QUANTIFYING ECOSYSTEM TRAJECTORIES: TREE GROWTH RESPONSE TO BIOPHYSICAL GRADIENTS AND DISTURBANCE

by

Laura Avery Ehlers Marshall

A Dissertation Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements For the Degree of

DOCTOR OF PHILOSOPHY

WITH A MAJOR IN NATURAL RESOURCES

In the Graduate College

THE UNIVERSITY OF ARIZONA

2019

THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by **Laura Avery Ehlers Marshall**, titled **Quantifying Ecosystem Trajectories: Tree Growth Response to Biophysical Gradients and Disturbance** and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

Donald A. Falk Date: February 5, 2019

Steven W. Leavitt Date: February 5, 2019

Nathan G. McDowell Date: February 5, 2019

David J. Moore Date: February 5, 2019

Valerie M. Trouet Date: February 5, 2019

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Date: February 5, 2019

Donald A. Falk
Dissertation Committee Chair
Professor, School of Natural Resources and the Environment

Acknowledgements

Thanks to my committee: Steven Leavitt, Valerie Trouet, David Moore, Nathan McDowell, and especially to my advisor Donald Falk for support and guidance over the many years of work that led to this completed dissertation.

For extensive help over many summers of fieldwork, assistance in the lab, and fellowship, thanks to Alex Arizpe, Mark Betancourt, Faith Campbell, Joshua Conver, Jacquie Dewar, Sharmila Dey, Alicia Durnin, Josh Farella, Ali Jaffery, Sarah Jorgensen, Erana Loveless, Kyle Miller, Jesse Minor, Rebecca Minor, Erica Newman, Cherry Niel, Christopher (Kit) O'Connor, Anastasia Rabin, Ben Schippers, Tyson Swetnam; Samantha S. Stutz, and Emma Williams.

Much thanks to Craig Allen, Chris Baisan, Margaret Evans, Ann Lynch, Ellis Margolis, and Tom Swetnam who contributed support, guidance, and ideas to the dissertation. Special thanks to Dorian Voorhees for help navigating my dissertation writing years.

For funding and support during my years as a graduate student, thanks to the University of Arizona School of Natural Resources and the Environment and the University of Arizona Graduate College, the USFS Collaborative Forest Restoration Program (CFRP) and the Rocky Mountain Research Station, the Joint Fire Science Program, the NM Forest and Woodlands Restoration Institute, and the US DoE Global Change Education Program.

For help keeping me fit and connected beyond the academy, thanks to my running friends in the Workout Group and the Tucson Trail Runners.

And a very special thank you to Rex Adams, for introducing me to tree rings.

—Laura Marshall, Tucson, Arizona, April 2019

Dedication

This dissertation is dedicated to Mom & Dad, for helping me get through.

Index

List of Figures

List of Tables

Abstract

Disturbance and climate are important drivers of tree physiological functioning, community assemblages and trends in recruitment and species presence across time and space. Fire exclusion-driven changes to the disturbance regime of frequent fire-adapted forests of the southern Rocky Mountains, North America, followed by modern megafires has strongly influenced stand structure and led to density increases in many forest types. Recent decadal drought has led to widespread mortality of some tree species, exacerbated fire extent and effects, and contributed to insect outbreaks. With climate change ongoing, hotter and drier conditions and droughts are expected, leading to increased risk of widespread tree mortality and vegetation type change.

Forest ecosystem changes result from compounding effects on individual tree establishment, growth, and survival, which leads to changes in stand structure and composition, and drives patterns appreciable at the broadest scale. Here I focus on tree-environment interactions in the context of disturbance and climate across three scales, from tree-stand, to stand-watershed, to forest-ecosystem. By working across scales we can observe how fine-scale tree responses to interact with the environment to create broad patterns.

At the tree scale, I considered the influence of increased forest density on tradeoffs of water and nutrient limitation affecting growth and physiological functioning in old-growth ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) (Appendix A). I identified a novel interaction in which lower leaf nitrogen in dense stands was associated with lower tree-ring growth yet higher carbon isotope discrimination, rather than the expected negative relationship between discrimination and density-driven water stress. Reduced leaf nitrogen

likely limited photosynthetic capacity, resulting in discrimination values more decoupled from water stress than is expected in the Southern Rockies.

At the stand level to watershed scale, I investigated climate-growth relationships and species distributions across a biophysical gradient in southwestern mixed-conifer forest (Appendix B). I used model selection to find how climate drivers of tree-ring growth varied by species, elevation, and aspect, and found differences were in accordance with relative species drought tolerance. I combined this with stand-level regeneration patterns to predict shifts in species dominance across the watershed. In the absence of fire, I found increased regeneration in pinyon pine (*Pinus edulis* Engelm.) at low elevations and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) at high elevations, while regeneration of ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) decreased everywhere across the study area.

At the ecosystem scale I used Forest Inventory and Analysis (FIA) data to derive the novel Community Mean Tolerance Index, based on relating species shade and drought tolerance to ecosystem changes and applied it to investigate demographic trends within and across forest types (Appendix C). With the index I mapped responses within and across forest ecosystems in the southern Rocky Mountains, and found areas at risk for vegetation type conversion to oak woodland following severe fire. Substantial shifts in mean drought and shade tolerance in tree regeneration was found in forest types that had exceeded their historic fire interval. Across forest types, drought tolerance in seedling groups increased at lower elevation sites, while shade tolerance increased at higher elevation sites. The difference in drought tolerance across demographic groups was significantly associated with PRISM-derived recent temperature and precipitation means, indicating the potential for climate-driven community shifts. Investigating the effects of disturbance and climate on trees, watersheds, and ecosystems allows for a holistic view across scales of the current state of southwestern forests, and the potential for future changes.

Chapter 1. Introduction

Central Focus of Dissertation

Disturbance and climate are important drivers of tree physiological functioning, growth, and demographic trends in recruitment and mortality. These factors contribute to species assemblages at the stand level to watershed scale, and over longer time scales are likely to contribute to range shifts and changes to vegetative communities across a given landscape. By studying current trends in radial tree growth and species composition across demographic groups at multiple scales, I interpret responses to shifting climate and disturbance regimes over the past century, and predict how these influences will contribute to the forest response to changing climate over the next century (Figure FRD-1).

Controls and influencing factors on tree growth and trends in regeneration can be understood through a state factor-interactive controls model as described by Amundson and Jenny (1997). The state factor model conceptualized and describes the relationship and effects of state factors (climate, topography, parent material of soils, potential biota at a site, and time) on ecosystem processes and structure, as modulated and influenced by interactive controls affecting and affected by the ecosystem (Amundson and Jenny 1997; Chapin et al. 2011). The summed effects of the model through time contribute to the development of an ecosystem, specific to place.

In this dissertation I consider the southern Rocky Mountain forest ecosystem, its development over recent centuries with a focus on fire, and the expected consequences of climate change on forest persistence. Within the state factor-interactive control model, I work through the five described state factors with a greater or lesser focus across each Appendix. Key to all sections are climate, topography of the mountainous region, and time on the scale of years to centuries required for the ecosystem processes driving forest growth and stand development. The primary interactive control I will be focusing on is fire, as in this system it combines the effects of disturbance regime and the history of human activities, the most notable in this system being fire exclusion from frequent fire-adapted forest systems.

Ponderosa pine and mixed-conifer forests in the southwestern USA have seen significant changes over the 20th century and the early 21st century, as determined by tree-ring and fire scar analysis (Speer 2010; Falk et al. 2011; Babst et al. 2018). In many areas, fire exclusion can be considered the greatest recent disturbance affecting these forest types, which are adapted to frequent, low severity fire (Covington and Moore 1994; Agee 1998; Keane et al. 2002; O'Connor et al. 2014). Fire exclusion came into effect in the late 1800s, from livestock grazing that removed fine fuels and altered soil structure, and active suppression that broadened in scope and area as technology and conditions allowed (Keane et al. 2002; Falk et al. 2011). Increasing density and the removal of fire from a system adapted to frequent fire favors elevated seedling survivorship, as well as the recruitment and persistence of different species, as stand-level pressures on survival change.

