a total of 270 plots across the study area. Each experimental block is 40 to 46 ha in size, and the total experimental area covers approximately 250 ha, making this site ideal for investigating the variation of stands at mid-scales (4 to 400 ha). Crews completed data collection in 2014, following methods described in detail in Fulé et al. (2002) and Roccaforte et al. (2015). Surveys recorded species, diameter at breast height (DBH: 1.37 m above the ground), diameter at stump height (DSH: 40 cm above the ground), total height, height to the base of the live crown, two crown radii measurements (long and short side) and condition (live tree, snag, log, cut stump, etc.) of all trees taller than breast height and all dead trees that may have predated Euro-American settlement (ca. 1879). Crews collected dendrochronological tree cores on all pre-settlement trees, trees larger than 40cm DBH, and 10% of all trees smaller than 40cm DBH.

Determining historic range of variability

To determine the historic range of variability of the dry mixed-conifer forests of the Mogollon Rim, I modeled the historical forest structure and composition using field plot data and dendroecological reconstruction techniques. These techniques were developed and discussed in detail by Fulé et al. (1997), Huffman et al. (2001), Bakker et al. (2008), Sánchez Meador et al.

(2010), and recently updated by Rodman et al. (2016) to incorporate additional species. This reconstruction model estimates the diameter of each tree during a set reconstruction year. I used 1879 for the reconstruction year, as the natural frequent fire regime on the Mogollon Rim burned regularly until this year (Huffman et al., 2015). Historical tree diameters were based on dendrochronological data (i.e., cross-dated increment cores collected from trees on field plots – see above) when available, and species-specific "back-growth" regression equations when dendrochronological data is not available. These "back-growth" equations estimate the historical diameter using species-specific growth equations, which took the following log-log regression form:

$$d_{\text{hist}} = \sqrt{d_{\text{inv}}^2 - (\frac{4}{\pi} * e^{(a+b*\log(d_{\text{inv}}))}) * (y_{\text{inv}} - y_{\text{hist}})}$$

where d_{hist} is the historical inside-bark diameter (cm), d_{inv}, is the inside-bark diameter (cm) at inventory year, y_{hist} is the targeted reconstruction year (1879), y_{inv} is the inventory year (2014), and *a* and *b* are species specific regression coefficients. In addition, the reconstruction model utilizes bark thickness equations developed by Myers (1963) and Laughlin et al. (2011), and locally developed DBH-DSH relationship equations. Historical diameters for dead trees were estimated by using current diameter and decomposition equations based on snag/log condition classes to determine death date (Parker and Thomas, 1979), and then input into the "back-growth" equations to estimate the diameter during the reconstruction year. While this method of reconstructing forest structure may have poor detection of small trees that died and decomposed prior to the contemporary surveys, comparisons to historical surveys indicate that 91 to 94% of pre-settlement trees can be identified by contemporary surveys (Huffman et al., 2001; Moore et al., 2004).

I used the results of the reconstruction model to summarize average diameter (cm), tree density (trees ha^{-1}), and basal area (m^2 per hectare) for each field plot. I quantified composition by calculating the ecological importance value (EIV) of each species in each plot, as described by Curtis and McIntosh (1951). EIV describes the importance of a given species group by accounting for the relative number of trees (abundance) as well as the relative basal area (dominance) of the species. This index ranges from 0 to 2 and is calculated using the following equation:

$$\mathrm{EIV}_{spp} = \frac{n_{spp}}{n_{total}} + \frac{BA_{spp}}{BA_{total}}$$

where EIV_{spp} is the species-specific ecological importance value; n_{spp} and BA_{spp} are the species-specific tree density and basal area, respectively; and n_{total} and BA_{total} are the total tree density and basal area, respectively. I summarized these measures of forest structure and composition across the study area to determine the historic range of variability of dry mixed-conifer forests, as well as the contemporary range of conditions at the Mogollon Rim site.

Measuring spatial variability

I evaluated spatial variability across the study area by quantifying spatial autocorrelation. I used the ‘spdep’ package in R (Bivand et al., 2013; Bivand and Wong, 2018) to calculate Moran’s I (Moran 1950; Cliff 1973), a commonly used measure of spatial patterns (Larson and Churchill, 2012). I calculated Moran’s I for each structure variable (average diameter, tree density, and basal area) and compared it to simulated complete spatial randomness to evaluate significance. Significantly positive values of Moran's I describe groups of similar plots, while significantly negative values of Moran's I describe mixtures of juxtaposed plot conditions (Mast and Wolf, 2006). Moran's I is useful for describing spatial heterogeneity across a network of patches, such as multiple stands at mid-scales.

When calculated globally (i.e., across the entire study area) this statistic describes the spatial autocorrelation of a variable – that is, whether the variable is distributed independently across a landscape or is dependent upon the value of its neighbors. When calculated at multiple neighborhood distances (locally), the local Moran's I can be plotted against distance to create a correlogram, describing the distance at which observations are independent from spatial autocorrelation. I calculated a local Moran's I at distances up to 1000m, at intervals of 60m (corresponding to the minimum distance between survey plots). Comparing the correlograms of the historical and contemporary data, I visually evaluated whether spatial variability had changed since the exclusion of natural frequent fire regimes.

The arrangement of the experimental blocks at the study site posed a challenge to using Moran's I in my analysis. Ideally, I could evaluate a complete range of distances up to the maximum distance between any two points in the study area, however there are significant gaps between some blocks. Blocks 2 through 5 are contiguous but Blocks 1 and 6 are disjunct from the others (see Figure 1). In Blocks 1 and 6, Moran's I cannot be calculated across distances larger than the maximum distance within the block, so I limited my analysis to 1000m, approximately the distance across one block. While this hinders my ability to make inferences about landscape spatial patterns, I was still able to evaluate variability across mid-scales.

Identifying drivers of variability

I used structural equation modeling (SEM) techniques in Amos software (Arbuckle, 2014) to identify the important relationships between environmental factors and forest structure and composition that drive variation in dry mixed-conifer forests on the Mogollon Rim. SEM is an analytical framework useful for investigating complex ecological systems because it can model multivariate relationships and feedback loops, explicitly evaluate direct and indirect causal relationships in ecological systems, and include unmeasured concepts as latent or composite variables (Grace 2006; Grace and Bollen 2008). SEM has been successfully used in southwestern forests to understand ponderosa pine regeneration (Puhlick et al., 2012) and relationships between environmental conditions, fire history, understory species richness and abundance (Laughlin and Grace, 2006; Laughlin et al., 2007).

To evaluate these relationships in prior to and following fire regime disruption, I built two independent models using reconstructed and contemporary field plot conditions: (1) a historical model, and (2) a contemporary model. These two models followed the same model building techniques, and started from the same a priori model, but used separate historical and contemporary datasets. While I could have tried multi-group modeling, which would focus on determining which pathways differ between time periods (Eisenhauer et al., 2015), I am more interested in a robust estimate of the historical drivers of variability.

SEM traditionally starts with an a priori conceptual model which is evaluated before making any modifications to arrive at a final model that adequately describes the relationships in the data. My conceptual model describes my hypothesis that environmental factors directly influence forest structure and composition, and indirectly influence forest structure through composition (see Figure 2). Measured variables were grouped into three broad environmental factors: topography, climate, and soils. The measured variables of each environmental factor were all correlated to each other, though this is not shown in the Figure 2 for simplicity. Each factor could have been represented by many measures, so I compiled a large pool of potential explanatory variables to select from (See Appendix A for a complete, detailed list).

Topographic variables were based on a high-resolution (1m x 1m), LiDAR-derived digital elevation model (DEM), and are calculated at 10m resolution in ArcMap10 software and in R (version 3.6.1) statistical software using the 'raster' (Hijmans, 2019) and 'SpatialEco' (Evans, 2019) packages. In the conceptual model I selected from Beer's aspect (or northeastness; Beers et al., 1966), heat load index (HLI; McCune and Keon 2002), and solar radiation index (SRI; Rich et al., 1994; calculated for the years 1879 and 2014) to represent 'aspect' as a composite variable; I selected from elevation, topographic slope position (TPI), and hierarchical slope position (HSP) to represent 'position' as a composite variable; and I selected from slope, roughness, and topographic ruggedness index (TRI; Riley et al., 1999; Blaszcynski 1997) to represent 'texture' as a composite variable.

Climate factors included seven different climate variables: precipitation, mean temperature, minimum and maximum temperature, mean dewpoint temperature, and maximum and minimum vapor pressure deficit. This data was acquired from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, 2019) for each month in 30-year periods from 1895 to 1924 (historical climate) and 1981 to 2010 (contemporary climate). PRISM data is used in ecological analyses where weather data has not been collected on site.

These climate variables were spatially downscaled from the native 800m x 800m resolution to the plot level resolution (60m x 60m) using gradient and inverse distance-squared weighting methods as described and implemented by Rodman et al. (2017). The downscaled climate variables were summarized as annual averages and seasonal averages for the 30-year periods and assigned to each corresponding plot. In the conceptual model I selected from precipitation, dewpoint temperature, minimum and maximum vapor pressure deficit variables into a 'water availability' composite variable; and selected from mean, minimum and maximum temperature variables into a 'temperature' composite variable.

Soil parent material is known to influence forest conditions (Abella and Denton, 2009; Rodman et al., 2017), however parent material does not vary significantly across the study area. In lieu of parent material, I used soil characteristics that do vary across the study area and are still important drivers of forest conditions (e.g., Laughlin et al., 2007; Puhlick et al. 2012). Soil factors were calculated from the SoilGrids 100m dataset (Ramcharan et al., 2017), making it possible to evaluate how changes in soil characteristic impact forest conditions over mid-scales. Soil factors included six soil properties (percent organic C, total N, bulk density, pH, percent sand, and percent clay) at seven standard soil depths (0, 5, 15, 30, 60, 100, and 200 cm). I selected from all these variables to represent a 'soil' composite variable.

I used average diameter and tree density from the historical reconstruction and the contemporary survey as indicators of forest structure in the SEMs. To aid in evaluating correlations between environmental variables and measures of forest structure I evaluated common data transformations to correct for skew in the distributions of average diameter and density. I log-transformed historical average diameter and contemporary density, and square root-transformed historical density and contemporary average diameter. I also calculated the means, 95% confidence intervals, and conducted t-test for significant difference from these transformed structure measures, then back-transformed them for reporting.

To represent forest composition in the SEMs, I used distance-based ordination techniques to reduce the complexity of the community data so that it would be easier to use in variable selection and structural equation modeling. I used the ‘vegan’ package (Oksanen et al., 2019) in R for this analysis. I transformed plot-level species count data using Wisconsin double standardization before calculating Bray-Curtis distance to describe the differences between plot overstory communities. I used nonmetric multi-dimensional scaling (NMDS) to calculate independent three-axis solutions for both the historical and contemporary community data and to calculate species scores within the ordination space. Each three-axis solution was rotated to place the maximum variation along the first axis, and I used this first axis score to summarize the community composition of each plot. The three measures of transformed average diameter, transformed density and the first axis scores from the community ordination, make up the response variables for the historical and contemporary models.

With over one hundred potential explanatory variables to include in each model, but needing to keep the models relatively parsimonious, I selected explanatory variables from each category to build each composite variable based on correlation with the response variables. I selected variables with the most extreme correlations greater than 0.1 or less than -0.1, making sure not to select redundant variables (e.g., the same soil characteristic at multiple depths, or the same climate variable at multiple seasons).

Using these criteria, I identified eleven measures of topography, climate, and soil to include in the historical model. For the topography factor, I selected Hierarchical Slope Position to represent position, Solar Radiation Index to represent aspect, and Topographic Ruggedness Index to represent texture. I selected percent organic C at 30cm, pH at 0cm, and percent clay at 30cm to represent the composite soil factor. For the composite climate factor, I selected winter minimum vapor pressure deficit and spring precipitation to represent water, and fall mean temperature, and winter maximum and minimum temperatures to represent temperature. For the contemporary model, I identified nine measures of topography, climate, and soil to include in the model. For topography, the same factors (HSP, SRI, and TRI) were selected. I selected pH at 0cm, and percent clay at 30cm to represent the soil factor. For climate, I selected spring precipitation and summer mean dewpoint temperature to represent water, and winter minimum and maximum temperatures to represent temperature.

After the variables were selected, I made several modifications to the model. To simplify the model where possible, I replaced all of the topography composite variables (aspect, position, and texture), which only one explanatory variable, with direct effects. I found that high collinearity between the explanatory variables of ‘temperature’ and ‘water’ caused illogical path coefficinents in the model, which I resolved by combining these into a single ‘climate’ composite. While my approach of correlating all environmental variables is conservative, this saturates the model, and model fit statistics cannot be calculated without any spare degrees of freedom. To evaluate model fit I removed the least significant correlation from the model, and calculated three model fit statistics (chi-squared significance, adjusted goodness-of-fit index (AGFI), and root mean square error of approximation (RMSEA)) over one degree of freedom.

Because there was no significant correlation in the paths removed, the final models behave essentially the same as a saturated model. While saturated models are traditionally not used as the final SEM, this is appropriate in this analysis because my objectives are to evaluate the relative importance of the environmental factors rather than test a novel theory of hypothesized relationships in the ecosystem.

Results

Historical and Contemporary Conditions

I successfully modeled historical forest conditions prior to fire regime disruption (1879) using dendrochronological reconstruction techniques. These conditions differed significantly from the contemporary conditions that were surveyed in 2014. Forest structure in both historical and contemporary time periods are summarized in Table 1 and Figure 3. Mean tree diameter across the Mogollon Rim averaged 27.5 (13.3 - 57.0) cm historically and varied widely (see Figure 4). Some stands were dominated by very large trees; the highest average diameter in 1879 was 93.0 cm. Contemporary average tree diameter was significantly lower (t-test $p < 0.01$) with an average of 20.1 (7.4 - 39.0) cm.

In 1879, basal area averaged 12.6 (2.0 – 79.4) m^2 ha^{-1} (see Figure 5). Again, there were extreme outliers characterized by large trees, with a maximum basal area of 117.6 m^2 ha^{-1}. Historical basal area was highly variable but significantly lower than contemporary conditions (t-test $p < 0.01$). Contemporary basal area averaged 30.8 (12.0 – 58.3) m^2 ha^{-1}.

The most drastic change in forest structure is seen in the density of trees (see Figure 6). Historical forests had an average density of 165 (48 – 352) trees ha^{-1}. Very sparse plots existed historically, and one plot was reconstructed with no trees (i.e. 0 trees ha^{-1}). The contemporary forest is significantly denser than the historical conditions (t-test $p < 0.01$), with an average density of 657 (188 – 2302) trees ha^{-1}. Some plots saw a tremendous increase in density, with a maximum tree density observed of 4025 trees ha^{-1}.

The historical forest overstory composition was typical of dry mixed-conifer in the Southwest (see Figure 7). Ponderosa pine accounted for about half of total EIV (0.934), with minor components of white fir (0.368), Douglas-fir (0.302), and Gambel oak (0.214). Contemporary composition is also characteristic of dry-mixed conifer, though ponderosa pine decreased in importance (0.622) and there has been a shift towards wet mixed-conifer species. White fir now accounts for about a third of total EIV (0.620), Douglas-fir increased to 0.370 EIV, and southwestern white pine increased from 0.018 to 0.102 EIV. There were also changes in the relative dominance of sprouting deciduous trees: Gambel oak (0.214 to 0.106) and aspen (0.118 to 0.008) decreased; bigtooth maple and New Mexico locust increased (0.042 to 0.146; and 0.004 to 0.024, respectively).

Spatial Variability

Overall, measurements of historical forest structure displayed low spatial autocorrelation which was consistent with a random arrangement. This heterogeneity can be seen in the maps of historical forest structure (Figures 4, 5, and 6). Historically, average diameter had low Moran's I and fell within the envelope of complete spatial randomness at all distances (Figure 8a). Basal area was significantly autocorrelated at distances of 90 and 210m but at all other distances was within the envelope of complete spatial randomness (Figure 8b). Interestingly, density was significantly negatively autocorrelated at 810m, but was otherwise spatially random (Figure 8c).

Unlike historical conditions, some contemporary conditions exhibited significant spatial autocorrelation. Average diameter was highly autocorrelated over distances of 0 to 360m and significantly autocorrelated at distances up to 1000m (Figure 8a). This homogeneity is apparent in the contemporary map in Figure 4. Density was significantly autocorrelated in contemporary forests at distances up to 360m and showed slight autocorrelation again at around 600m, but was otherwise random (Figure 8c). This homogeneity is also apparent in the contemporary map in Figure 6. Unlike average diameter and density, contemporary basal area remained largely random, only showing slight autocorrelation at distances of 210m and 570m (Figure 8b). Overall, contemporary conditions appear highly autocorrelated at distances up to 360m, and show some autocorrelation up to 1000m.

Drivers of Variability

Both historical and contemporary community ordinations successfully described composition in three axes, with final stresses of 0.11 and 0.12 (respectively). Each ordination was rotated to orient the most variation along the first axis (Axis 1). Using Axis 1 explained sufficient variation in overstory composition (r^2 of 0.425 and 0.511 for historic and contemporary ordinations, respectively). In both ordinations Axis 1 described a continuum ranging from ponderosa pine dominated sites at the far negative end, to sites dominated by relatively rare sprouting species (bigtooth maple and New Mexico locust) at the positive end. Intermediate values described sites with Douglas-fir, white fir, southwestern white pine, Gambel Oak, and aspen (see Figure 9a and 9b). In the historical ordination, Gambel oak and aspen were grouped at one end of Axis 2, and Douglas-fir, white fir and southwestern white pine were grouped at the other end. Gambel oak and Douglas-fir were grouped at one end of Axis 3, and southwestern white pine, white fir, and aspen were grouped at the other end (Figure 9c). In the contemporary ordination, there was less differentiation of species along Axis 2 or Axis 3. Gambel oak is differentiated on Axis 2 (Figure 9b), and southwestern white pine is differentiated on Axis 3 (Figure 9d), but the other species are clustered together.

In both the historical and contemporary datasets, environmental variables had stronger correlation with composition than with structure or composition (see Figure 10). Historical correlation coefficients were lower than contemporarily. Additionally, the relationships between average diameter and most environmental variables switched signs, changing from weakly positive to moderately negative, or weakly negative to moderately positive between historical and contemporary time periods.

The historical SEM has adequate fit: $p > 0.05$, RMSEA < 0.001, and AGFI > 0.9 (see Table 2). The historical model has moderate descriptive power for composition ($r^2 = 0.483$) but had low descriptive power for average diameter ($r^2 = 0.088$) and basal area ($r^2 = 0.101$).

Topography and climate factors had relatively high importance in driving historical forest structure and composition, while the soil factor had a lower impact on forest conditions (see Figure 11). The climate-to-composition had the highest single path coefficient in the historical model (0.66), while topography has a higher overall impact on historical composition than climate, from the cumulative effect of Aspect, Position, and Texture (total absolute value of 0.73). Climate was a significant driver of historical density (0.28) and diameter (0.37), but were of roughly equal importance with topography for these structural variables (0.24 and 0.32, respectively). Aspect and texture were not significant drivers of tree density or diameter. Soil had an impact on historical density (0.35) and diameter (0.38) that was similar to that of climate and topography. Soil had a relatively small, though still significant, impact in driving historical forest composition (0.39). Composition did not significantly drive variation in historical tree density but did have an impact on average tree diameter. While statistically significant, this path coefficient (-0.23) was the smallest driver of historical average diameter. See Appendix B for full details of path components.

The contemporary model also converged at a solution with good fit ($p > 0.05$, RMSEA < 0.001, and AGFI > 0.9; see Table 2), though again these measures of goodness of fit were evaluated on one degree of freedom. The model had good descriptive power for density (r^2 = 0.296) and diameter (r^2 = 0.317), and even better description of forest composition (r^2 = 0.632).

In the contemporary model, climate factors have the strongest relative importance for composition, while topography has the highest relative importance for forest structure (Figure 12). The pathway from climate to composition has the strongest path coefficient in the model (0.79) while pathways that lead from climate to density (0.21) and average diameter (0.21) have relatively low importance. Topography had the strongest influence on contemporary forest density (-0.36) and average diameter (0.32). Like the historical model, neither aspect nor texture were significant drivers of contemporary forest structure. The cumulative effects of position and aspect on composition (-0.59), was a relatively important pathway, however, texture is not an important driver of contemporary composition. Soil has a relatively weak importance to both contemporary forest density (0.20) and diameter (0.26); this differs from the historical model, where soil was a relatively equal driver of forest structure. The pathway from soil to composition (0.35) is the weakest driver of contemporary composition. The relationship between contemporary forest composition and structure differs from the one suggested by the historical model. Contemporarily, composition is a significant driver of forest density (0.26), but not forest diameter. See Appendix B for full details of path components.

Discussion

My results suggest that the abrupt disruption to the historical frequent fire regime has drastically altered the forests on the Mogollon Rim, as has been reported in dry mixed-conifer forests across the Southwest (Fulé et al., 2003, 2009; Cocke et al., 2005; Heinlein et al., 2005; Rodman et al., 2016, 2017). My analysis of the historical reconstruction data describes the conditions that existed in the forest prior to fire regime disruption, while the analysis of the contemporary survey data describes the forest conditions after an extended period of fire exclusion. The differences between contemporary conditions and the historical range of variability, and the changes to forest composition emphasize the need for forest restoration initiatives.

The reconstruction of the plots in the study area suggested that the historical dry mixed-conifer forests on the Mogollon Rim were consistently low density, with large and variable average tree sizes, leading to a low but variable basal area across the rim. This draws a picture of relatively open forests with a variety of small and large trees, possibly describing stands with multiple cohorts. The historical range of variability found in the study area is similar to the ranges found in other studies of dry mixed-conifer. Basal area ranged from about 2 to 79 m^2 ha^{-1} and averaged 12.6 m^2 ha^{-1}, and density averaged 165 trees ha^{-1} and ranged from 48 to 352 trees ha^{-1} (Table 2). The average density and basal area on Mogollon Rm fall also fall within the ranges described by both Reynolds et al., (2013) and Wassermann et al., (2019).

The average basal area and tree density that I found in the study area are slightly higher than the conditions reconstructed at dry mixed-conifer sites elsewhere on the Mogollon Rim (Rodman et al., 2016), at Black Mesa (Strahan et al., 2016), and in the San Juan mountains (Fulé et al., 2009). The historical conditions in dry mixed-conifer at the Grand Canyon, however, are generally denser than those found in the study area (Fulé et al., 2002, 2003). Interestingly, the historical conditions from the study area are slightly denser than those reported in Williams and Baker (2012) for the Mogollon Rim. When compared to mixed-conifer reference conditions outside the Southwest, my results are similar to those found on the Front Range of northern Colorado and southern Wyoming (Brown et al., 2015; Battaglia et al., 2018), and considerably less dense than the results reported from parts of the Sierras (Lydersen et al., 2013). Historical conditions from other parts of the Sierras (Collins et al., 2015; Stephens et al., 2015, 2018), and in Oregon (Hagmann et al., 2013, 2014, 2017), had higher basal area and lower tree density than in the study area suggesting those forests had fewer and larger trees than those found on the Mogollon Rim.

I found that historical tree diameter also varied widely, averaging 27.5 cm but ranging from 13.3 to 57.0 cm. Other studies in the Southwest typically report just basal area and tree densities – while tree size can be inferred from these two statistics, I have reported these for easy interpretation. The diversity of tree sizes indicates that some plots were dominated by very large trees, but few sites were dominated by very small trees. This gives empirical support to the restoration strategy of keeping large trees, which should help to recreate the full range of variability on a site.

Contemporary forest conditions diverged significantly from the historical range of variability in all three measures of forest structure. Average diameter is significantly lower in contemporary conditions reflecting the legacy of harvesting larger trees for timber and the influx of many small trees due to fire exclusion. Basal area and tree density increased significantly. This is consistent with other comparisons of historical and contemporary forest conditions in dry mixed-conifer forests across the Southwest; Fulé et al. (2003), Heinlein et al. (2005), Rodman et al. (2016, 2017), and Strahan et al. (2016) all recorded massive increases in the density and basal area in dry mixed-conifer forests over a similar time frame.

I recorded a shift in forest composition away from dry-mixed conifer, towards a more wet-mixed conifer composition. Based on changes to EIV, ponderosa pine has decreased in importance, while white fir has increased greatly, and now the two species are roughly equally important. Southwestern white pine and Douglas-fir also experienced modest increases. This trend has been recorded before on the Mogollon Rim (Huffman et al., 2015; Rodman et al., 2016) and in other mixed conifer forests across the Southwest (Fulé et al., 2003; Heinlein et al., 2005; Strahan et al., 2015; Margolis and Malevich 2016). Sprouting hardwoods did not all respond equally to the disruption of the historical fire regime. Aspen were historically present in small numbers across the study area but are now almost completely absent. Fulé et al. (2003) concluded that a majority of aspen stands are initiated by fire. The lack of frequent fires over the last hundred years may be the cause of this decline on the Mogollon Rim, though this could also be due to a combination of drought, ungulate browsing, insect damage, and disease (USDA, 2019a). Increasing density may explain the decrease in oak and the increase in bigtooth maple, which has a higher shade tolerance than oak (USDA, 2019b). Similar conversion from oak dominance to maple dominance has been recorded in Utah (Nixon, 1967). My results support the interpretation that in dry mixed-conifer forests, white fir is limited by fire more than site conditions (Reynolds et al., 2013; Huffman et al., 2015). Frequent fires kept these mesic, fire-intolerant species in check, but when released from fire they have begun filling in areas where they were previously excluded.

These changes to forest structure and composition are accompanied by changes to the spatial pattern to forest conditions. Spatial patterns occur at multiple, nested scales, from fine- (<4 ha) to mid- (4 to 400 ha) and landscape-scales (>400 ha) (Reynolds et al., 2013). Most of the previous research on spatial patterns in western forests has focused on describing the patterns of groups of trees, individual trees, and openings, which are typically exhibited at scales from 0.4 to 4 ha (Larson and Churchill, 2012). Rodman et al. (2016), for example, analyzed stem-mapped plots to evaluate the aggregation of trees, and found both random and aggregated patterns on the Mogollon Rim. My results indicate that prior to fire regime disruption, the forests on the Mogollon Rim exhibited random spatial patterns across mid-scales, up to 1000m (~314 ha). Similarly, Strahan et al. (2016) analysis of community traits in dry mixed-conifer forests at Black Mesa also found no significant autocorrelation at similar resolutions, and at distances up to 2500m. The resolution of my correlogram analysis is not particularly suited to detecting fine-scale patterns, which is better analyzed by stem mapped plots. However, patterns on the upper end of fine-scale (4 ha) would have shown up at lag distances of around 200m, suggesting that even at fine-scales the forests on the Mogollon Rim are randomly arranged. Rodman et al. (2017) also suggested that these forests exhibit random fine-scale patterns.