Fire exclusion has altered stand dynamics, leading to extreme increases in stand density in many areas, and increasing risk of severe fire and insect outbreaks (Veblen 2000; Keane et al. 2002; O'Connor et al. 2014). Persistent regional drought enhanced by climate change leads to heightened risk of widespread mortality, especially at lower forest ecotones (Allen et al. 2010; Allen et al. 2015). The return of fire to a landscape with decades of fuel buildup and increasing stand density results in larger and more severe fires. Large fuel loads interact with climate conditions to create the modern "megafires", where fire behavior and size become extreme and threaten forest ecosystems and communities in wildland-urban-interface areas (Radeloff et al. 2005; Williams 2013). Fire, climate, and the interaction between the two are strong, top-down controls on the survival of individual trees and on broader stand dynamics.

Large, severe fires are an important potential trigger for vegetation type change as severe fires are more likely to kill mature trees across large patches, removing nearby seed sources (Stephens et al. 2013; Falk et al. 2017). Following severe fire, a transition to a shrub- or grass-dominated system is then more likely to occur. In coming decades, hotter droughts will contribute to tree die-off events, another path towards vegetation type change and altered ecosystem dynamics (Millar et al. 2007; Hurteau et al. 2014; Allen et al. 2015; Millar and Stephenson 2015). Tree- and stand-level response to changing climate interacting with disturbance regimes can result in changes to species distribution, through extinction in some areas and expansion in others.

Extinction debt and immigration credit are ideas suggesting that that range shifts are a function of demography. Movement of climate envelopes leads to remnant adult populations in some areas (extinction debt), with dispersal is unable to keep up with the leading edge or rate of change (immigration credit). These paired concepts are useful for identifying areas where change of vegetation type may occur (Jackson and Sax 2010). The longevity of trees contributes to lag in species range movement. Recruitment of less-resilient seedlings is more likely to fail in marginal habitat, but extirpation of mature trees in that area may only occur following drought or a disturbance event (Bell et al. 2014; Talluto et al.

2017). Different requirements for survival across demographic groups is a component of niche theory and is the basis for interpreting relative species composition differences across demographic groups in terms of climate and disturbance drivers (Colwell and Rangel 2009; Jackson et al. 2009). By studying differences in species response and composition across demographic groups and spatial gradients subject to climate and disturbance pressures, we can find areas responding to increasing climate stress and thus more likely subject to extinction debt.

Mountain systems are particularly useful in gradient studies due to the steep climatic gradient that occurs with increasing elevation. An increase of 100 m elevation is accompanied by a drop in temperature of approximately 1°C (the dry lapse rate) (Pruppacher and Klett 2010). In complex mountain terrain, lapse rates tend to vary through time, and exact temperature values often depend on local microsite effects (Minder et al. 2010; Strachan and Daly 2017). Mountains also create moisture gradients as air masses are lifted over them and water condenses into clouds and rain (Smith 1979). High-precision weather data are not widely available across the mountains of the western United States and long time series comparable to tree-ring chronologies are rare, so modeled climate data are commonly used for fine-scale comparisons across gradients as the best option available for capturing site-specific climate variability across time and space (Daly et al. 1994; Daly et al. 2008). Elevation in mountain gradient studies tends to correspond to climate variability, given the expectation of cooler and more mesic (moister) conditions at higher altitudes.

Species-level tradeoffs in tolerance for drought or shade are common across Northern Hemisphere tree species (Niinemets and Valladares 2006). These life-history tradeoffs are common across species, genera, and continents (Niinemets 2010). Evolved morphological and physiological traits tend to favor tolerance of either drought or shading by mutually exclusive characteristics (Smith and Huston 1989). Given such a strong tradeoff, differential species recruitment favoring drought- or shade-tolerant species can identify areas where drought (climate) or shade (increasing density from fire exclusion) is a dominant driver of species distribution across gradients (Barton 1993; O'Connor et al. 2017). Tree-scale physiological response can also be used to parse the effects of climate variability and disturbance history on growth and photosynthesis, which then contributes to tree survival or mortality, and across broader scales to species presence or extirpation. The summation of species traits is revealed in overall tendency and degree of drought or shade tolerance. In turn, the overall effect on the plant community of environmental and stand developmental pressures, like fire exclusion, can be intuited through the general functional trait-based tolerance of a species assemblage.

The central focus of this dissertation is on understanding tree responses to interactions of disturbance history, climate, and topographic setting, in southwestern US montane forests, with a focus on ponderosa pine and mixed-conifer forests (Figure FWD-1). I approach this question across multiple scales, to interpret how tree-level growth, physiological response, and regeneration trends contribute to species presence and survival across mountain gradients and landscapes subject to changing climate and disturbance pressures.

Disturbance: Increased Density Following Fire Exclusion

Disturbance regime changes driven by decades to over a century of fire exclusion in the fire-adapted forests of the southern Rocky Mountains, North America have resulted in substantial increases in stand density and altered ecosystem functioning (Bailey et al. 1994; Keane et al. 2002; Kolb et al. 2007; O'Connor et al. 2014). Climate is an important driver of fire activity: large-scale circulation patterns have been shown to drive the widespread occurrence of fire on the American Pacific coast (Trouet et al. 2009), and seasonal climate is a strong control on annual wildfire area burned (Kitzberger et al. 2017). Interactions between climate, fuel availability, and ignition sources are broad controls on fire regimes, moderated by human ability to affect forest conditions and fire occurrence or absence, on the scale of years to centuries (Schoennagel et al. 2004; Falk et al. 2011; Swetnam et al. 2016). The evolution of current overly-dense forest conditions in many parts of the southern Rocky Mountains is tied intrinsically to human presence and actions as inhabitants of the forest landscape.

Ponderosa pine forests, one of the most widespread forest types in the southern Rocky Mountains, undergo episodic periods of mass seedling establishment during wet periods (Brown and Wu 2005). The historic fire regime of this ignition-saturated environment involves frequent low-severity ground fire that tends to occur in dry years following wet years with fuels buildup (Covington and Moore 1994). Fire thins out the seedling population in patches, creating mixed-age stands with grass and herbaceous groundcover between widely spaced trees (Covington and Moore 1994; Swetnam et al. 2016). As a result of fire exclusion, extreme stand density increases have occurred across large areas of ponderosa pine forest in the southern Rocky Mountains (Kolb et al. 2007). Extreme density increases competition, heightening drought mortality risk for overstory trees (Allen et al. 2010; van Mantgem et al. 2018). The degree to which a ponderosa pine stand increases in density in the absence of fire is largely driven by abiotic site characteristics, especially soil parent material, along with aridity of the site (Rodman et al. 2017).

Mixed-conifer forests in the southern Rocky Mountains follow similar patterns of frequent fire, but with more variability in species composition and stand structure, and moderate fire severity in denser stands (Agee 1998; Veblen 2000; Fulé et al. 2009). In mixed-conifer forests in the southern Rocky Mountains and in California, which are subject to similar pressures of fire exclusion, species composition has shifted over decades to favor shade tolerant firs over more drought tolerant and fire-adapted pines (Niinemets and Valladares 2006; Fulé et al. 2009; Serra-Diaz et al. 2016). Reduced species diversity across demographic groups in mixed-conifer forests can reveal community-level responses to shifting disturbance regimes.

An example of increasing stand density following the cessation of frequent fire in southern Rocky Mountains mixed-conifer forest is shown in the stand-age structure for 1040 trees sampled at elevation-stratified random plots (Figure FRD-2) (for further details see Appendix B Supplemental Information). In this figure, tree establishment is grouped into 10-year age bins, with bar color indicating species drought tolerance, from brown (high) to green (low). The last widespread fire in this watershed occurred in 1879, as indicated by the vertical dotted line (Margolis et al. 2007). Most individuals surveyed in this stratified random-sampling study became established after fire exclusion, although older individuals persist on the landscape. The extensive post-fire establishment demonstrates changing stand structure common to 20th century mixed-conifer forests.

Reestablishing frequent, low-severity fire in forests that have increased in density following fire exclusion, without going through a damaging high-severity event, is important for promoting forest resilience (Falk 2017). Increased tree and fuel density contributes to modern extreme fires that burn larger areas with more severe fire behavior than is expected based on understanding of historic fire regimes (Litschert et al. 2012; Williams 2013; O'Connor et al. 2014). Along with altered disturbance regimes, climate change is an important factor in modern fire activity. A hotter climate has resulted in drier fuels and increased area burned in the western US (Abatzoglou and Williams 2016; Kitzberger et al. 2017).

Increasing density can affect tree physiological functioning, resulting in reduced growth, leaf area, and gas exchange, as increased competition reduces the ability of trees to access water and nutrients (McDowell et al. 2003; Sala et al. 2005). Competition-mediated drought stress results in increased stomatal closure and reduced carbon acquisition, heightening the risk of death from hydraulic failure and/or carbon starvation under extended drought (McDowell 2011). The density-stress-mortality relationship reveals the interactions between tree responses to changing disturbance regimes and climate, as trees in denser stands will be more greatly affected by drought (Allen et al. 2010).

Climate: Drought Tolerance, Species Distribution, and Gradients

Temperature and precipitation are key climatic variables driving plant species distributions across gradients, with tolerances derived from genetic, morphological, physiological, and functional traits (Whittaker 1967; Thuiller et al. 2004; Albert et al. 2010). Gene flow contributing to variation along a gradient can occur, with greater variation found at larger scales (Ohsawa and Ide 2008; King et al. 2013). At a species level, plants make tradeoffs in stress response strategies, as traits and characteristics favoring drought tolerance do not support shade tolerance, and vice versa (Niinemets and Valladares 2006). Measurements of variation across gradients in functional traits, such as drought or shade tolerance, are useful as biodiversity indicators and for showing response to land-use change, including altered fire regimes (Albert et al. 2010; Vandewalle et al. 2010).

Sessile plants must grow and respond to shifting climate and disturbance factors in place (Colwell and Rangel 2009). Beyond the individual scale, species respond to changing external conditions through range shifts, which occur via dispersal and mortality events. Specific demographic events often have their own climatic requirements for occurrence, and introduce lag into the aggregate species response to changing mean conditions (Jackson et al. 2009). Climate conditions, variability, and historical trends control where species populations are located. Extreme weather and disturbance events such as drought or wildfire influence mortality and dispersal, and thereby influence where species are found. Such lags between climate and niche can be understood demographically through extinction debt and immigration credit (Jackson and Sax 2010).

In conifers, biodiversity and community structure vary greatly across mountain and climatic gradients (Barton 1993; Lomolino 2001). A stronger tree growth-climate relationship is found near lower elevational ecotones (Fritts et al. 1965; Adams 2005). It follows that within a species elevational range, drought effects and the potential for mortality events driving species presence will be stronger near the lower species ecotone, i.e., at lower elevations with hotter temperatures and less precipitation. At higher elevations within a species range, conditions are more mesic and further from the species extremes of drought tolerance and so other stand-level factors like disturbance history are more likely to be equal or greater influences than climate on growth, survival, and reproduction.

Climate is a major control on species distribution. A commonly-used framework to understand species distribution is the bioclimatic niche, the specific climatic requirements of a species for survival and reproduction applied to find the climatically suitable area for that species (Grinnell 1917; Woodward 1987; Leibold 1995). Bioclimatic approaches can also estimate the variance in area of suitable climate across demographic groups as seedlings tend to be more climate-sensitive than adults (Jackson et al. 2009; Bell et al. 2014; Law et al. 2019). Bioclimatic envelope modeling of species shifts is useful for predicting the potential for climate-driven species range changes, although the models are only as good as their assumptions (Araújo and Peterson 2012). The inclusion of disturbance events in models such as drought-related die offs can improve bioclimatic models and provide a better reflection of species range shift potential, given the lag that can occur between disturbance-driven mortality and dispersal events (Jackson et al. 2009; Law et al. 2019).

Although climate controls where species may occur across a landscape, species-specific factors drive their ability to tolerate drought and the overall climate response. Physiological, morphological, and genetic factors all contribute to varying drought tolerance in conifer species (Niinemets 2010; McDowell 2011; Moran et al. 2017). Key attributes of drought tolerance are the controls on plant water balance and gas exchange, notably stomatal conductance (Farquhar and Sharkey 1982; Klein 2014). More drought tolerant species and individuals are able to maintain leaf turgor under a more negative leaf water potential, avoiding wilting, and also to maintain stem hydraulic connectivity to avoid cavitation (McDowell 2011; Bartlett et al. 2012). Stomatal conductance must also balance water loss with carbon acquisition for photosynthesis. Under extended drought, trees risk mortality from hydraulic failure and/or carbon starvation, depending on species-level safety margins in stomatal conductance and individual variation (McDowell et al. 2011; Sevanto et al. 2013).

Severe multidecadal droughts are an established factor in the history and development of southwestern forests (Cook et al. 2004; Stahle et al. 2007). Climate change is likely to make extreme droughts the new normal. As background climate conditions warm, the added stress of hotter drought influences plant water balance and results in a greater risk of widespread forest mortality (Allen et al. 2015).

Climate Change Exacerbates Drought and Disturbance Effects

Anthropogenic climate change is a complex issue touching on all aspects of the global system, with substantial potential to affect forests. Greenhouse gas emissions, land-use change, and other forcings are contributing to increasing surface temperature and precipitation changes, and observable changes to physical, biological, and human systems including North American forests (IPCC 2014). On the current emissions trajectory, 1.5ºC of warming will be reached by approximately 2040, and is expected to result in substantial changes to natural and human systems (IPCC 2018). Long-term climate reconstructions from the western US show evidence of past extreme drought periods exceeding those seen in the relatively short instrumental record (Cook et al. 2004; Stahle et al. 2007). With climate change raising average temperatures, extreme drought is projected to become more common and widespread, and major changes to forests can be expected with increased risk of widespread species die-offs (Allen et al. 2015).

Climate change can interact with fire regimes and other forest disturbances in many ways, especially in fire-prone forests (Hurteau et al. 2014). Interactive effects of disturbance and climate change can lead to fire regime changes, widespread drought-driven mortality, and changes to patterns of regeneration and recruitment (Seidl et al. 2017; Kane et al. 2017).

These effects contribute to changes in community composition, and with time result in vegetation type conversion, potentially leading to novel species assemblages (Millar and Stephenson 2015; Seidl et al. 2017; O'Connor et al. 2017). Recent decadal drought has led to widespread mortality of certain tree species (Breshears et al. 2005; Allen et al. 2010). In the near future, extreme drought driven by climate change is expected to cause widespread terrestrial species die-offs and has the potential to drastically decrease global biodiversity (Bellard et al. 2012; Allen et al. 2015; Ruthrof et al. 2018).

With climate change ongoing, hotter and drier conditions are expected, with correspondingly hotter and drier droughts leading to changes in species distribution, increased risk of widespread tree mortality, and vegetation type conversion from forests to grasslands or shrubfields (Allen et al. 2015; Millar and Stephenson 2015). Species range movements up in elevation and northward have been noted, and sometimes in other directions depending on local drivers (Breshears et al. 2008; Lenoir and Svenning 2015). Changes in relative composition across demographic groups, without overall range shifts have also been noted (Bertrand et al. 2011; Bell et al. 2014). Demographic composition shifts align with the idea of extinction debt and immigration credit, presaging species range shifts and a heightened potential for vegetation type conversion in the near future (Jackson and Sax 2010; Talluto et al. 2017).

Climate change-driven drought contributes to increases in severe fire weather, and will increase the length of the fire season and the flammability of the forests, affecting fire severity and spread (Collins 2014; Hurteau et al. 2014). In recent years, extreme conditions have led to changing fire behavior, resulting in fast-spreading record-breaking fires and severe effects to certain forest types and wildland-urban interface areas across multiple western US states and Canada (Williams 2013; O'Connor et al. 2014; Keeley and Syphard 2016; Kirchmeier-Young et al. 2017). In the past few years California has repeatedly broken records of fire size, structures burnt, and lives lost in 2017 and 2018, in events where weather (extreme wind events) and climate (extended drought) interact to create the potential for extreme fire (Nauslar et al. 2018). The modern era of record-breaking fires derives in large part from human alterations of the fire regime in many systems, resulting in a buildup of fuels and a fire deficit, compounded by anthropogenic climate change making extreme fire weather more common, and contributing to larger areas burned in dry years (Abatzoglou and Williams 2016; Kitzberger et al. 2017; Tett et al. 2018; Balch et al. 2018).