This random arrangement of forest conditions describes a multi-scalar level of structural heterogeneity that has been theorized (Reynolds et al., 2013), but not well documented. Both aggregated and random fine-scale spatial patterns have been recorded in previous studies of dry mixed-conifer reference conditions (Rodman et al., 2017; Binkley et al., 2008, Lydersen et al., 2013).

I found contemporary forest conditions on the Mogollon Rim to be strongly autocorrelated at distances to 360m, giving a general sense that these forests have formed large homogeneous patches, roughly 40ha in size. Some autocorrelation at distances up to 1000m suggests that there is low variation between these patches. Disruption to the historical frequent fire regime, which maintained the forest patterns is the probable explanation for this change. Strahan et al. (2016) describe a similar shift in the mid-scale variability of community traits, reporting significant spatial autocorrelation up to 250m. Managers seeking to restore historical spatial patterns should not use the existing large and homogeneous stands as the units of management – rather, these patches should be broken up into many variable stands, and restoration prescriptions need to incorporate random variation (i.e., not aggregated) of forest structure within each stand.

Fire was likely the primary driver of historical variability on Mogollon Rim, more so than environmental factors such as topography, climate, and soils. My model of historical drivers of variability has poor explanatory power for describing variation in forest structure, and moderate power for composition (see Table 2). This weak relationship between environment and forest structure is also seen in the low bivariate correlations between average diameter, density and almost all of the environmental predictors. One reason for poor explanation of structure is the low variability in historical densities. Historically there was little variation in density, which could have been kept consistently low by a natural fire regime of frequent, low- to mixed-severity fires. I was unable to include site-specific measures of fire in my models, and the relative importance of fire versus environmental factors in determining historical structure and composition needs further research.

My SEM suggested that climate and topography were the most important drivers of variation in historical forest structure and composition, while soil factors were relatively unimportant drivers. The importance of climate is supported by studies that use climate to explain up to half of the variation in overstory species abundances (Laughlin et al., 2011), or linked sites with high historical density to higher water availability and lower water demand (Stephens et al., 2018). Historical climate factors indicate that warm and dry winters, high spring precipitation, and warm fall temperatures correlate with low ponderosa pine dominance. Pathways leading from climate towards density and diameter indicate that sites with more water availability have higher densities, and sites with cold and dry winters are associated with larger trees. Winter temperatures may be associated with how well a site is able to keep snowpack into the spring, which is known to be important in determining forest density (Stephens et al., 2018). Spring precipitation is important for the timing of ponderosa pine seedling establishment on the Front Range (League and Veblen, 2006), and fall temperatures could be important to wildfire behavior by influencing fuel moisture. The strength of fire-climate relationships in historical fire regimes could also explain the relative importance of climate factors for driving historical forest conditions. Periods of severe drought are understood to influence the timing of widespread fire years in mixed-conifer forests by making fuels available to burn (Swetnam and Baisan, 1996; Fulé et al., 2009; Margolis and Malevich, 2016).

Topography was also an important driver of historical variation on the Mogollon Rim. Position was consistently a top driver, which makes sense because microsite variability is important to forest conditions (Korb et al., 2013, Urban et al., 2000). Aspect is also a logical driver of variation; sites with more solar radiation dry out faster, so more drought tolerant species like ponderosa pine and Gambel oak are able to occupy these sites. Additionally, this increased drying could increase the availability of existing fuels, making these sites able to carry fire more frequently. Interestingly, Rodman et al. (2017) did not find any topographic factors to be important to describing historical forest conditions on the Mogollon Rim, nor did Abella and Covington (2006) at other sites in northern Arizona. The selective plot selection used in these studies may have avoided topographically complex sites, while the systematic grid in my study area captured a wider variety of topographic conditions that drove greater variation in forest structure and composition.

Soil was a significant, but relatively unimportant driver of variability both the historical as well as the contemporary models. Rodman et al. (2017), Abella and Denton (2009), Kimsey et al. (2019), and Laughlin et al. (2007) demonstrate that soil parent material drives significant variation in forest structure and composition. There is limited variation in soil parent material across the study site, which likely is why soil was a relatively unimportant factor in my analysis.

Environmental factors exhibited a stronger influence on contemporary forest conditions than on historical structure and composition, likely due to anthropogenic exclusion of frequent fire. The contemporary model had stronger explanatory power than the historical model (see Table 2), which is reflected by the stronger correlations between contemporary environmental variables and forest measures (see Figure 10). Climate was distinctly the most important driver of forest composition on the contemporary landscape, and indicated that sites with high spring precipitation, cold winter low temperatures, and dry summers are associated with low ponderosa pine dominance. Forest composition may have previously been constrained by fire adaptedness, but without that constraint climate dominated as a key driver of forest composition; this narrative of compositional release from fire constraints has been described in other studies (Fulé et al., 2003; Reynolds et al., 2013; Huffman et al., 2015; Rodman et al., 2016; Strahan et al., 2016). Mueller et al. (2020) described a strengthening fire-climate relationship, whereas others report changes in the timing of widespread fire years relative to periods of drought or above average precipitation since fire-regime disruption (Meunier et al., 2014; Swetnam et al., 2016). Similarly, I found that climate has increased in relative importance, and different components of climate have become more important, supporting an interpretation of strengthening relationship between climate and forest structural characteristics.

Topography was less important to contemporary forest composition than it was in the past, perhaps because microsite variability that used to interact with fire is no longer a driving force (Korb et al., 2013). While weaker, this path describes the same relationship that was found historically: sunny sites and sites on upper slopes and ridgetops drive forest composition towards ponderosa pine dominance. Topography is the strongest driver of both density and diameter, but this relationship has changed dramatically since Euro-American settlement. While lower slopes and valleys historically had lower density and larger trees, contemporarily they are dominated by high densities of smaller diameter trees. Historical logging targeted large, commercially valuable trees, which may have been concentrated in lower sites. While density has increased significantly across the entire study area, Rodman et al. (2017) and Stephens et al. (2018) both found that density increases were greatest at mesic sites like valleys and lower slopes. The increase in density on the Mogollon Rim is also related to compositional changes. Composition is now a significant driver of forest density, and intermediate conifers and sprouting species that would have previously been kept in low densities by frequent fire are now filling up lower sites.

Conclusions

The drastic changes to forest structure and composition on the Mogollon Rim exemplify the changes seen in dry mixed-conifer forests across the Southwest and demonstrate the need for extensive restoration efforts. Current distributions of average tree diameter, basal area and density are all outside of the historical range of variability. These over-dense forests are at a heightened risk of large, severe wildfire, which could cause a transition to unforested ecosystem types, and reduce the functioning of ecosystem services.

The historic range of variability described in this study can serve as a guide for restoration projects on the Rim, emphasizing the need to reduce forest density, and maintain a wide range of conditions. The reduction in average diameter on the Mogollon Rim suggests that restoration treatments should seek to preserve large trees, and focus thinning on smaller diameter trees, this agrees with the strategy currently used. The historical importance of topography indicates that large tree preservation and aggressive density reductions should be focused in valley bottoms and lower slopes.

Additionally, my spatial analysis provides much needed expansion of the understanding of reference scales of heterogeneity at the mid-scale, which is comparable to stands and thus useful for forest managers. The random historical patterns observed on the Mogollon Rim, combined with the low descriptive power of SEM, suggests that that structural patterns were not strongly driven by environmental factors, so perhaps fire was the main driver of this structural variation. The significantly autocorrelated contemporary pattern, combined with the strong descriptive power of the environmental drivers model suggests that the large homogeneous stands are formed and maintained by environmental conditions – especially climate factors. This interpretation advocates for the reintroduction of fire as a restoration tool to maintain ecologically appropriate spatial patterns in dry mixed-conifer forests.

Reintroduction of fire could not only serve as a tool to recreate random spatial patterns but could serve to reduce the density of small diameter trees and restore historical forest composition. Small diameter trees have higher fire-related mortality than large trees, and the incursion of shade tolerant species would also be limited by fire, because these trees are generally not very fire tolerant (Fulé and Laughlin, 2006). Low severity fire, even multiple burns at low severity, do not always result in forest density that approximates historical conditions, so it is important to allow moderate severity fire to burn on the Mogollon Rim (Huffman et al., 2017, 2018). However, recent research suggests that this can also have mortality on larger trees (Stoddard et al., 2020). Some loss of large trees may be acceptable in dry mixed-conifer forests where some of the large trees that die in the fire may be species that are undesirable from a restoration perspective; however, further research and applied management experiments are needed to better understand how mixed-severity fire can be used to achieve multiple restoration objectives.

While contemporary forest conditions are also driven by environmental factors, these relationships were weaker and different in the past, suggesting that a site's contemporary environmental template cannot be used to entirely describe its historical condition. Climate has a strengthening and changing relationship to forest conditions and should not necessarily be used to guide historically based restoration treatments. Restoration treatments cannot ignore climate, especially given the strengthening relationship and climate change, and historical climate relationships may be an unreliable guide under some circumstances. While topography would serve as a poor guide for forest structure, topographic position may serve as a useful guide for restoring historical forest composition. It was very important in the past, is still relatively important, and the basic relationship between position and composition has remained essentially unchanged. This indicates that restoration treatments should seek to encourage pine-dominated stands on ridgetops and upper slopes, while allowing a more mixed composition of conifers and shade tolerant hardwoods in valley bottoms and lower slopes. The topographically complex Mogollon Rim has a diversity of microsites that could serve as refugia for mesic mixed-conifer species as climate change intensifies over coming decades.

Overall, my research paints a picture of highly variable, heterogeneous, and open dry mixed-conifer forests in the past on the Mogollon Rim, with ponderosa pine dominating stands on ridgetops, and more mixed composition persisting in valley bottoms. This should serve as a guide for restoration treatments on the Mogollon Rim. Future restoration treatments should seek to restore these conditions through targeted thinning operations, and the reintroduction of low- and mixed-severity fires through resource objective fire or allowing prescribed burns to burn at increased severity. Restoring these forests will increase resilience to large and severe wildfires, a growing threat under climate change. However, past climate relationships may not serve as an effective guide under novel climate situations, so managers seeking to adapt these forests to new conditions may be advised to try a wide variety of treatments and opportunistically make use of microsites. My increased understanding of historic ranges, patterns, and environmental drivers of variability may be useful for maintaining dry mixed-conifer forests across the Southwest.

Figures

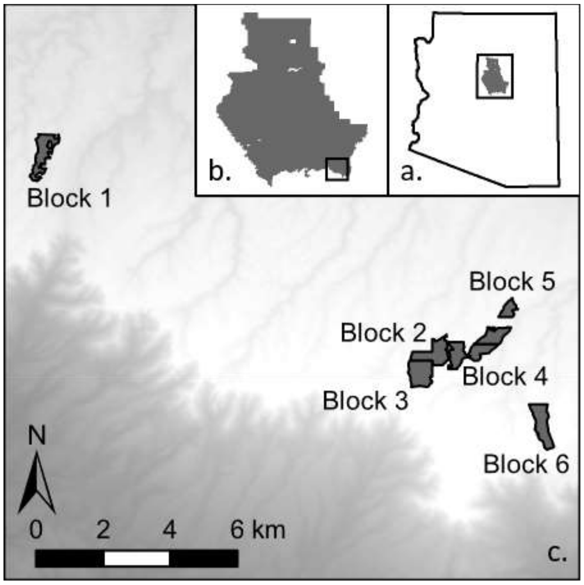

Figure 1: Map of study area. Location of Coconino National Forest within Arizona (a.), location of Mogollon LEARN blocks within the Coconino National Forest (b.), and the location of the Mogollon LEARN blocks on the Mogollon Rim, overlain on DEM.

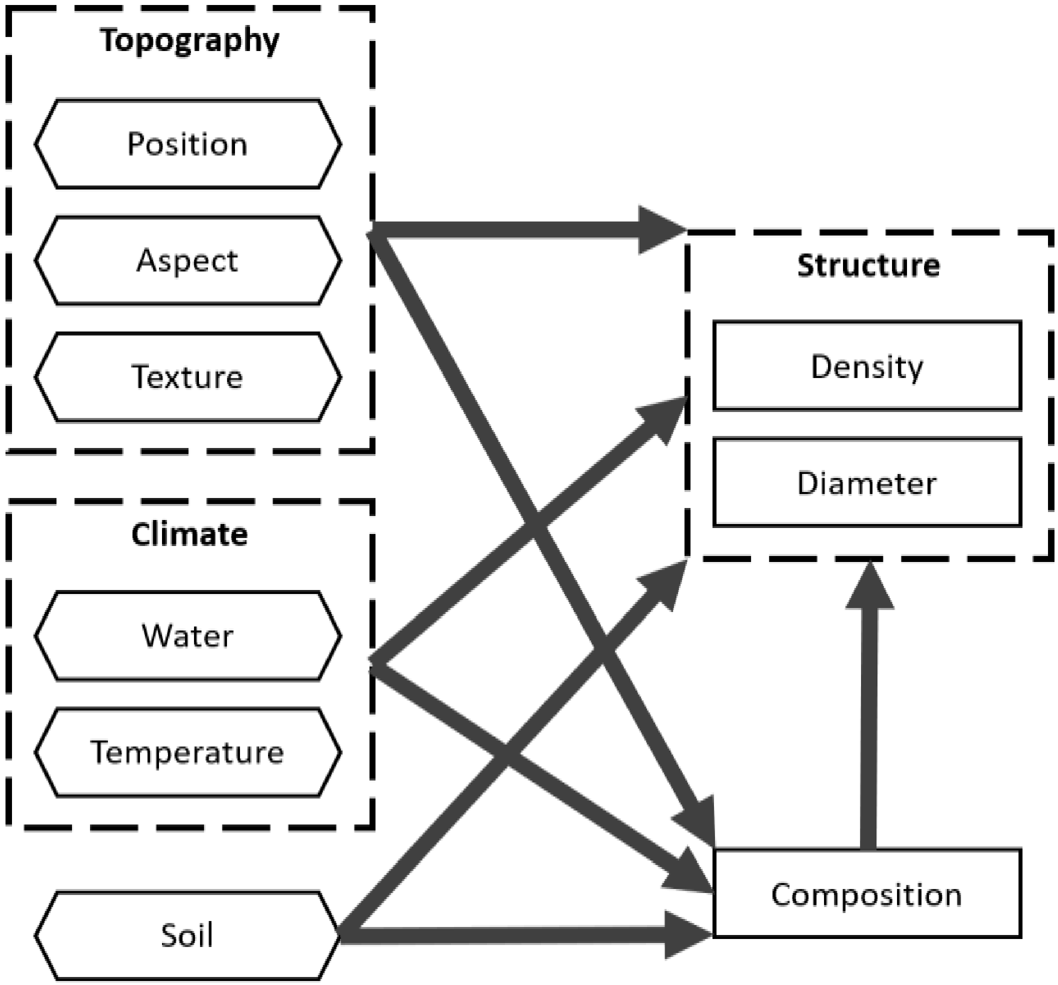

Figure 2: The conceptual model used at the beginning of structural equation modeling. This model visualizes my initial hypothesis that measures of topography, climate, and soil directly drive variation in structure and composition, and indirectly drive variation in structure through composition. Dashed boxes represent conceptual groupings of variables, solid boxes represent measured variables, hexagons represent composites of multiple measured variable, and arrows indicate causal relationships in the data. Correlation between all environmental variables is included in the model, but for simplicity is not shown in the diagram.