Along with the effects of hotter drought driving mortality and species range shifts, anthropogenic greenhouse gas emissions, particularly increasing carbon dioxide, can affect plant physiological functioning directly. Higher atmospheric carbon dioxide alters plant assimilation, growth, and water relations, and net positive or negative overall effects are possible, depending on complex interacting factors (Franklin et al. 2016). Initially, it was thought that increased net primary productivity was likely with higher atmospheric carbon dioxide, found experimentally across a global range of forest types, but with time and further stand development, nitrogen limitation can constrain carbon acquisition (Norby et al. 2005; Norby et al. 2010). Recent comprehensive reviews addressing the issue from the perspective of stoichiometry suggest that forests will not be able to fully take advantage of atmospheric carbon dioxide increases, due to nutrient limitation (primarily nitrogen) lowering the global potential for carbon storage through forest growth (Huang et al. 2015; Yue et al. 2017).

Physiological factors likely to be altered by climate change are important for growth and survival at the scale of the individual tree. Increases in plant water-use efficiency are expected as atmospheric carbon dioxide increases, and this could in part counteract drought effects on forest processes (Frank et al. 2015; Allen et al. 2015; Swann et al. 2016). The broader-scale changes driven by increasing temperature and changing water availability parlay the effects on the individual into the potential for range shifts or adaptation at the species level. Identifying areas that are likely to transition to other vegetation types, species assemblages, or functional types is important for reaching management goals and promoting resilience (Millar et al. 2007; Falk 2017). Some areas may be less likely to see climate-driven changes in the near term, and can be considered resistant to changes thanks to site-specific microclimate factors. These climate refugia are important to identify as they may help to maintain biodiversity and land-based carbon stocks (Millar et al. 2018).

The effects of fire exclusion-driven increasing stand density on forest health and ecosystem processes can be hard to disentangle from the effects of climate change. Climate and disturbance can both alter forest dynamics, structure, and biodiversity (Millar and Stephenson 2015; Clark et al. 2016). Promoting forest resilience against change, and restoration efforts following unwanted changes, can help to address both climate change and past disturbance effects such as an interrupted fire regime (Reyer et al. 2015; Falk et al. 2017). In forests adapted to frequent, low-intensity fire that have been subject to fire exclusion, the restoration of fire to the forest can be an important step in promoting resilience and ecosystem services (Hurteau et al. 2014; O'Connor et al. 2017). Looking more broadly at disturbance, many stressors may interact with climate change to magnify the negative effect on forest health (Trumbore et al. 2015; Kane et al. 2017).

Drought is a major factor influencing to tree growth and survival. Fire exclusion constitutes a major disturbance to natural fire regimes and has resulted in increased forest density in frequent-fire systems. The compounding effects of drought and disturbance threaten forest resilience and persistence under climate change, and increase the risk of widespread forest mortality. Understanding the effects of drought and disturbance on trees and forests in western US montane systems is important to understanding how the forest has developed into its present state. This is a necessary first step to understanding how the forests are likely to change over the 21st century, as the effects of climate change become increasingly evident.

Approach

Multi-Scale Analysis of Tree Response to Climate and Disturbance

This dissertation focuses on tree growth and species distribution in the context of disturbance and climate across three scales: tree, stand-watershed, and forest-landscape, in the montane forests of the southern Rocky Mountains, USA (Figure FRD-3). At each scale, data are interpreted through the individual tree response to varying climate, stand-level topographic setting factors, and disturbance regimes. Working across scales can show how fine-scale tree response to disturbance and climate drivers amplifies effects at broader scales, to create widespread systemic response patterns (Babst et al. 2018). In Figure FRD-1, the project design framework linking climate and disturbance drivers to tree processes and the interpretation of response variables across broader scales is summarized. Findings and conclusions of all studies are broadly applicable to similar forest types across the Rocky Mountains and the intermountain western USA.

Appendix A considers fine-scale tree physiological response mechanisms to interactive disturbance and drought effects over the 20th century period of fire exclusion in an old-growth ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forest. Appendix B examines watershed-scale growth and species composition shifts in response to disturbance and climate, across the elevational range of ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and covering the same time frame as Appendix A. Appendix C develops and applies a community index relating mean functional trait response to ecosystem-level disturbance and climate, across and between forest types occurring in the southern Rocky Mountains across elevation ranges from pinyon-juniper woodland to rocky mountain bristlecone pine (*Pinus aristata* Engelm.) near treeline. All three appendices address aspects of how individual tree response to climate and disturbance shapes the current forest landscape, and how knowledge of past drivers and responses can inform on changes to the forest that might be expected from 21st century climate and disturbance pressures.

The southern Rocky Mountains was chosen as the system of study because it has experienced substantial changes over the past century from altered disturbance patterns and fire exclusion (Veblen 2000; Keane et al. 2002; Kolb et al. 2007). It is a system with extensive history of human occupation and influences from uses like grazing, logging, and recreation, and from fire exclusion. Sociological factors have altered fire regimes and forest ecology likely from the time of first human occupation, with effects becoming more widespread as technology allowed (Bowman et al. 2011; Litschert et al. 2012; Swetnam et al. 2016).

The southern Rocky Mountains region is well suited to gradient studies, where elevational change and climatic variation align with forest type change and corresponding variation in controls on tree growth and species distributions (Barton 1993; Lomolino 2001;

Adams 2005; Fukami and Wardle 2005; Bell et al. 2014). Elevational gradients are especially useful in ecological studies as variation in growth or species composition across altitudes tends to reflect variation in other factors that are changing over the gradient (Körner 2007). For this dissertation, variation in response to climate (temperature and precipitation) or disturbance (fire exclusion leading to stand density increases), and tradeoffs between the different factors across the mountain gradient are the primary focus of study.

Full methods and results are found in each appendix. Generally, tree rings are used in Appendix A and Appendix B for time series analysis of tree growth and climate response (Speer 2010). In Appendix A, stable carbon isotope analysis of tree rings is also used to identify changes in water stress and limiting factors over the period of analysis across forests with different stand densities (McCarroll and Loader 2004; Leavitt 2010). A notable finding in Appendix A is that in some very dense stands, carbon isotope discrimination does not always indicate water stress as expected, but rather a nitrogen limitation effect on trees' ability to photosynthesize.

Gradient analysis is the focus of Appendix B, developing species-specific tree-ring climate models and investigating demographic variation in species composition. Here we found a species-specific climate-growth response that was strongest at lower species ecotones, in accordance with expectations from the literature. Species composition shifts across demographic groups followed the trend of climate being a more important driver at lower elevations, with increased dominance of drought tolerant *Pinus edulis*, and fire exclusion-driven density increase being more important at higher elevations, with increased dominance of *Abies concolor* and reductions in *Pinus ponderosa* across the gradient. Here the potential for *Pinus edulis* expansion upwards, in an area that has seen regional die-off of the species, was the most novel finding (Breshears et al. 2005).

Appendix C incorporates Forest Inventory and Analysis (FIA) data into a novel community mean index of species drought or shade tolerance, used as an ecosystem response metric tracking demographic trends (Garnier et al. 2004; Kunstler et al. 2012; Burrill et al. 2017). The findings fit with expectations developed from elevation-related conclusions in Appendix B and from the literature. By forest type, lower elevations tended to shift towards drought tolerance, a climate response, and higher elevations to shift towards shade tolerance, thus responding to disturbance. Demographic shifts were especially notable in forest types most affected by fire exclusion, which had gone substantially outside the range of their expected historic fire interval. The index was used to identify areas and forest types that might be more likely to undergo vegetation type change. In general, mid-elevation mixed-conifer showed the greatest potential for change, either to oak woodland following fire, or to substantially increased density and fir dominance.

Broad forest ecosystem changes result from a conflation of factors affecting individual trees, which then lead to changes in stand structure and composition, in turn resulting in patterns appreciable at the broadest scale. Investigating the effects of disturbance and climate on individual trees, stands across watershed gradients, and forest types that make up larger ecosystems allows for a holistic view of the current state of southwestern forests, and the potential for change in the near future as the global and local effects of climate change become more apparent every year.

Chapter 2. Present Study

Detailed methods, results, theoretical framings, specific grounding in the literature, and conclusions of this research project are presented in three manuscripts appended to this dissertation. The following chapter summarizes the research focus and describes the most important findings from the dissertation appendices, and interprets the contributions each manuscript makes to the dissertation as a whole.

Appendix A: "Nitrogen Can Limit Overstory Tree Growth Following Extreme Stand Density Increase in a Ponderosa Pine Forest"

Author's note: The following summarizes the results of a multi-authored journal manuscript of which I was the primary author. Manuscript coauthors were collaborators who contributed assistance in the form of funding, editorial, and analytical support. The manuscript was published in January 2019 in Tree-Ring Research 75(1) 49-60, a peer-reviewed publication of the Tree-Ring Society.

Environmental variation and gradients in physical settings are interpreted through the physiological response of an organism. In trees, environmental variation is apparent in interannual growth and stand dynamics, and across longer time scales, the mortality or survival of individuals. The growth and survival of individual trees contributes to the species composition of the stand, and across broader scales to the distribution of a given species' range. In ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forests across the western United States, fire exclusion has led to extreme stand density increases starting in the early 20th century (Kolb et al. 2007; Hurteau et al. 2014). For individual overstory trees, the increase in competition resulted in reduced access to water and nutrients reducing tree growth and affecting physiological functioning. In general, water stress is considered to be the primary factor driving reduced growth and physiological changes in dry ponderosa pine forests (McCarroll and Loader 2004). We found that nitrogen was at times the more important driver based on relative changes in tree growth and discrimination between dense and open stands.

This study investigates the physiological drivers of increased competition on overstory ponderosa pine, using stable carbon isotope analysis of tree rings to track tradeoffs in water and nitrogen limitation over time. At Monument Canyon Research Natural Area, an old-growth ponderosa pine-dominant forest in the Jemez Mountain in northern New Mexico, USA, we compared growth and carbon isotope discrimination response in overstory trees between dense and open stands. Using tree rings, we tested change over three time periods: before the density increase, after the increase with similar climate, and a later period with high stand density and regional drought. At the time of tree ring sampling we also tested soil and leaf nitrogen to find the effects of competition on nutrient limitation as well as water stress.

In the initial sampling period, before density increased, overstory trees in stands that became dense or stayed open acted similarly in growth and discrimination. After density increased, we found reduced growth in dense stands, but discrimination was greater in dense stands, contrary to expectations supposing water stress the primary driver. In the later period with drought and completion affecting growth, we found a mixed response, in which growth stayed low in dense stands but discrimination was not different from open stands. Trends in nitrogen sampling suggested greater per-stem nitrogen stress in dense stands.

We were not able to track variation in nitrogen availability in soils and use by trees over time, as we were with growth and discrimination using the tree-ring record. However, water stress alone does not explain our findings. In the later sampling period nitrogen, growth, discrimination patterns align to suggest a tradeoff in limiting factors over time. This could lead to the unexpected discrimination findings through the mechanism of nitrogen limitation affecting carbon assimilation through reduced photosynthetic capacity, rather than water limitation reducing stomatal conductance. Though water limitation is generally the primary concern in dense ponderosa pine forests, we found evidence suggesting nitrogen limitation is also important, which could influence management decisions in ponderosa pine forests.

Appendix B: "Modeled Climate-Growth Relationship and Topographic Influence on Changing Species Distributions"

Author's note: The following summarizes the results of a multi-authored journal manuscript of which I will be the primary author. Manuscript coauthors will be collaborators who contributed assistance in the form of funding, editorial, and analytical support. The manuscript is being prepared for submission to the Journal of Ecology, a peer-reviewed journal of the British Ecological Society, or similar peer-reviewed journal addressing ecological change over time and space.

At the watershed scale, the response of individual trees is summed across the landscape through the investigation of species composition shifts across demographic groups. In southwestern mixed-conifer forests, changing species composition is a result of the past disturbance and altered fire regimes, combined with increasing drought stress as the region moves into an era dominated by a warming, drying climate (Allen et al. 2010; Williams et al. 2010; Allen et al. 2015). Fire exclusion is a critical factor that has led to increased stand density and species composition changes in forest types adapted to frequent fire, including southwest mixed-conifer forests that historically had fire return intervals of approximately 25 years (Covington and Moore 1994; Margolis and Balmat 2009; O'Connor et al. 2014; Law et al. 2019). With climate change affecting tree growth, survival, and recruitment, further changes are expected in species distribution and community composition compared to today. Across mountain gradients, climate is anticipated to affect lower-elevation ecotones and contribute to shifting species distributions (Lomolino 2001; Breshears et al. 2008).

Along a southwest mixed-conifer forest elevation-aspect gradient, we investigated 20th century growth-climate relations using tree rings from the two dominant species. We also investigated the community dynamics contributing to relative species dominance across the watershed. Our study area was the Little Tesuque Watershed in the Sangre de Cristo Mountains, New Mexico, USA, in a watershed gradient encompassing the lower to upper elevation limits of the distribution of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

We used model selection to pick between temperature and climate drivers as primary predictors of mean tree-ring growth series for ponderosa pine and Douglas-fir. Plots were stratified by elevation and randomly selected, and were split into five topographically similar groups for analysis using a classification tree. Tree growth responded to climate more strongly at lower ecotone boundaries, in accordance with Fritts et al. (1965). Differences in climatic drivers of tree growth indicated species-specific stressors at the warmer limits of species distribution, which has implications for species-level resilience across its present range, and the potential for type change following disturbance or widespread drought-related mortality (Allen et al. 2010; Millar and Stephenson 2015).

To find the potential for changing species composition, we compared relative species dominance in the six major mixed-conifer tree species present in the watershed, between tree and regeneration classes using the same elevation-aspect groups to species and areas where the regeneration community had substantially different relative dominance. Survival of seedlings in a given area is not guaranteed with increasing climate change stress and the potential for widespread mortality and vegetation type change (Millar and Stephenson 2015; Law et al. 2019). Current trends in regeneration set up the potential 21st century forest and can provide a snapshot of current trends in species distribution and regeneration patterns.

We found differences in the climate drivers of tree growth at low elevations and southwest aspects only. Ponderosa pine growth was best modeled by precipitation across all elevation-aspect groups. Douglas-fir was best modeled by temperature variables at the low and mid elevations with southwest aspects, and elsewhere by precipitation. This likely tracked the degree to which each species expressed drought tolerance. Douglas-fir is less drought tolerant than ponderosa pine and so at its lower elevation limits temperature became more important (Niinemets and Valladares 2006). Increasing temperature stress from climate change will likely affect Douglas-fir at these low elevation sites first, potentially resulting in mortality events and changes to species distribution.

We found a substantial proportion of trees (stem diameter at breast height > 2.5 cm) in the study area had establishment dates after the last major fire in the watershed, in the late 1800s. Similar density increase following fire suppression *ca.* 1900 is common in forests across the western US (Swetnam et al. 2016). Establishment dates for individuals in the regeneration group likely came from the 30-40 year period before sampling (approximately 1970-2010), based on size-age relationships for conifer species (Shepperd et al. 2006).

Comparing relative species proportions of trees and regeneration, we found changes in composition that varied by elevation and aspect. At lower elevations and southwest aspects, we found a greater proportion of drought-tolerant pinyon pine (*Pinus edulis* Engelm.) in the regeneration class despite recent regional dieoffs affecting the species (Breshears et al. 2005; Allen et al. 2010). These plots were near the upper elevation limit of pinyon pine, where increasing dominance was likely a combined effect of fire exclusion and suitable climate for regeneration. At high elevations, we found significant increases in white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.). Fire exclusion is likely the dominant driver of shade-tolerant white fir success, as it is able to fill in gaps as the overstory canopy closes. The increase in tree density means there is an increased risk of severe fire with extreme fire behavior, when fire returns to the forest, unless management actions are taken to reduce the fuel load and break up continuous stands. Across the gradient, we found a significantly lower presence of ponderosa pine and Douglas-fir in the regeneration group, indicating that conditions were less suitable for regeneration in recent decades for those species.

Demographic patterns in regeneration across the watershed tended to differ from the relative dominance in the tree community, increasing the chance that different community structures with different dominant species will develop. Over time, species distributions are increasingly likely to change as lags in shifting species distribution resolve. This may occur gradually with climate change, over a period of years of drought, or suddenly following an extreme event like a severe, widespread fire.

Appendix C: "Demographic Trends in Community Functional Tolerance Reflects Tree Responses to Climate and Disturbance"

Author's note: The following summarizes the results of a multi-authored journal manuscript of which I will be the primary author. Manuscript coauthors will be collaborators who contributed assistance in the form of funding, editorial, and analytical support. The manuscript is being prepared for submission to Ecological Applications, a peer-reviewed journal of the Ecological Society of America, or to a similar peer-reviewed journal addressing metrics of ecological response to climate and disturbance.