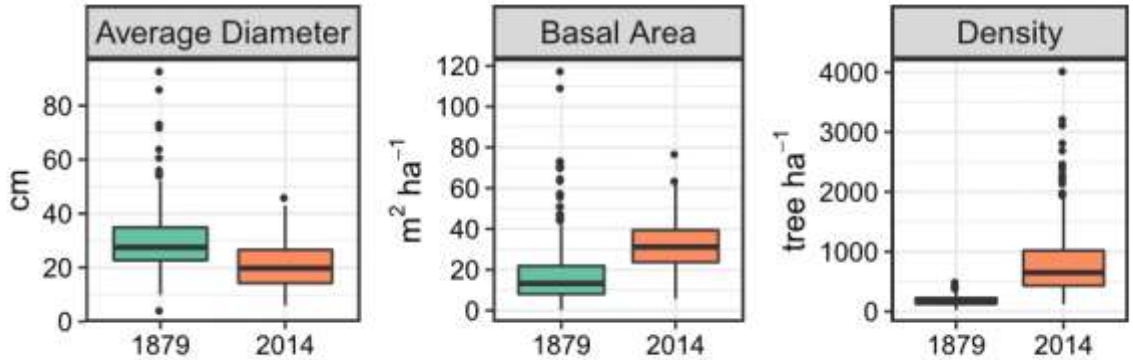

Figure 3: Historical and contemporary forest structure. Box plots depicting average diameter, basal area, and density for both historical (1879) and contemporary (2014) forest conditions. Comparisons between the two time periods indicate a decrease in average tree diameter, an increase in basal area, and a drastic increase in density.

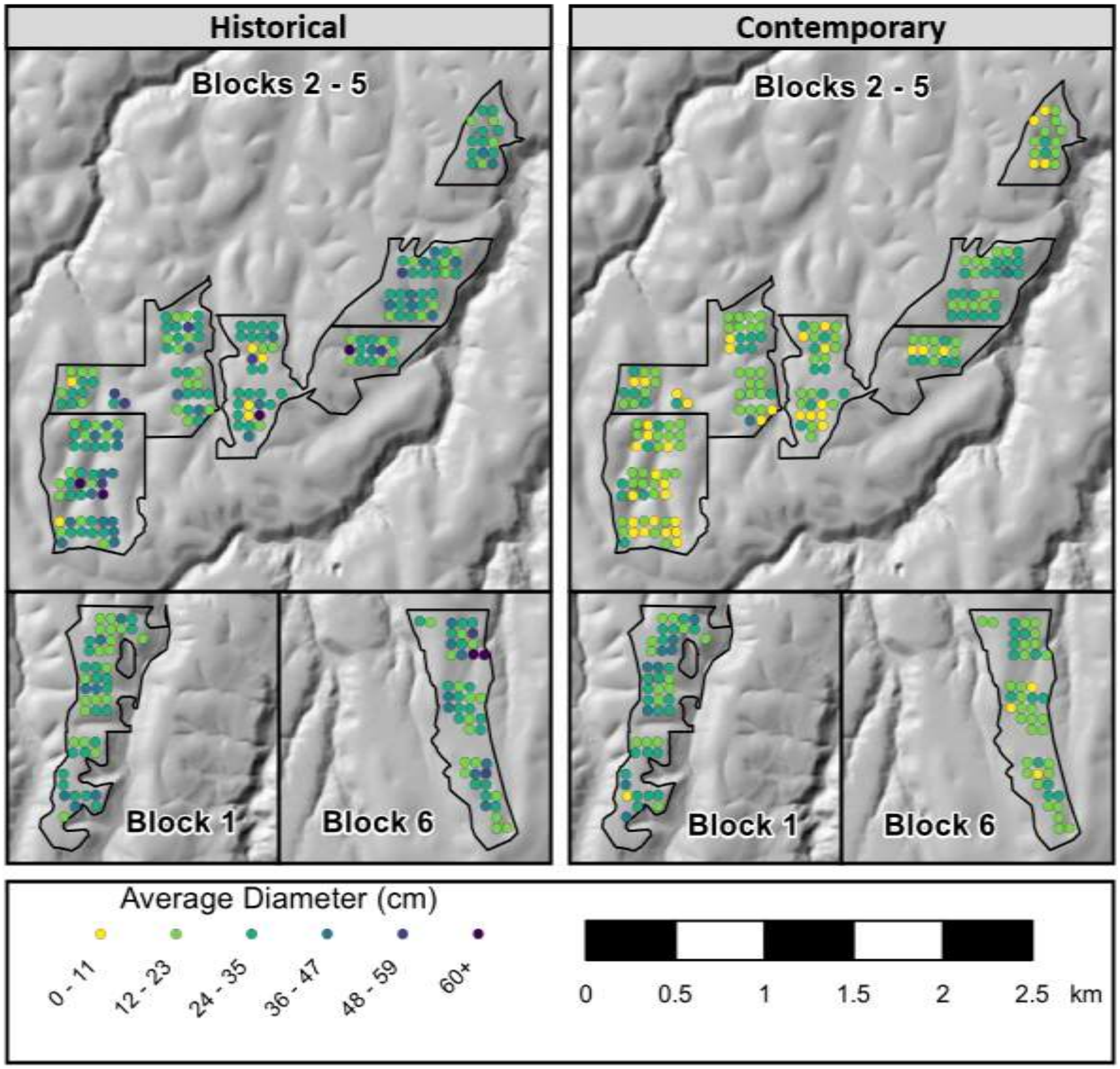

Figure 4: Maps of historical (left) and contemporary (right) average diameter. Comparison between the two panels shows a decrease in average diameter from 1879 to 2014.

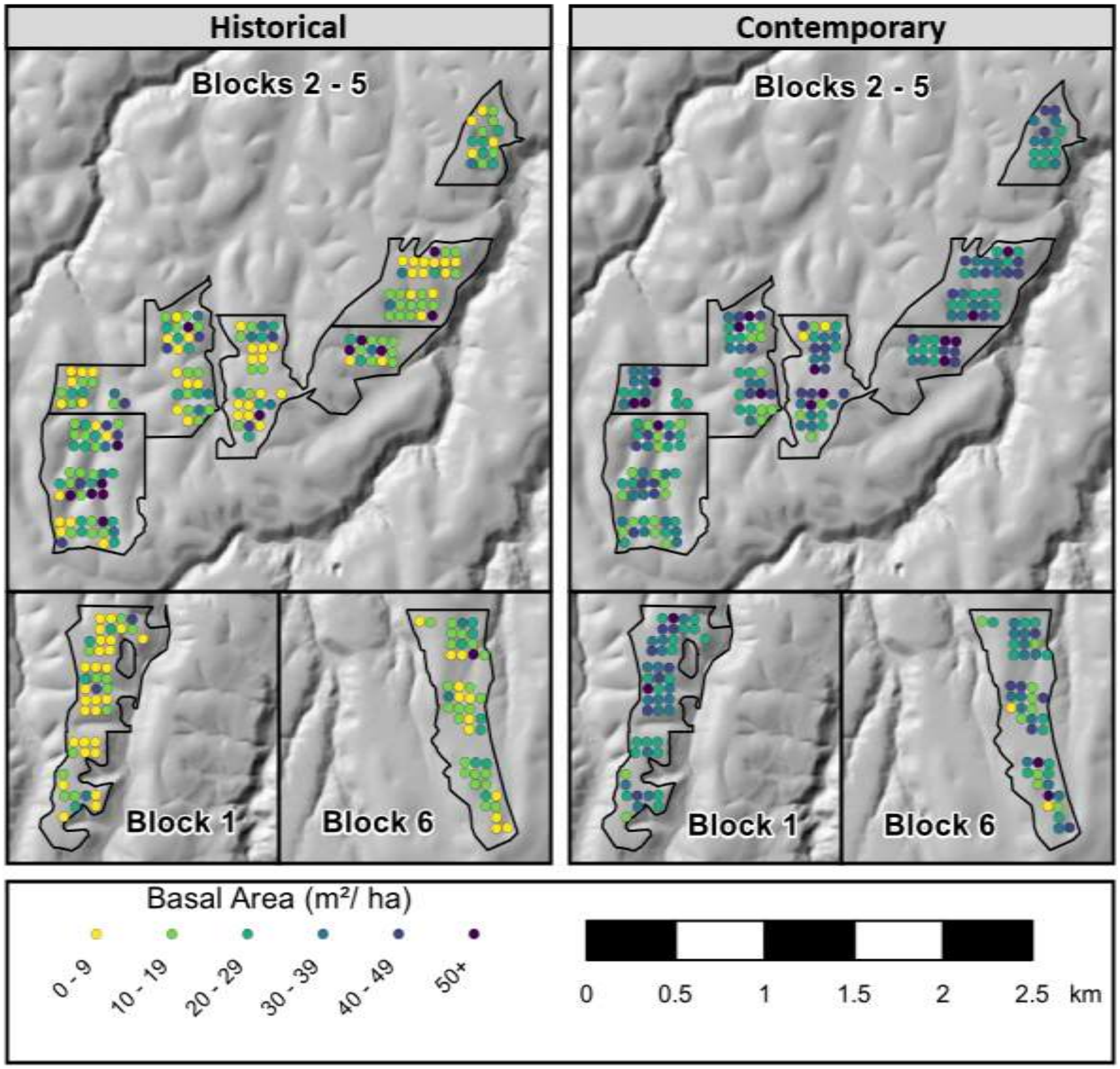

Figure 5: Maps of historical (left) and contemporary (right) basal area. Comparison between the two panels shows an increase in basal area from 1879 to 2014.

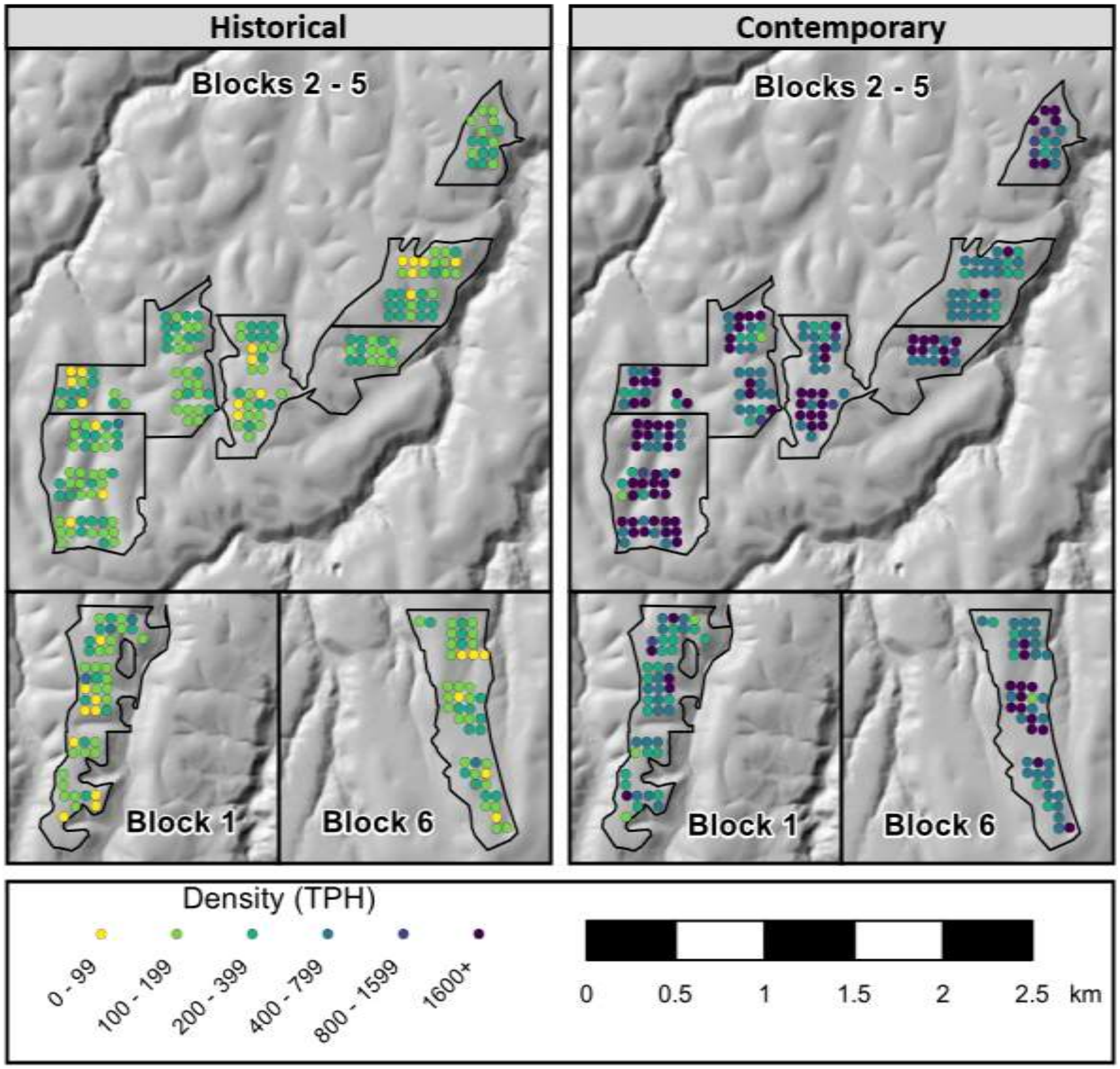

Figure 6: Maps of historical (left) and contemporary (right) density. Comparison between the two panels shows an increase in density from 1879 to 2014.

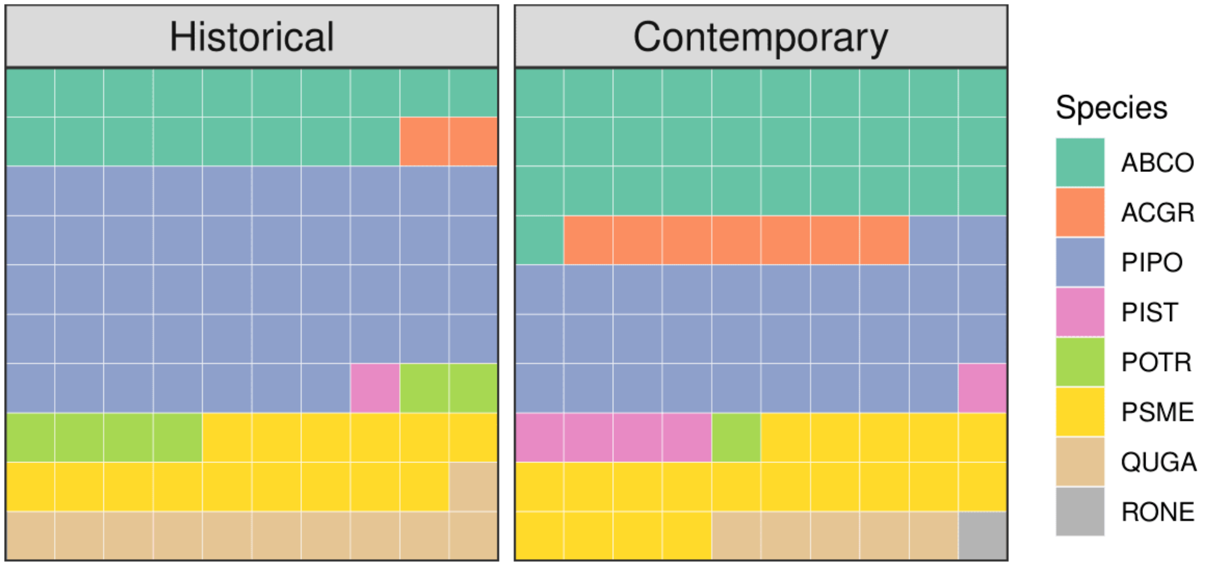

Figure 7: Historical and contemporary forest community composition. Squares are color coded by species, and each square represents 1 percent of total ecological importance values for the given time period. Species are identified by four letter codes: ABCO (white fir; *Abies concolor*), ACGR (bigtooth maple; *Acer grandidentatum*), PIPO (ponderosa pine; *Pinus ponderosa*), PIST (southwestern white pine; *Pinus strobiformis*), POTR (quaking aspen; *Populus tremuloides*), PSME (Douglas-fir; *Pseudotsuga menziesii*), QUGA (Gambel oak; *Quercus gambelii*), and RONE (New Mexico locust; *Robinia neomexicana).* Comparison between the two panels shows a decrease in fire adapted species from 1879 to 2014.

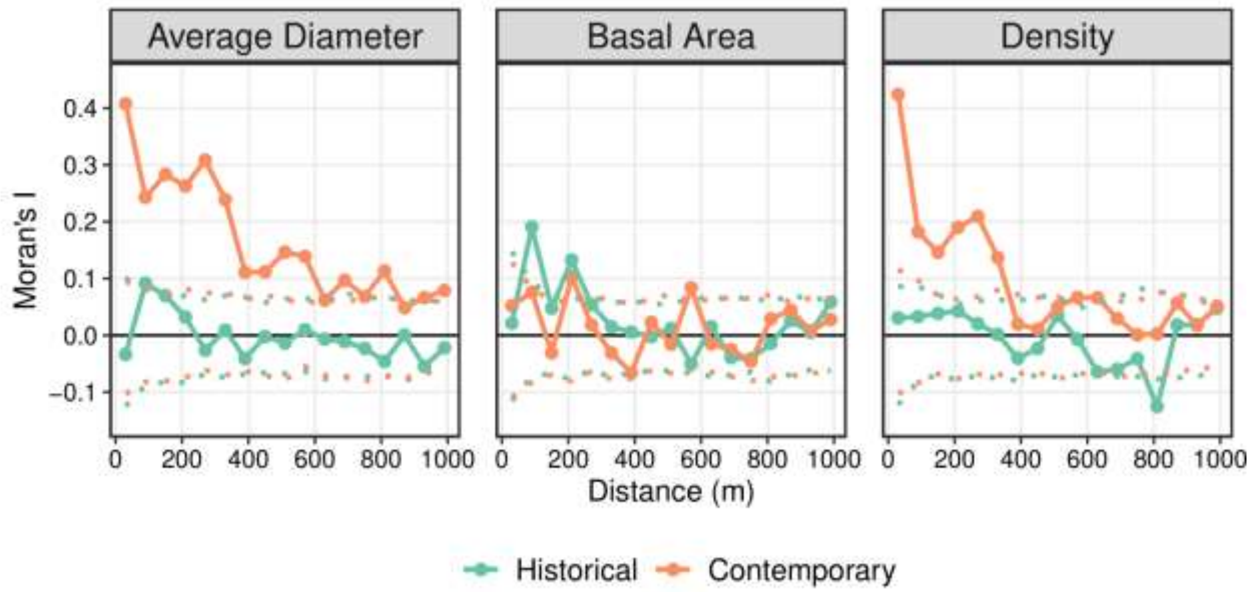

Figure 8: Correlograms of historical and contemporary forest structure. Each panel displays the spatial autocorrelation (as measured by Moran's I) for historical and contemporary conditions (differentiated by color). Points connected by solid lines indicate the Moran’s I at a given lag distance, and the dotted lines indicate the upper and lower limits of a simulated complete spatial randomness threshold. Points that are above the threshold are significantly spatially autocorrelated, points that are below the threshold are significantly negatively autocorrelated. Historically, measures of forest structure were generally not autocorrelated. Contemporarily, average diameter and density are both significantly autocorrelated.

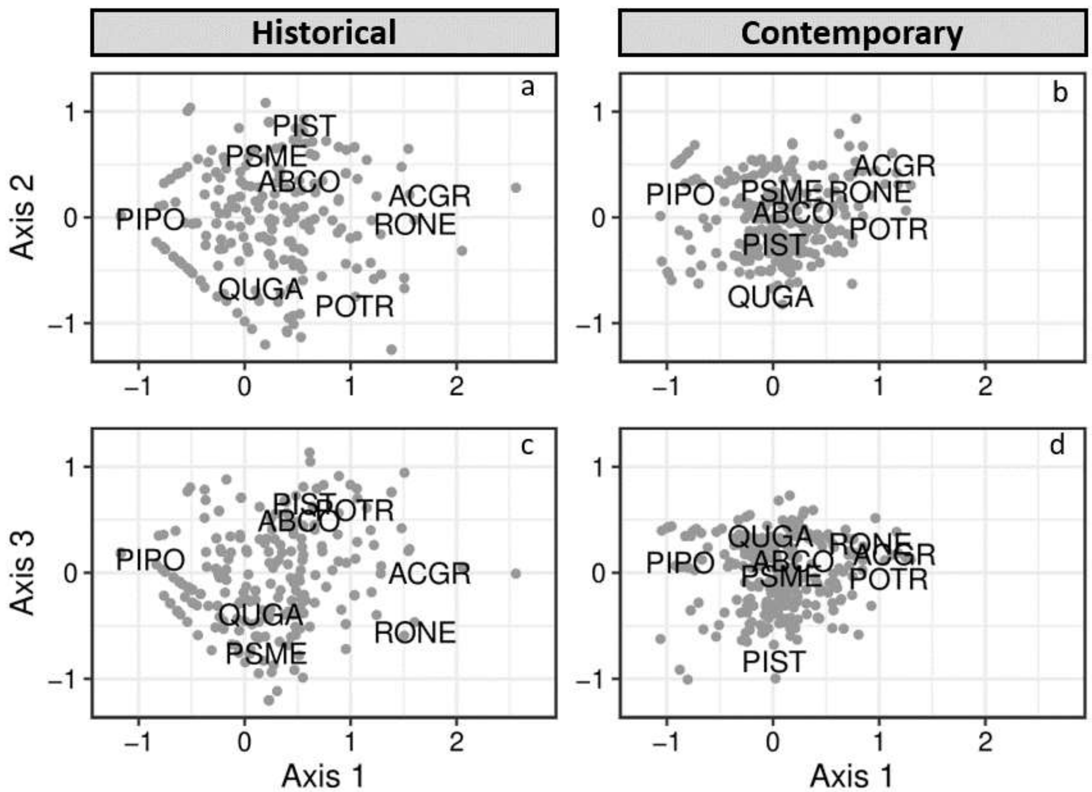

Figure 9: Ordinations of historical and contemporary forest community data. Points represent the composition of each site, the distance between points represents the similarity between the composition of each site; points that are close together are similar, points that are far apart are dissimilar. The three-axis ordination space is displayed as Axis 1 by Axis 2 (a and b), and Axis 1 by Axis 3 (c and d). Four letter species codes indicate the species scores within the ordination space: ABCO (white fir; *Abies concolor*), ACGR (bigtooth maple; *Acer grandidentatum*), PIPO (ponderosa pine; *Pinus ponderosa*), PIST (southwestern white pine; *Pinus strobiformis*), POTR (quaking aspen; *Populus tremuloides*), PSME (Douglas-fir; *Pseudotsuga menziesii*), QUGA (Gambel oak; *Quercus gambelii*), and RONE (New Mexico locust; *Robinia neomexicana)*

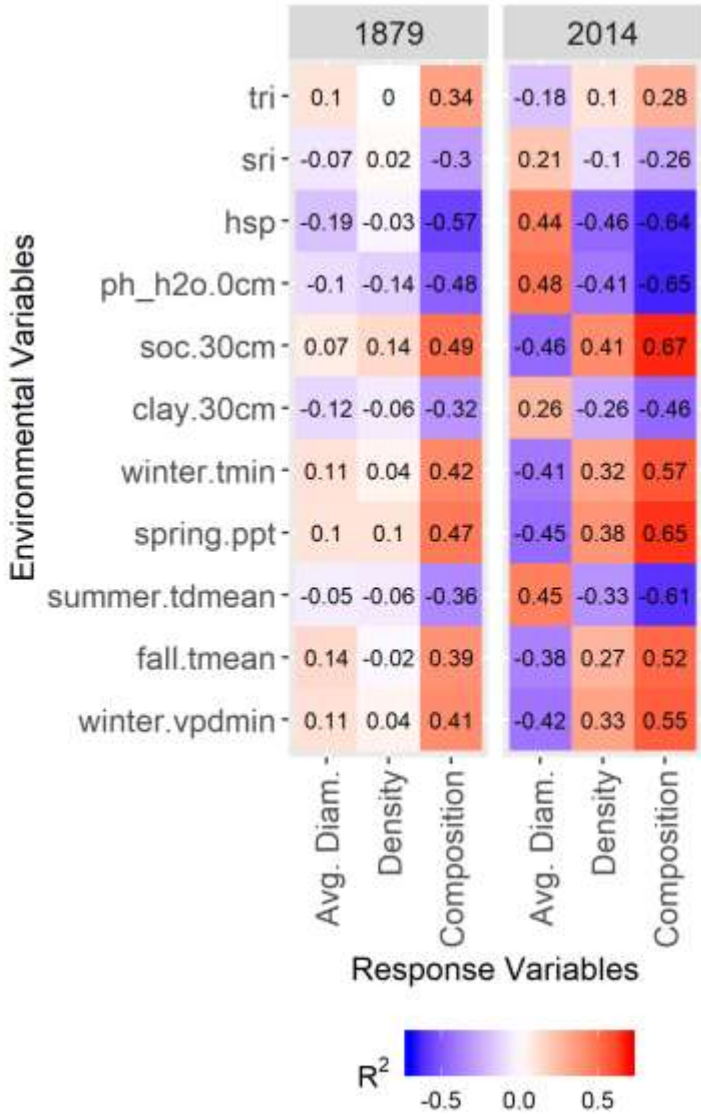

Figure 10: Correlation between selected predictors and model responses. Correlation between pairs of environmental variables selected for inclusion in either of the historical and contemporary models, and measures of forest structure and composition included in the models. Strength and direction of the correlation is indicated by color and reported by the correlation coefficient. Historical correlation coefficients tended to be lower than contemporarily, indicating

that the relationship between a site’s environment and its structure may not have been as strong in the past as it is now.