Mean changes in functional traits across forest types and forested ecosystems can inform overall trends in forest community response to climate and disturbance. We investigated change in drought and shade tolerance across the southern Rocky Mountains by developing the novel Community Mean Tolerance Index (CMTI), based on tree species composition in a plot, interpreted through species-level functional tradeoffs between drought and shade tolerance. Community means are useful for interpreting change across different systems with one unified metric. The drought-shade tolerance tradeoff is a function of species physiology and life history variation, and has been well established in temperate forest species, genera, and across continents (Niinemets and Valladares 2006). By aligning functional tolerance with major drivers of forest change, we can interpret ecosystem variability across forest types and age classes (Garnier et al. 2004; Kunstler et al. 2012).

CMTI difference across age classes indicates ecosystem response to regional drought affecting recent climate (drought tolerance) or disturbance history, where fire exclusion has led to increasing stand density in forests adapted to frequent fire (shade tolerance) (White and Vankat 1993; Fulé et al. 2002; Allen et al. 2015). Mean tolerance trends are determined by the factors at a site contributing to individual tree and seedling survival and reproduction, from which the mean is derived. Where the seedling CMTI is especially different from the tree CMTI, there is a substantial difference in functional tolerance across demographic groups. In some cases, this may indicate a greater chance of vegetation type change if trends in ecosystem stressors continue or a disturbance occurs favoring a differential survival of seedlings (Millar and Stephenson 2015; Falk et al. 2017).

We applied the CMTI to the Sangre de Cristo Range portion of the Southern Rockies ecoregion, a mountainous forested region in Colorado and New Mexico, USA, south of the Arkansas River and east of the Rio Grande (Bailey et al. 1994). Using Forest Inventory and Analysis (FIA) program data, we obtained counts and species for trees and seedlings at all plots within the area of interest, a total of 864 unique plot-conditions sampled since 2003 when exact seedling counts were implemented in FIA sampling practices (Burrill et al. 2017). We calculated the CMTI difference across demographic groups of seedlings and trees at each plot for drought and shade using established relative tolerance values by species (Niinemets and Valladares 2006). The CMTI difference across demographic groups was used to identify areas and conditions of substantial change in drought and shade tolerance, within and across forest types. Notably, seedling tolerance index values tended to move away from the middle towards the extremes of drought tolerance, shade tolerance, or low tolerance/aspen dominated species assortments. The divergence in CMTI values in the seedling group facilitates broad-scale interpretation of where plots are driven more by climate or by disturbance history.

The greatest difference in CMTI across demographic groups was found in forest types where fire exclusion has pushed the fire regime furthest from the expected historic fire interval. For the drought tolerance CMTI, we found a change in drivers at 2500 m elevation, within the mixed-conifer forest type, which is adapted to high-frequency mixed severity fire. Below 2500 m in elevation we found a consistent climate relationship and increasing drought tolerance in the regenerative seedling group, while above 2500 m we observed a greater influence of stand-driven variation. The shade tolerance CMTI had a similar inflection point at 2300 m, within the ponderosa pine forest type, which is adapted to high-frequency low severity fire. Assuming a general cessation of fire in the region around 1900, peak index difference in these forest types indicates a relationship between demographic trends in tolerance and altered fire regimes.

We used the CMTI to find areas with a high risk of vegetation type conversion following a severe fire, based on the dominance of Gambel oak (*Quercus gambelii* Nutt.) in the regeneration group. Root sprouting Gambel oak has a tendency to form an understory shrub layer, resprout after fire, and persist in shrub form (Guiterman et al. 2018). FIA sampling protocol counted each Gambel oak root sprout from a single point as a seedling, without consideration for whether the species persisted at the plot in understory or tree form. As a result, mean CMTI values for the regeneration group were significantly affected at plots with a substantial oak regeneration presence, making the potential for change after severe fire clear. We mapped CMTI difference across demographic groups, and flagged plots where oak contributed to seedling CMTI shifts, areas that after fire are likely to transition to oak shrubfield.

Determining the potential for species distribution shifts and vegetation type change, particularly in response to disturbance and climate stress, is a critical area of study given current projections of climate change and the potential effects on forested ecosystems resulting in widespread tree mortality (Allen et al. 2015; IPCC 2018). The difference in functional drought tolerance between tree and seedling groups can be considered a bellwether of the trajectory of ecosystem change, across broad areas and multiple forest types.

References Cited

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, *113*(42), 11770-11775.

Adams, H. D. (2005). Tree growth response to drought and temperature along an elevation gradient on a mountain landscape. *Journal of Biogeography*, *32,* 1629-1640.

Agee, J. K. (1998). The landscape ecology of western forest fire regimes. *Northwest Science*, *72,* 24-34.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, *98*(3), 604-613.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. T., & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660-684.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 1-55.

Amundson, R., & Jenny, H. (1997). On a state factor model of ecosystems. *BioScience, 47*(8), 536-543.

Araújo, M. B., & Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology*, *93*(7), 1527-1539.

Babst, F., Bodesheim, P., Charney, N., Friend, A. D., Girardin, M. P., Klesse, S., Moore, D. J., Seftigen, K., Björklund, J., Bouriaud, O., & Dawson, A. (2018). When tree rings go global: Challenges and opportunities for retro-and prospective insight. *Quaternary Science Reviews, 197,* 1-20.

Balch, J., Schoennagel, T., Williams, A., Abatzoglou, J., Cattau, M., Mietkiewicz, N., & St Denis, L. (2018). Switching on the Big Burn of 2017. *Fire*, *1*(1), 18.

Bailey, R. G., Avers, P. E., & King, T. (1994). Ecoregions and subregions of the United States (map; scale 1: 7,500,000) (supplementary table of map unit descriptions compiled and edited by McNab WH, Bailey RG). United States Department of Agriculture Forest Service, Washington, DC.

Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, *15*(5), 393-405.

Barton, A. M. (1993). Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. *Ecological Monographs*, *63*(4), 367-397.

Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, *23*(2), 168-180.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365-377.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., Pierrat, J.C., & Gégout, J.C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature, 479*(7374), 517.

Bowman, D. M., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'antonio, C. M., DeFries, R., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., & Kull, C. A. (2011). The human dimension of fire regimes on Earth. *Journal of Biogeography*, *38*(12), 2223-2236.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., & Anderson, J. J. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, *102*(42), 15144-15148.

Breshears, D. D., Huxman, T. E., Adams, H. D., Zou, C. B., & Davison, J. E. (2008). Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences*, *105*(33), 11591-11592.

Brown, P. M., & Wu, R. (2005). Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*, *86*(11), 3030-3038.

Burrill, E. A., Wilson, A. M., Turner, J. A., Pugh, S. A., Menlove, J., Christiansen, G., Conkling, B. L., & David, W. (2017). The Forest Inventory and Analysis Database: Database description and user guide version 7.2 for Phase 2. U.S. Department of Agriculture, Forest Service. 946 p. [Online]. [Available at: http://www.fia.fs.fed.us/library/database-documentation/].

Chapin III, F. S., Matson, P. A., & Vitousek, P. (2011). 1. The Ecosystem Concept In: *Principles of terrestrial ecosystem ecology*. (pp. 3-17). Springer Science & Business Media.

Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., D'amato, A. W., Davis, F. W., Hersh, M. H., Ibanez, I., & Jackson, S. T. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, *22*(7), 2329-2352.

Collins, B. M. (2014). Fire weather and large fire potential in the northern Sierra Nevada. *Agricultural and Forest Meteorology*, *189*, 30-35.

Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences, 106*(Supplement 2), 19651-19658.

Cook, E. R., Woodhouse, C. A., Eakin, C. M., Meko, D. M., & Stahle, D. W. (2004). Long-term aridity changes in the western United States. *Science*, *306*(5698), 1015-1018.

Covington, W. W., & Moore, M. M. (1994). Postsettlement changes in natural fire regimes: ecological restoration of old-growth ponderosa pine forests. *J. Sustain. Forest, 2*, 153-181.

Daly, C., Neilson, R. P., & Phillips, D. L. (1994). A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorologymeteorology*, *33*(2), 140-158.