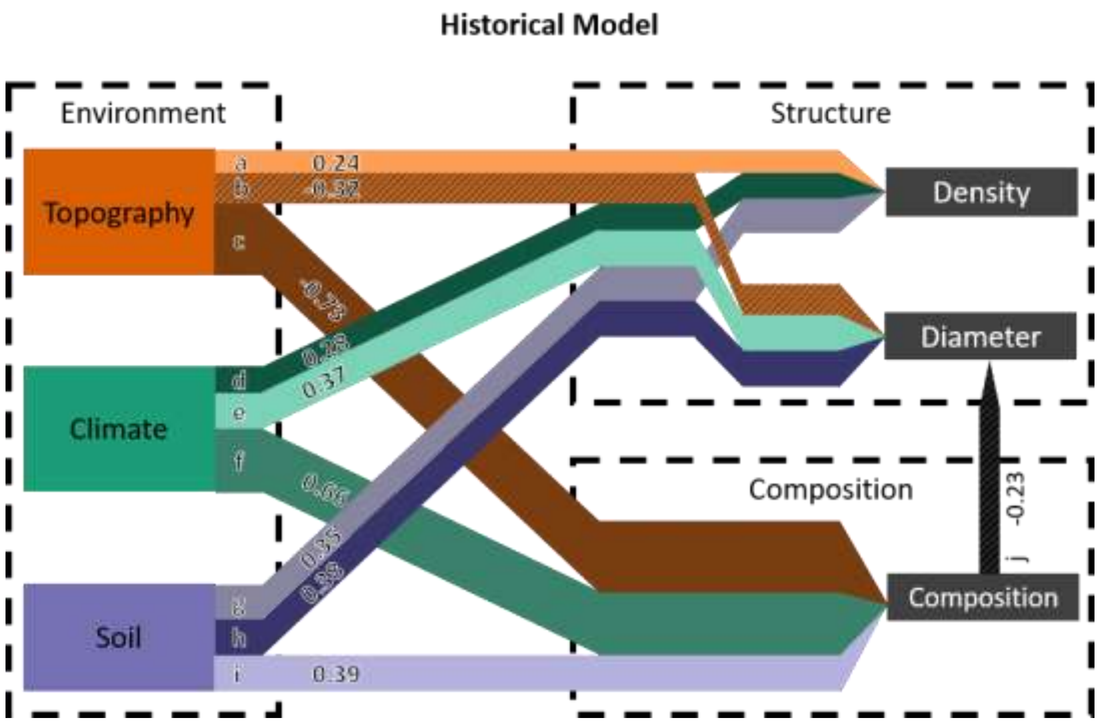

Figure 11: Historical model diagram. The relative importance of each environmental factor (Topography, Climate, and Soil) can be interpreted by the width of the pathways leading to Structure and Composition, which have been scaled to indicate the magnitude of the path coefficient. Paths with negative coefficients are marked with diagonal stripes. Only paths with coefficients significantly different from 0 are included in the diagram. Coefficients are also reported on the paths, and letters on the path correspond to entries in Appendix B: Historic and contemporary model pathway details. Topography and climate have the greatest influence on forest composition, and climate and soil have the greatest influence on forest structure.

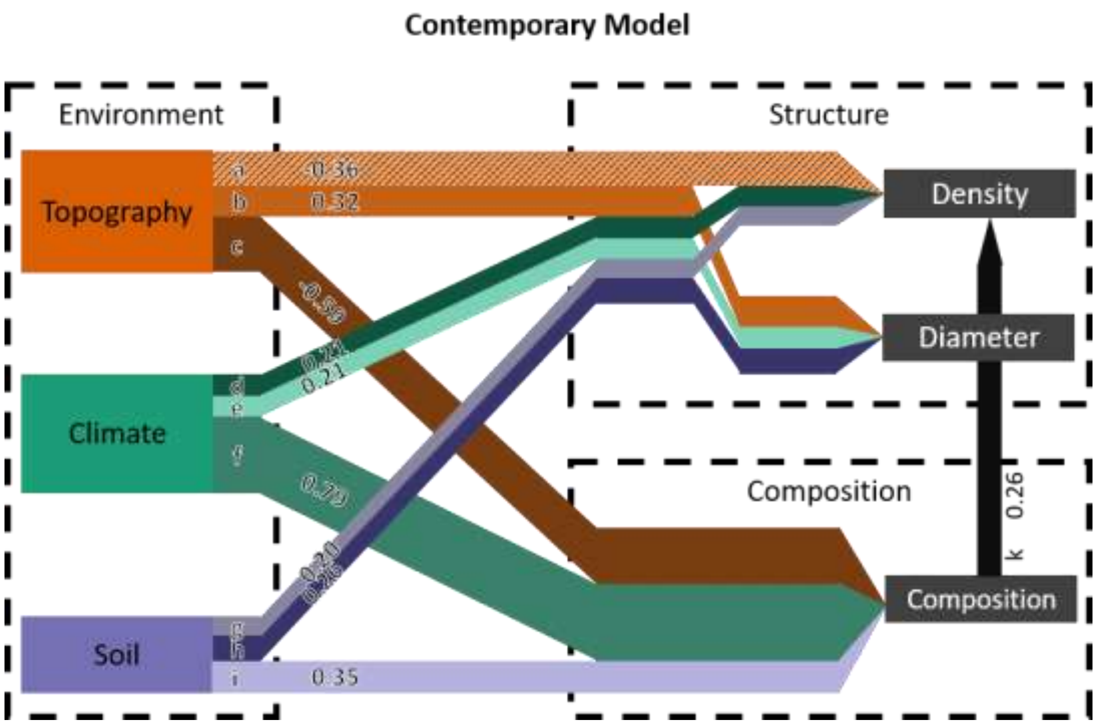

Figure 12: Contemporary model diagram. The relative importance of each environmental factor (Topography, Climate, and Soil) can be interpreted by the width of the pathways leading to Structure and Composition, which have been scaled to indicate the magnitude of the path coefficient. Paths with negative coefficients are marked with diagonal stripes. Only paths with coefficients significantly different from 0 are included in the diagram. Coefficients are also reported on the paths, and letters on the path correspond to entries in Appendix B: Historic and contemporary model pathway details. Topography and climate have the greatest influence on forest composition, and climate and soil have the greatest influence on forest structure.

Tables

Time Period	**Average Diameter* (cm)**	**Basal Area* (m^2 ha^{-1})**	**Density* (trees ha^{-1})**
Historical	27.5 (13.3 – 57.0)	12.6 (2.0 – 79.4)	165 (48 – 352)
Contemporary	20.1 (7.4 – 39.0)	30.8 (12.0 – 58.3)	657 (188 – 2302)

Table 1: Summary of historical and contemporary forest structure. The mean value and 95%confidence interval are given for average diameter, basal area, and density, for both historical and contemporary time periods. Variables marked with * are statistically different ($p > 0.01$) between time periods.

	Model Fit			Response Variable r^2		
Model	**Chi^2 p-value**	**RMSEA**	**AGFI**	**Density**	**Average Diameter**	**Composition**
Historical	0.447	<0.001	0.968	0.088	0.101	0.483
Contemporary	0.424	<0.001	0.980	0.296	0.317	0.632

Table 2: Summary of model performance. Measures of model fit (p-value, Root Mean Square Error of Approximation (RMSEA), and Adjusted Goodness-of-Fit Index (AGFI) are reported, as are measures of the predictive power of the models (r^2 for Average Diameter, Density, and Composition). Model fit statistics are calculated over one degree of freedom for both Historical and Contemporary models. While both models fit the data well, the historical model does not have strong predictive capability for structural measures. The contemporary model has better predictive capability than the historical model for all response variables.

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Chapter 4: Management Implications

Introduction

Forests across the Southwest have changed drastically over the last century, and now pose a monumental challenge for forest managers. Extensive overgrazing by Euro-American settlers disrupted a frequent fire regime near the end of the nineteenth century (Covington et al., 1994; Bahre, 1998). Low-intensity, frequent surface fires are a primary disturbance agent in these dry forests (Reynolds et al., 2013) and the prolonged exclusion of fire has led to significant increases in forest density (eg: Fulé et al.,2003, 2009; Cocke et al., 2005; Heinlein et al., 2005, Rodman et al., 2016). These overly dense forests have decreased resiliency to drought, and increased risk of uncharacteristic, high-severity wildfire (Reynolds et al., 2013; Bryant et al., 2019)

Ecological restoration is a common approach that managers have used to increase the resiliency of forests in the Southwest. This practice has many definitions but is defined most generally as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed,” and uses reference conditions to set restoration goals and evaluate success (SER, 2004). A historical range of variability (HRV) describes the range of conditions that naturally occurred in the past and are widely used as reference conditions (Landres, et al., 1999). The use of HRV is based on the assumption that historical conditions are relevant to the current conditions and that approximating the range of conditions that were present during a species evolutionary history will likely create suitable conditions for sustaining that species or ecosystem into the future (Landres, et al., 1999; Keane et al., 2009).

There is concern that the novel conditions predicted under a changing climate make historical conditions less relevant to current and future ecosystems, calling into question a strict adherence to historical conditions in restoration (Millar et al., 2007, 2014). However, reestablishing historical conditions and processes in southwestern forests may be appropriate for the increasing droughts and severe wildfire expected as climate change continues (Fulé et al., 2008). Restoration guided by these conditions can increase resilience to disturbance (Bryant et al., 2019), reduce the risk of conversion to non-forested ecosystems (Walker et al., 2018), and protect watershed resources (O'Donnell et al., 2018).

My study (presented in Chapter 3) seeks to improve the understanding of variability in southwestern dry mixed-conifer forests by addressing the following research questions: (1) What was the historical range of variability in warm/dry mixed-conifer forests on the Mogollon Rim? (2) How did forest conditions vary spatially across mid-scales, and has spatial variation changed since fire exclusion? and (3) What were the drivers of variability in historical dry mixed-conifer forests of the Southwest, and how have they changed? I utilized data from a network of forest survey plots on the Mogollon Rim in northern Arizona to reconstruct the historical conditions of dry mixed-conifer forests, and used structural equation modeling (SEM) to evaluate the relative importance of environmental drivers before and after frequent fire regime disruption. Contemporary forest structure and composition differ significantly from historical conditions, and environmental drivers of variation have changed in strength and relative importance after prolonged fire exclusion. The historical conditions that I report can be used to guide restoration treatments and evaluate their success. My historical and contemporary models describe which ecosystem relationships are still relevant and might be useful for tailoring restoration treatments.

Additional research into HRV and restoration experimentation can help forest managers address the challenges of landscape-scale restoration.

Changes in dry mixed-conifer forest conditions

The results of my reconstruction and spatial heterogeneity analysis emphasizes the need for restoration in dry mixed-conifer forests and can be used by restoration managers to serve as targets for restoration treatments. While the historical conditions reported from the study area are not drastically different than the HRV described in reviews such as Reynolds et al. (2013) and Wassermann et al. (2019), my analysis of mid-scale heterogeneity is a useful addition to managers' understanding of historical variation in dry mixed-conifer forests.

Current forest conditions on the Mogollon Rim are significantly outside the HRV for dry mixed-conifer forests in the Southwest. In the study area, contemporary forest structure is significantly different from the reconstructed conditions and are outside the HRV suggested by reviews. Average basal area increased from 12.6 to 30.8 m^2 ha^{-1}, and average tree density increased from 165 to 657 trees ha^{-1}. The historical averages on the Mogollon Rim are within the ranges described in Reynolds et al. (2013) (7.8 to 28.5 m^2 ha^{-1}; and 89 to 247 trees ha^{-1}) and in Wassermann et al. (2019) (11.6 to 19.1 m^2 ha^{-1}; and 109 to 180 trees ha^{-1}); however, contemporary structure – especially tree density – are outside these ranges. Similar increases in basal area and tree density have been found elsewhere on the Mogollon Rim (Rodman et al., 2016) and across the Southwest (Cocke et al., 2005; Heinlein et al., 2005; Fulé et al., 2009; Strahan et al., 2016). This widespread departure from HRV emphasizes the need for landscape-scale restoration.

The range of historical conditions found in the study area on the Mogollon Rim can be used to help design restoration treatments. The wide range of basal area and density conditions that historically were present on the landscape suggests that treatments should seek to establish a variety of conditions, with some relatively open stands and some relatively dense stands. The large historical average diameter (27.5 cm) suggests that treatments should seek to increase the average diameter of stands. Additionally, the upper end of the range of average diameters (57.0 cm) demonstrates that some stands were dominated by very large trees, and large, especially large and old, trees should be preserved when possible. Future research can use the conditions reported in my study to evaluate the success of the future restoration treatments planned at these sites, as well as the success of forest-wide restoration on the Mogollon Rim, such as the Four Forest Restoration Initiative and the Cragin Watershed Protection Project.