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P.P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology: a Journal of the Royal Meteorological Society*, *28*(15), 2031-2064.

Falk, D. A., Heyerdahl, E. K., Brown, P. M., Farris, C., Fulé, P. Z., McKenzie, D., Swetnam, T. W., Taylor, A. H., & Van Horne, M. L. (2011). Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment*, *9*(8), 446-454.

Falk, D. A. (2017). Restoration ecology, resilience, and the axes of change. *Annals of the Missouri Botanical Garden*, *102*(2), 201-216.

Farquhar, G. D., & Sharkey, T. D. (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiologyphysiology*, *33*(1), 317-345.

Frank, D. C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., Treydte, K., Zimmermann, N. E., Schleser, G. H., Ahlström, A., & Ciais, P. (2015). Water-use efficiency and transpiration across European forests during the Anthropocene. *Nature Climate Change*, *5*(6), 579.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, *113*(14), 3725-3734.

Fritts, H. C., Smith, D. G., Cardis, J. W., & Budelsky, C. A. (1965). Tree‐ring characteristics along a vegetation gradient in northern Arizona. *Ecology*, *46*(4), 393-401.

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*(1577), 2105-2115.

Fulé, P. Z., Covington, W. W., Moore, M. M., Heinlein, T. A., & Waltz, A. E. (2002). Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography*, *29*(1), 31-47.

Fulé, P. Z., Korb, J. E., & Wu, R. (2009). Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. *Forest Ecology and Management*, *258*(7), 1200-1210.

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., & Neill, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*(9), 2630-2637.

Grinnell, J. (1917). Field tests and theories concerning distributional control. *Am Nat, 51*, 115–128.

Guiterman, C. H., Margolis, E. Q., Allen, C. D., Falk, D. A., & Swetnam, T. W. (2018). Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. *Ecosystems, 21*(5), 943-959.

Huang, W., Houlton, B. Z., Marklein, A. R., Liu, J., & Zhou, G. (2015). Plant stoichiometric responses to elevated CO_2 vary with nitrogen and phosphorus inputs: evidence from a global-scale meta-analysis. *Scientific Reports*, *5*, 18225.

Hurteau, M. D., Bradford, J. B., Fulé, P. Z., Taylor, A. H., & Martin, K.L. (2014). Climate change, fire management, and ecological services in the southwestern US. *Forest Ecology and Management,* 327, 280-289.

IPCC, (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

IPCC, (2018). Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, T. Waterfield (eds.)]. In Press.

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, *106*(Supplement 2), 19685-19692.

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153-160.

Kane, J. M., Varner, J. M., Metz, M. R., & van Mantgem, P.J. (2017). Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western US Forests. *Forest Ecology and Management, 405*, 188-199.

Keane, R. E., Ryan, K. C., Veblen, T. T., Allen, C. D., Logan, J. A., Hawkes, B., & Barron, J. (2002). Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-91, 24 pp.

Keeley, J., & Syphard, A. (2016). Climate change and future fire regimes: examples from California. *Geosciences*, *6*(3), 37.

Klein, T. (2014). The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Functional Ecology*, *28*(6), 1313-1320.

King, G. M., Gugerli, F., Fonti, P., & Frank, D. C. (2013). Tree growth response along an elevational gradient: climate or genetics?. *Oecologia*, *173*(4), 1587-1600.

Kirchmeier-Young, M. C., Zwiers, F. W., Gillett, N. P., & Cannon, A. J. (2017). Attributing extreme fire risk in Western Canada to human emissions. *Climatic Change*, *144*(2), 365-379.

Kitzberger, T., Falk, D. A., Westerling, A. L., & Swetnam, T. W. (2017). Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. *PloS One*, *12*(12), e0188486.

Kolb, T. E., Agee, J.K., Fulé, P. Z., McDowell, N. G., Pearson, K., Sala, A., & Waring, R.H. (2007). Perpetuating old ponderosa pine. *Forest Ecology and Management, 249*, 141-157.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution, 22*(11), 569-574.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J., & Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters, 15*(8), 831-840.

Law, D. J., Adams, H. D., Breshears, D. D., Cobb, N. S., Bradford, J. B., Zou, C. B., Field, J. P., Gardea, A. A., Williams, A. P., & Huxman, T. E. (2019). Bioclimatic envelopes for individual demographic events driven by extremes: Plant mortality from drought and warming. *International Journal of Plant Sciences*, *180(1), 53-62.*

Leavitt, S. W. (2010). Tree-ring C–H–O isotope variability and sampling. *Science of the Total Environment, 408*, 5244-5253.

Leibold, M. A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology*, *76*(5), 1371-1382.

Lomolino, M. V. (2001). Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, *10*(1), 3-13.

Litschert, S. E., Brown, T. C., & Theobald, D. M. (2012). Historic and future extent of wildfires in the Southern Rockies Ecoregion, USA. *Forest Ecology and Management, 269,* 124-133.

Margolis, E. Q., Swetnam, T. W., & Allen, C. D. (2007). A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research*, *37*(11), 2227-2241.

Margolis, E. Q., & Balmat, J. (2009). Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecology and Management*, *258*(11), 2416-2430.

McCarroll, D., & Loader, N. J. (2004). Stable isotopes in tree rings. *Quaternary Science Reviews, 23,* 771-801.

McDowell, N., Brooks, J. R., Fitzgerald, S. A., & Bond, B. J. (2003). Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell & Environment, 26,* 631−644.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. *New Phytologist, 178*, 719-739.

McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology, 155*, 1051−1059.

Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: managing in the face of uncertainty. *Ecological applications*, *17*(8), 2145-2151.

Millar, C. I., & Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, *349*(6250), 823-826.

Millar, C. I., Charlet, D. A., Westfall, R. D., King, J. C., Delany, D. L., Flint, A. L., & Flint, L. E. (2018). Do Low-Elevation Ravines Provide Climate Refugia for Subalpine Limber Pine (*Pinus flexilis*) in the Great Basin, USA?. *Canadian Journal of Forest Research, 48*(6), 663-671.

Minder, J. R., Mote, P. W., & Lundquist, J. D. (2010). Surface temperature lapse rates over complex terrain: Lessons from the Cascade Mountains. *Journal of Geophysical Research: Atmospheres*, *115*(D14).

Moran, E., Lauder, J., Musser, C., Stathos, A., & Shu, M. (2017). The genetics of drought tolerance in conifers. *New Phytologist, 216*(4), 1034-1048.

Nauslar, N., Abatzoglou, J., & Marsh, P. (2018). The 2017 North Bay and Southern California Fires: A Case Study. *Fire*, *1*(1), 18.

Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, *260*(10), 1623-1639.

Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs*, *76*(4), 521-547.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J., Ceulemans, R., & De Angelis, P. (2005). Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences*, *102*(50), 18052-18056.

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., & McMurtrie, R. E. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences*, *107*(45), 19368-19373.

O'Connor C. D., Falk D. A., Lynch A. M., & Swetnam, T.W. (2014). Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleño Mountains, Arizona, USA. *Forest Ecology and Management, 329,* 264-278.

O'Connor, C. D., Falk, D. A., Lynch, A. M., Swetnam, T. W., & Wilcox, C. P. (2017). Disturbance and productivity interactions mediate stability of forest composition and structure. *Ecological Applications*, *27*(3), 900-915.

Ohsawa, T., & Ide, Y. (2008). Global patterns of genetic variation in plant species along vertical and horizontal gradients on mountains. *Global Ecology and Biogeography*, *17*(2), 152-163.

Pruppacher, H. R., & Klett, J. D. (2010). Cooling of moist air. In *Microphysics of Clouds and Precipitation* (pp. 485-501). Springer, Dordrecht.

Radeloff, V. C., Hammer, R. B., Stewart, S. I., Fried, J. S., Holcomb, S. S., & McKeefry, J. F. (2005). The wildland–urban interface in the United States. *Ecological Applications*, *15*(3), 799-805.

Reyer, C. P., Brouwers, N., Rammig, A., Brook, B. W., Epila, J., Grant, R. F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., & Medlyn, B. (2015). Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology*, *103*(1), 5-15.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rodman, K. C., Meador, A. J. S., Moore, M. M., & Huffman, D. W. (2017). Reference conditions are influenced by the physical template and vary by forest type: A synthesis of *Pinus ponderosa*-dominated sites in the southwestern United States. *Forest Ecology and Management, 404,* 316-329.