Species composition is often used as an indicator of restoration success and is part of Reynolds et al. (2013) restoration framework. The changes to forest structure in southwestern dry mixed-conifer forests are associated with changes to the overstory composition. Species composition in the study area shifted from ponderosa pine dominance towards a more mixed species composition. Historically, ponderosa pine was clearly dominant, while in the contemporary forest ponderosa pine shares dominance with white fir. The shift in species composition observed in my study is consistent with other studies on the Mogollon Rim (Huffman et al., 2015; Rodman et al., 2016) and across the Southwest (Fulé et al., 2003, 2009; Heinlein et al., 2005; Margolis and Malevich, 2016). These changes represent a decrease in the forest’s ability to resist fire and drought (Strahan et al., 2016). Treatments that restore historical overstory species composition would likely increase the forests resilience to these disturbances that are expected to increase as climate change intensifies.

My analysis of mid-scale heterogeneity offers important insight into historical variability at a scale useful for managers. Spatial patterns are nested at multiple scales: fine scale patterns (<4 ha) typically describe the arrangement of trees into groups, individuals, and openings, and are nested into stands, which make up mid-scale patterns (4-400 ha). These mid-scale patterns describe variation in stands, and are further nested within landscape-scale patterns (400+ ha) that describe the patterns of stands across a landscape (Reynolds et al., 2013). A majority of studies that quantify spatial patterns in southwestern forests examine the fine-scale patterns of trees and how they form a matrix of individuals, groups and openings at scales smaller than 4 ha (Larson and Churchill, 2012). Both random and aggregated spatial patterns have been described in dry mixed-conifer forests (Binkley et al., 2008; Lydersen et al., 2013; Rodman et al., 2016, 2017). My results indicate that historical forests on the Mogollon Rim varied randomly across mid-scales; historical structure varied randomly at distances from 60 to 1000m, loosely corresponding to scales of 1 to 300 ha. Contemporary forest patterns differ significantly from historical conditions and are significantly autocorrelated at distances up to 360m, roughly 40 ha. A similar shift toward stronger autocorrelation at distances up to 250m has also been reported for community traits at Black Mesa (Strahan et al., 2016), and a shift towards fine-scale aggregation has been reported on the Mogollon Rim (Rodman et al., 2017).

This discrepancy between historical and contemporary patterns poses a challenge for restoration of these forests. In addition to restoring an appropriate range of conditions, restoration goals often seek to restore heterogeneity (Landres et al., 1999; Reynolds et al., 2013).

My results suggest that managers should seek to create random variation across mid-scales. However, the contemporary forest has formed larger, more homogeneous stands which may not be an appropriate unit of management for reintroducing historical random conditions. When designing treatments, managers should consider breaking up these large stands, or allowing density and diameter distributions to vary randomly within stands. It is important to remember that treatments should vary across multiple scales to prevent an even application of fine-scale patterns without being appropriately nested within higher-order scales (Larson et al., 2012).

Drivers of historical and contemporary variability

My models of historical and contemporary drivers of variability offer insights for managers. My historical model's low descriptive power suggests that environmental factors were not drivers of large variation in historical forest structure. Low-intensity, frequent surface fire is, however, understood to be the primary disturbance agent in southwestern dry mixed-conifer forests. Fire drives variation in forest conditions through impacts on stand initiation (Fulé et al., 2009), recruitment (Tepley and Veblen, 2015; Owen et al., 2017), and pattern (Malone et al., 2018). In my study I was unable to include plot-specific measures of fire frequency or severity, and were thus unable to explicitly include fire as a factor in my models. The low descriptive power of my historical model agrees with the understanding of fire as the main driving force shaping historical forests.

Ecological restoration not only seeks to recreate functional conditions, but to also reestablish the processes that maintain those healthy conditions (SER, 2004). The importance of fire to historical forest conditions calls for the reintroduction of fire into dry mixed-conifer forests. While a combination of mechanical thinning and prescribed burning is effective at brining forest structure in line with HRV (Stoddard et al., 2015) and reducing the risk of severe wildfire (Kalies and Yocom Kent, 2016), there is renewed interest in allowing natural wildfires to burn unimpeded in low risk areas to achieve restoration objectives (van Wagtendonk, 2007). These fires, also known as resource objective fires, are effective at reducing basal area and tree density in dry mixed-conifer forests, targeting small diameter trees, and shifting species composition towards ponderosa pine dominance (Fulé and Laughlin, 2006). These restoration benefits can also be persistent more than 10 years after the fire, however, there is concern about delayed mortality of large diameter trees (Stoddard et al., 2020). Additionally, moderate severity wildfire may be more effective at restoring ponderosa pine forests to HRV than multiple low severity fires (Huffman et al., 2017, 2018). Further experimentation may be needed to evaluate how resource objective fires may be used to achieve multiple restoration objectives in dry mixed-conifer forests, and whether resource objective fires can restore historical relationships between environmental factors and forest structure and composition.

My historical and contemporary models describe a dynamic relationship between forest conditions and climate factors, suggesting that climate is a poor guide for historically based ecological restoration. My contemporary model indicates that climate is the primary driver of contemporary forest composition, and that the relative importance of climate has increased since fire exclusion. Historically, environmental factors only explain moderate variation in composition and little variation in forest structure. Additionally, these relationships change between the historical and contemporary models, with a shift in which climate variables are important and the direction of these relationships. The historical modeled indicate that warm and dry winters (high winter minimum and maximum temperatures; high winter vapor pressure deficit), high spring precipitation, and warm fall average temperatures correlate with low ponderosa pine dominance, while the contemporary model indicated that sites with high spring precipitation, cold winter lows, and dry summers (low summer average dewpoint temperature) are associated with low ponderosa pine dominance (see Appendix B). The relationship between climate conditions and forest conditions is variable and therefore an unreliable tool for guiding historically based restoration treatments. Managers should not use historical forest-climate relationships to guide restoration because the relationship driving variation on the contemporary landscape is fundamentally different, and may send treated areas down an unexpected trajectory.

This is not to say that climate conditions should be ignored when seeking to improve forest resilience. As climate moves further from the evolutionary conditions that these forests developed under, the relationship between forest conditions and climate factors becomes increasingly uncertain. When making decisions in the face of uncertainty, forest managers can hedge their bets against climate change by adopting variable treatments in the hopes that some will create conditions that are sustainable under a new climate (Millar et al., 2007, 2014). Further research and experimentation may be needed to evaluate whether restoring historical forest conditions reestablishes the historical climate-forests relationships, and whether these treatments help forests adapt to novel climate conditions.

While climate may be a poor guide for historically based restoration, topography may be a useful guide for restoration of dry mixed-conifer forests in the Southwest. Topography was the most important driver of historical composition and a significant driver of contemporary composition. Similar relationships between position and aspect were identified in both models:

sunny sites (high solar radiation index) or sites on ridgetops and upper slopes (high hierarchical slope position) are dominated by ponderosa pine, while shady sites (low solar radiation index) or sites in valley bottoms and lower slopes (low hierarchical slope position) have a more mixed composition. This relationship has remained consistent even through fire regime disruption and changes in forest composition, making it a good tool for guiding the desired composition of restoration treatments across variable topography. Stands on sunny sites, or on ridges and upper slopes should be the target of more aggressive composition management, with a target composition dominated by ponderosa pine. On shady sites and valley bottoms, managers can allow a more mixed composition to persist. Managers should opportunistically make use of microsite variability to vary treatments and create heterogeneity across the restored landscape.

Variations in local topography have been linked to variations in forest conditions and fire regimes (Korb et al., 2013). Mesic sites, like those found in valley bottoms have experienced more drastic increases in density than xeric sites like those found on ridge tops and upper slopes (Rodman et al., 2017). My historical and contemporary models also agree with this narrative: historically, sites on lower slopes were characterized by fewer, larger trees, while contemporarily these same sites are characterized by numerous, smaller trees. This reversal could be due to the logging history of the Southwest which targeted large trees. If these larger trees were concentrated in lower sites, these sites would experience changes to structure more acutely.

There are limitations to my study that managers should be aware of when considering my results. Foremost, I was unable to explicitly include measures of disturbances in my models of the drivers of variability. Fire is the primary disturbance agent in dry mixed-conifer forests, but I did not have plot-level estimates of fire history in the study area and thus could not include fire as a factor in my models. The importance of fire is well established and fire's impact to the study area may be inferred by comparison of the two time periods, the historical forest conditions and drivers describing a forest with an intact frequent fire regime, while the contemporary forest conditions and drivers describing a forest after a prolonged disruption to the fire regime. A thorough survey of fire scars and stand age structure overlapping the study area would provide a fine- to mid-scale measure of fire history, and could more explicitly evaluate the relative importance and interaction of fire and environmental drivers of variability. I was unable to include other disturbances, such as insects, disease, logging, grazing or other management history into my models due to a similar lack of plot-level data.

My analysis of the Mogollon Rim did not capture variation in soil parent material, another important driver of forest variation. Parent material is associated with differences in understory composition (Abella and Covington, 2006; Laughlin et al., 2007), differences in overstory growth and regeneration (Abella and Covington, 2006; Puhlick et al., 2012), overstory structure and pattern (Abella and Denton, 2009; Rodman et al., 2017) and stand density index (Kimsey et al., 2019). While parent material did not vary across the study area, I was able to include soil characteristics including pH, organic carbon, total nitrogen, water capacity, and percent silt, clay. My results are most directly applicable to dry mixed-conifer sites on similar limestone-based soils and are likely relevant to managers operating across a single parent material.

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Appendix A: Descriptions and summary statistics for all potential variables

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Temperature	Annual tmax	15.18	14.58	15.92	0.32	Annual average of daily maximum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Annual tmax	15.55	14.95	16.31	0.33	Annual average of daily maximum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Spring tmax	13.91	13.28	14.65	0.33	Spring average of daily maximum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Spring tmax	14.44	13.80	15.22	0.34	Spring average of daily maximum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Summer tmax	24.67	23.98	25.48	0.36	Summer average of daily maximum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Summer tmax	25.44	24.75	26.27	0.36	Summer average of daily maximum temperature (1981 to 2010)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Temperature	Fall tmax	15.97	15.43	16.69	0.31	Fall average of daily maximum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Fall tmax	16.27	15.72	17.01	0.31	Fall average of daily maximum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Winter tmax	6.17	5.63	6.86	0.31	Winter average of daily maximum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Winter tmax	6.07	5.54	6.76	0.30	Winter average of daily maximum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Annual tmean	8.96	8.85	9.05	0.03	Annual average of daily average temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Annual tmean	9.31	9.20	9.40	0.04	Annual average of daily average temperature (1981 to 2010)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Temperature	Spring tmean	7.35	7.23	7.50	0.05	Spring average of daily average temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Spring tmean	7.84	7.73	8.00	0.05	Spring average of daily average temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Summer tmean	18.06	17.94	18.14	0.04	Summer average of daily average temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Summer tmean	18.53	18.40	18.63	0.05	Summer average of daily average temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Fall tmean	9.82	9.68	9.91	0.06	Fall average of daily average temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Fall tmean	10.16	9.99	10.29	0.08	Fall average of daily average temperature (1981 to 2010)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Temperature	Winter tmean	0.60	0.45	0.76	0.05	Winter average of daily average temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Winter tmean	0.71	0.63	0.84	0.04	Winter average of daily average temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Annual tmin	2.77	1.96	3.25	0.32	Annual average of daily minimum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Annual tmin	3.07	2.25	3.61	0.33	Annual average of daily minimum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Spring tmin	0.79	0.11	1.21	0.26	Spring average of daily minimum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Spring tmin	1.24	0.57	1.68	0.26	Spring average of daily minimum temperature (1981 to 2010)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Temperature	Summer tmin	11.45	10.61	12.05	0.35	Summer average of daily minimum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Summer tmin	11.62	10.79	12.26	0.36	Summer average of daily minimum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Fall tmin	3.67	2.67	4.29	0.40	Fall average of daily minimum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Fall tmin	4.04	3.00	4.76	0.44	Fall average of daily minimum temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Temperature	Winter tmin	-4.98	-5.70	-4.69	0.26	Winter average of daily minimum temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Temperature	Winter tmin	-4.64	-5.34	-4.25	0.27	Winter average of daily minimum temperature (1981 to 2010)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Annual ppt	921	760	975	71	Annual total precipitation (1895 to 1924)	millimeters	PRISM
Climate: Water	Annual ppt	887	752	932	59	Annual total precipitation (1981 to 2010)	millimeters	PRISM
Climate: Water	Spring ppt	169	131	187	17	Spring total precipitation (1895 to 1924)	millimeters	PRISM
Climate: Water	Spring ppt	169	136	184	15	Spring total precipitation (1981 to 2010)	millimeters	PRISM
Climate: Water	Summer ppt	267	203	286	29	Summer total precipitation (1895 to 1924)	millimeters	PRISM
Climate: Water	Summer ppt	242	182	259	27	Summer total precipitation (1981 to 2010)	millimeters	PRISM
Climate: Water	Fall ppt	195	179	200	7	Fall total precipitation (1895 to 1924)	millimeters	PRISM
Climate: Water	Fall ppt	190	177	194	5	Fall total precipitation (1981 to 2010)	millimeters	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Winter ppt	289	246	316	19	Winter total precipitation (1895 to 1924)	millimeters	PRISM
Climate: Water	Winter ppt	286	255	306	14	Winter total precipitation (1981 to 2010)	millimeters	PRISM
Climate: Water	Annual tdmean	-3.95	-4.02	-3.88	0.03	Annual average of daily dewpoint temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Water	Annual tdmean	-2.29	-2.38	-2.21	0.04	Annual average of daily dewpoint temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Water	Spring tdmean	-7.40	-7.48	-7.32	0.04	Spring average of daily dewpoint temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Water	Spring tdmean	-5.45	-5.54	-5.30	0.06	Spring average of daily dewpoint temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Water	Summer tdmean	3.02	2.86	3.16	0.07	Summer average of daily dewpoint temperature (1895 to 1924)	degrees Celsius	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Summer tdmean	4.41	4.28	4.53	0.07	Summer average of daily dewpoint temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Water	Fall tdmean	-2.59	-2.67	-2.50	0.04	Fall average of daily dewpoint temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Water	Fall tdmean	-0.78	-0.89	-0.65	0.05	Fall average of daily dewpoint temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Water	Winter tdmean	-8.82	-8.89	-8.75	0.02	Winter average of daily dewpoint temperature (1895 to 1924)	degrees Celsius	PRISM
Climate: Water	Winter tdmean	-7.36	-7.41	-7.26	0.03	Winter average of daily dewpoint temperature (1981 to 2010)	degrees Celsius	PRISM
Climate: Water	Annual vpdmax	14.65	13.94	15.51	0.37	Annual average of daily maximum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Annual vpdmax	14.94	14.19	15.75	0.35	Annual average of daily maximum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Spring vpdmax	13.51	12.87	14.24	0.32	Spring average of daily maximum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Spring vpdmax	13.73	13.11	14.40	0.29	Spring average of daily maximum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Summer vpdmax	24.22	23.03	25.61	0.61	Summer average of daily maximum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Summer vpdmax	25.03	23.56	26.49	0.66	Summer average of daily maximum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Fall vpdmax	14.35	13.72	15.21	0.35	Fall average of daily maximum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Fall vpdmax	14.38	13.73	15.16	0.32	Fall average of daily maximum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Winter vpdmax	6.53	6.15	6.99	0.20	Winter average of daily maximum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Winter vpdmax	6.61	6.36	6.93	0.13	Winter average of daily maximum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Annual vpdmin	3.26	2.84	3.56	0.18	Annual average of daily minimum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Annual vpdmin	3.09	2.92	3.27	0.09	Annual average of daily minimum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Spring vpdmin	3.10	2.78	3.32	0.13	Spring average of daily minimum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Spring vpdmin	3.15	2.97	3.30	0.07	Spring average of daily minimum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Summer vpdmin	5.30	4.61	5.84	0.31	Summer average of daily minimum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Summer vpdmin	5.13	4.88	5.46	0.15	Summer average of daily minimum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Fall vpdmin	3.16	2.66	3.53	0.22	Fall average of daily minimum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM
Climate: Water	Fall vpdmin	2.86	2.64	3.11	0.12	Fall average of daily minimum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Climate: Water	Winter vpdmin	1.48	1.30	1.55	0.06	Winter average of daily minimum vapor pressure deficit (1895 to 1924)	hectopascals	PRISM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Climate: Water	Winter vpdmin	1.20	1.15	1.23	0.02	Winter average of daily minimum vapor pressure deficit (1981 to 2010)	hectopascals	PRISM
Soil	BD 0cm	666	527	948	67	Bulk density of the fine earth fraction (<2 mm) at 0cm soil depth	grams per cubic centimeter	Soil Grids
Soil	BD 5cm	891	766	1002	51	Bulk density of the fine earth fraction (<2 mm) at 5cm soil depth	grams per cubic centimeter	Soil Grids
Soil	BD 15cm	1131	1023	1212	36	Bulk density of the fine earth fraction (<2 mm) at 15cm soil depth	grams per cubic centimeter	Soil Grids
Soil	BD 30cm	1228	1162	1287	25	Bulk density of the fine earth fraction (<2 mm) at 30cm soil depth	grams per cubic centimeter	Soil Grids
Soil	BD 60cm	1336	1219	1418	44	Bulk density of the fine earth fraction (<2 mm) at 60cm soil depth	grams per cubic centimeter	Soil Grids

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Soil	BD 100cm	1447	1364	1504	25	Bulk density of the fine earth fraction (<2 mm) at 100cm soil depth	grams per cubic centimeter	Soil Grids
Soil	BD 200cm	1439	1362	1507	30	Bulk density of the fine earth fraction (<2 mm) at 200cm soil depth	grams per cubic centimeter	Soil Grids
Soil	Clay 0cm	16	11	21	2	Percent clay at 0cm soil depth	Percent by weight	Soil Grids
Soil	Clay 5cm	16	11	21	2	Percent clay at 5cm soil depth	Percent by weight	Soil Grids
Soil	Clay 15cm	17	13	21	2	Percent clay at 15cm soil depth	Percent by weight	Soil Grids
Soil	Clay 30cm	24	16	37	5	Percent clay at 30cm soil depth	Percent by weight	Soil Grids
Soil	Clay 60cm	36	24	50	6	Percent clay at 60cm soil depth	Percent by weight	Soil Grids
Soil	Clay 100cm	37	25	49	6	Percent clay at 100cm soil depth	Percent by weight	Soil Grids

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Soil	Clay 200cm	36	24	50	6	Percent clay at 200cm soil depth	Percent by weight	Soil Grids
Soil	N Total 0cm	70	48	81	5	Total Nitrogen at 0cm soil depth	Percent by weight	Soil Grids
Soil	N Total 5cm	37	29	43	3	Total Nitrogen at 5cm soil depth	Percent by weight	Soil Grids
Soil	N Total 15cm	21	16	25	2	Total Nitrogen at 15cm soil depth	Percent by weight	Soil Grids
Soil	N Total 30cm	13	8	18	2	Total Nitrogen at 30cm soil depth	Percent by weight	Soil Grids
Soil	N Total 60cm	10	6	15	2	Total Nitrogen at 60cm soil depth	Percent by weight	Soil Grids
Soil	N Total 100cm	9	4	14	2	Total Nitrogen at 100cm soil depth	Percent by weight	Soil Grids
Soil	N Total 200cm	11	5	15	2	Total Nitrogen at 200cm soil depth	Percent by weight	Soil Grids

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Soil	pH 0cm	58.3	55.1	62.7	1.7	pH in 1:1 soil–water solution at 0cm soil depth	pH	Soil Grids
Soil	pH 5cm	56.8	53.7	61.0	1.6	pH in 1:1 soil–water solution at 5cm soil depth	pH	Soil Grids
Soil	pH 15cm	57.0	54.5	61.0	1.5	pH in 1:1 soil–water solution at 15cm soil depth	pH	Soil Grids
Soil	pH 30cm	57.0	55.0	60.3	1.3	pH in 1:1 soil–water solution at 30cm soil depth	pH	Soil Grids
Soil	pH 60cm	57.1	55.2	60.6	1.3	pH in 1:1 soil–water solution at 60cm soil depth	pH	Soil Grids
Soil	pH 100cm	57.2	55.1	61.6	1.5	pH in 1:1 soil–water solution at 100cm soil depth	pH	Soil Grids
Soil	pH 200cm	57.4	55.1	61.9	1.6	pH in 1:1 soil–water solution at 200cm soil depth	pH	Soil Grids

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Soil	Sand 0cm	27	18	36	4	Percent sand at 0cm soil depth	Percent by weight	Soil Grids
Soil	Sand 5cm	28	19	36	4	Percent sand at 5cm soil depth	Percent by weight	Soil Grids
Soil	Sand 15cm	27	18	36	4	Percent sand at 15cm soil depth	Percent by weight	Soil Grids
Soil	Sand 30cm	27	20	35	4	Percent sand at 30cm soil depth	Percent by weight	Soil Grids
Soil	Sand 60cm	28	20	37	4	Percent sand at 60cm soil depth	Percent by weight	Soil Grids
Soil	Sand 100cm	31	22	40	4	Percent sand at 100cm soil depth	Percent by weight	Soil Grids
Soil	Sand 200cm	32	23	40	4	Percent sand at 200cm soil depth	Percent by weight	Soil Grids
Soil	SOC 0cm	294	186	338	23	Soil organic Carbon at 0cm soil depth	Percent by weight	Soil Grids

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Soil	SOC 5cm	72	44	96	14	Soil organic Carbon at 5cm soil depth	Percent by weight	Soil Grids
Soil	SOC 15cm	28	18	37	6	Soil organic Carbon at 15cm soil depth	Percent by weight	Soil Grids
Soil	SOC 30cm	17	8	25	4	Soil organic Carbon at 30cm soil depth	Percent by weight	Soil Grids
Soil	SOC 60cm	10	5	14	2	Soil organic Carbon at 60cm soil depth	Percent by weight	Soil Grids
Soil	SOC 100cm	8	4	13	2	Soil organic Carbon at 100cm soil depth	Percent by weight	Soil Grids
Soil	SOC 200cm	9	3	16	3	Soil organic Carbon at 200cm soil depth	Percent by weight	Soil Grids
Topography: Aspect	Beer's Aspect	1.44	0.00	2.00	0.56	Cosine transformed aspect	NA	DEM
Topography: Aspect	Heat Load Index (HLI)	0.83	0.71	0.97	0.05	Slope-aspect transformation	NA	DEM

Factor	Variable	Mean	Min	Max	SD	Description	Units	Source
Topography: Aspect	Solar Radiation Index (SRI)	1715499	1593948	1810763	41603	Amount of incoming solar insolation	Watt hours per square meter	DEM
Topography: Position	Elevation	2332	2223	2399	41	Elevation above sea level	meters	DEM
Topography: Position	Hierarchical Slope Position (HSP)	3295	-10371	14386	5249	Multi-scalar measure of topographic exposure	NA	DEM
Topography: Position	Topographic Position Index (TPI)	0.55	-11.53	9.75	3.61	Local measure of topographic exposure	NA	DEM
Topography: Texture	Roughness	17.1	1.4	31.2	5.8	Maximum elevational difference	meters	DEM
Topography: Texture	Slope	5.5	0.0	10.5	2.3	Steepness of terrain	degrees	DEM
Topography: Texture	Terrain Ruggedness Index (TRI)	19.3	2.0	42.0	7.2	Average of elevational differences	meters	DEM

Table 3: Summary of all potential environmental variables. Variables are organized by environmental factor, and subgroup if applicable. Summary statistics (mean, minimum, maximum, and standard deviation, brief description, units and data source are provided for each variable. Historical and contemporary climate variables are listed separately.

Appendix B: Historical and contemporary model pathway details

Diagram Key	Pathway		Model	Coefficient	Components
	From	To			
a	Position	Density	Historical	0.245*	HSP
			Contemporary	-0.358*	HSP
b	Position	Diameter	Historical	-0.324*	HSP
			Contemporary	0.321*	HSP
c	Position	Composition	Historical	-0.371*	HSP
			Contemporary	-0.405*	HSP
NA	Texture	Density	Historical	-0.065	TRI
NA			Contemporary	-0.095	TRI
NA	Texture	Diameter	Historical	0.053	TRI
NA			Contemporary	-0.020	TRI
c	Texture	Composition	Historical	0.126*	TRI
NA			Contemporary	0.068	TRI
NA	Aspect	Density	Historical	0.008	SRI
NA			Contemporary	0.010	SRI
NA	Aspect	Diameter	Historical	-0.124	SRI
NA			Contemporary	0.072	SRI
c	Aspect	Composition	Historical	-0.233*	SRI
			Contemporary	-0.184*	SRI
d	Climate	Density	Historical	0.276*	Winter Tmin (-0.491); Winter Tmax (0.657); Fall Tmean (0.473); Spring Precip (3.546); Winter VPDmin (-3.462)
			Contemporary	0.212*	Winter Tmin (-2.566); Winter Tmax (-3.615); Spring Precip (-1.742); Summer Tdmean (-0.035)
e	Climate	Diameter	Historical	0.370*	Winter Tmin (-2.052); Winter Tmax (-0.228); Fall Tmean (0.27); Spring Precip (0.773); Winter VPDmin (1.821)

Diagram Key	Pathway		Model	Coefficient	Components
	From	To			
			Contemporary	0.212*	Winter Tmin (2.423); Winter Tmax (3.568); Spring Precip (2.202); Summer Tdmean (1.224)
f	Climate	Composition	Historical	0.657*	Winter Tmin (6.969); Winter Tmax (1.124); Fall Tmean (-0.769); Spring Precip (2.375); Winter VPDmin (-6.687)
			Contemporary	0.792*	Winter Tmin (-0.855); Winter Tmax (0.185); Spring Precip (1.512); Summer Tdmean (-0.486)
g	Soil	Density	Historical	0.352*	Clay.30cm (0.207); ph.0cm (-0.726); SOC.30cm (0.437)
			Contemporary	0.203*	ph.0cm (-0.793); SOC.30cm (0.233)
h	Soil	Diameter	Historical	0.383*	Clay.30cm (-0.482); pH.0cm (0.441); SOC.30cm (-0.863)
			Contemporary	0.259*	pH.0cm (0.723); SOC.30cm (-0.309)
i	Soil	Composition	Historical	0.389*	Clay.30cm (0.26); pH.0cm (0.924); SOC.30cm (0.116)
			Contemporary	0.345*	pH.0cm (0.661); SOC.30cm (-0.373)
j	Composition	Diameter	Historical	-0.228*	Axis 1
NA			Contemporary	-0.058	Axis 1
NA	Composition	Density	Historical	0.104	Axis 1
k			Contemporary	0.255*	Axis 1

Table 4: Summary of pathways in Historic and contemporary models. Letters in the Diagram Key column correspond to the letters on pathways in figures 10 and 11. Values of NA indicate that this pathway is not included in these model diagrams. Pathway: From and Pathway: To describe the directional relationship between model components that each pathway represents. The Model column indicates whether the following values correspond to the pathway in the historical model or the Contemporary model. The Coefficient column contains the path coefficient, which describes the relative magnitude and direction of each pathway's relationship. Values with

* are statistically significant from 0 ($p < 0.05$). The Components column contains the predictors used to calculate each pathway; if more than one predictor was used, the path coefficients used to calculate the composite are given in parentheses.