Ruthrof, K. X., Breshears, D. D., Fontaine, J. B., Froend, R. H., Matusick, G., Kala, J., Miller, B. P., Mitchell, P. J., Wilson, S. K., van Keulen, M., & Enright, N. J. (2018). Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. *Scientific Reports*, *8*(1), 13094.

Sala, A., Peters, G. D., McIntyre, L. R., & Harrington, M. G. (2005). Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Physiology,* 25, 339–348.

Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *AIBS Bulletin*, *54*(7), 661-676.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., & Lexer, M. J. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 395.

Serra-Diaz, J. M., Franklin, J., Dillon, W. W., Syphard, A. D., Davis, F. W., & Meentemeyer, R. K. (2016). California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography*, *25*(2), 164-175.

Sevanto, S., McDowell, N. G., Dickman, L. T., Pangle, R., & Pockman, W. T. (2014). How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment& environment*, *37*(1), 153-161.

Shepperd, W. D., Edminster, C. B., & Mata, S. A. (2006). Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. *Western Journal of Applied Forestry*, *21*(1), 19-26.

Smith, R. B. (1979). The influence of mountains on the atmosphere. In *Advances in Geophysics* (Vol. 21, pp. 87-230). Elsevier.

Smith, T., & Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, *83*, 49-69.

Speer, J. H. (2010). *Fundamentals of Tree-Ring Research.* University of Arizona Press, Tucson.

Stahle, D. W., Fye, F. K., Cook, E. R., & Griffin, R. D. (2007). Tree-ring reconstructed megadroughts over North America since AD 1300. *Climatic Change*, *83*(1-2), 133.

Stephens, S. L., Agee, J. K., Fulé, P. Z., North, M. P., Romme, W. H., Swetnam, T. W., & Turner, M. G. (2013). Managing forests and fire in changing climates. *Science*, *342*(6154), 41-42.

Strachan, S. & Daly, C. (2017). Testing the daily PRISM air temperature model on semiarid mountain slopes. *Journal of Geophysical Research: Atmospheres*, *122*(11), 5697-5715.

Swann, A. L., Hoffman, F. M., Koven, C. D., & Randerson, J. T. (2016). Plant responses to increasing CO2 reduce estimates of climate impacts on drought severity. *Proceedings of the National Academy of Sciences*, *113*(36), 10019-10024.

Swetnam, T. W., Farella, J., Roos, C. I., Liebmann, M. J., Falk, D. A., & Allen, C. D. (2016). Multi-scale perspectives of fire, climate and humans in Western North America and the Jemez Mountains, U.S.A. *Philosophical Transactions of the Royal Society* B*: Biological Sciences*, *371*(1696), 20150168.

Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, 1(7), 0182.

Tett, S. F., Falk, A., Rogers, M., Spuler, F., Turner, C., Wainwright, J., Dimdore-Miles, O., Knight, S., Freychet, N., Mineter, M. J., & Lehmann, C. E. (2018). Anthropogenic Forcings and Associated Changes in Fire Risk in Western North America and Australia During 2015/16. *Bulletin of the American Meteorological Society*, *99*(1), S60-S64.

Thuiller, W., Lavorel, S., Midgley, G. U. Y., Lavergne, S., & Rebelo, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology*, *85*(6), 1688-1699.

Trouet, V., Taylor, A. H., Carleton, A. M., & Skinner, C. N. (2006). Fire-climate interactions in forests of the American Pacific coast. *Geophysical Research Letters*, *33*(18).

Trumbore, S., Brando, P., & Hartmann, H. (2015). Forest health and global change. *Science*, *349*(6250), 814-818.

Vandewalle, M., De Bello, F., Berg, M. P., Bolger, T., Doledec, S., Dubs, F., Feld, C. K., Harrington, R., Harrison, P. A., Lavorel, S., & Da Silva, P. M. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, *19*(10), 2921-2947.

van Mantgem, P. J., Falk, D. A., Williams, E. C., Das, A. J., & Stephenson, N. L. (2018). Pre-fire drought and competition mediate post-fire conifer mortality in western US National Parks. *Ecological Applications*, *28*(7), 1730-1739.

Veblen, T. (2000). Disturbance patterns in southern Rocky Mountain forests, In: RL Knight et al. (Eds) *Forest Fragmentation in the Southern Rocky Mountains*,(pp. 31-54), Colorado University Press, Boulder.

White, M. A., & Vankat, J. L. (1993). Middle and high elevation coniferous forest communities of the North Rim region of Grand Canyon National Park, Arizona, USA. *Vegetatio, 109*(2), 161-174.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews*, *42*(2), 207-264.

Williams, A. P., Allen, C. D., Millar, C. I., Swetnam, T. W., Michaelsen, J., Still, C. J., & Leavitt, S. W. (2010). Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*, *107*(50), 21289-21294.

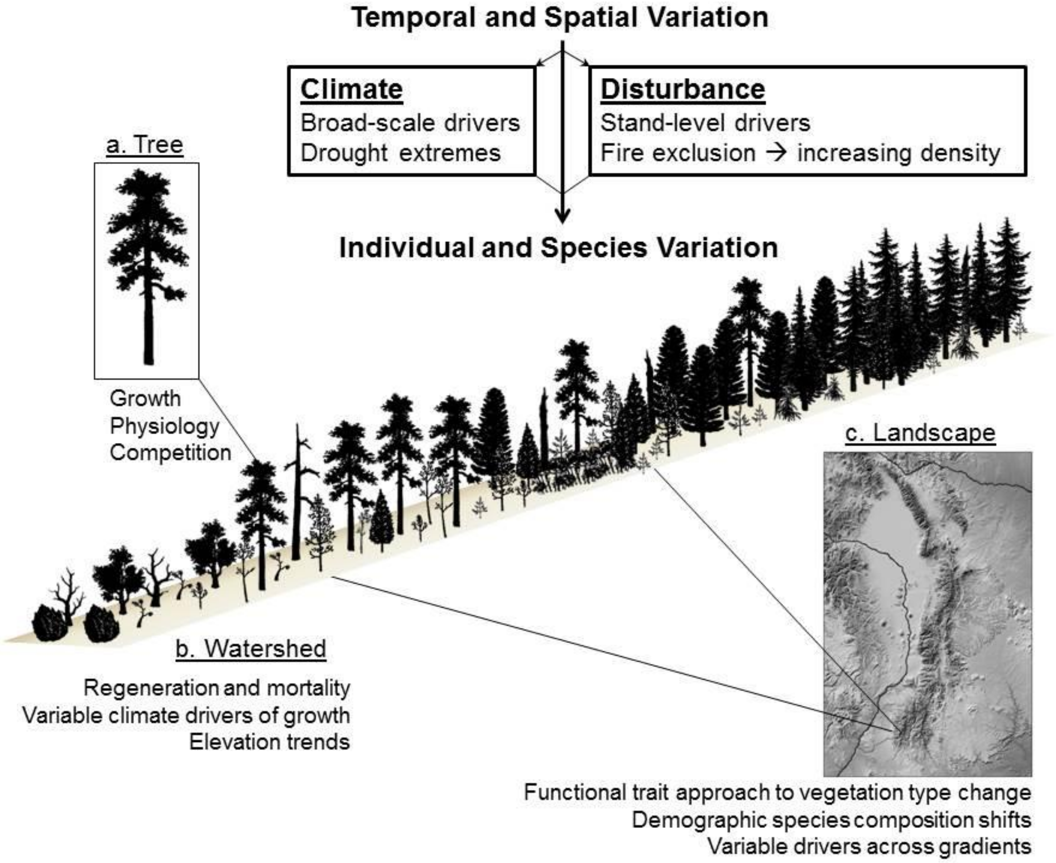
Williams, J. (2013). Exploring the onset of high-impact mega-fires through a forest land management prism. *Forest Ecology and Management*, *294,* 4-10.

Woodward, F. I. (1987). *Climate and plant distribution*. Cambridge University Press, Cambridge.

Yue, K., Fornara, D. A., Yang, W., Peng, Y., Li, Z., Wu, F., & Peng, C. (2017). Effects of three global change drivers on terrestrial C: N: P stoichiometry: a global synthesis. *Global Change Biology*, *23*(6), 2450-2463.

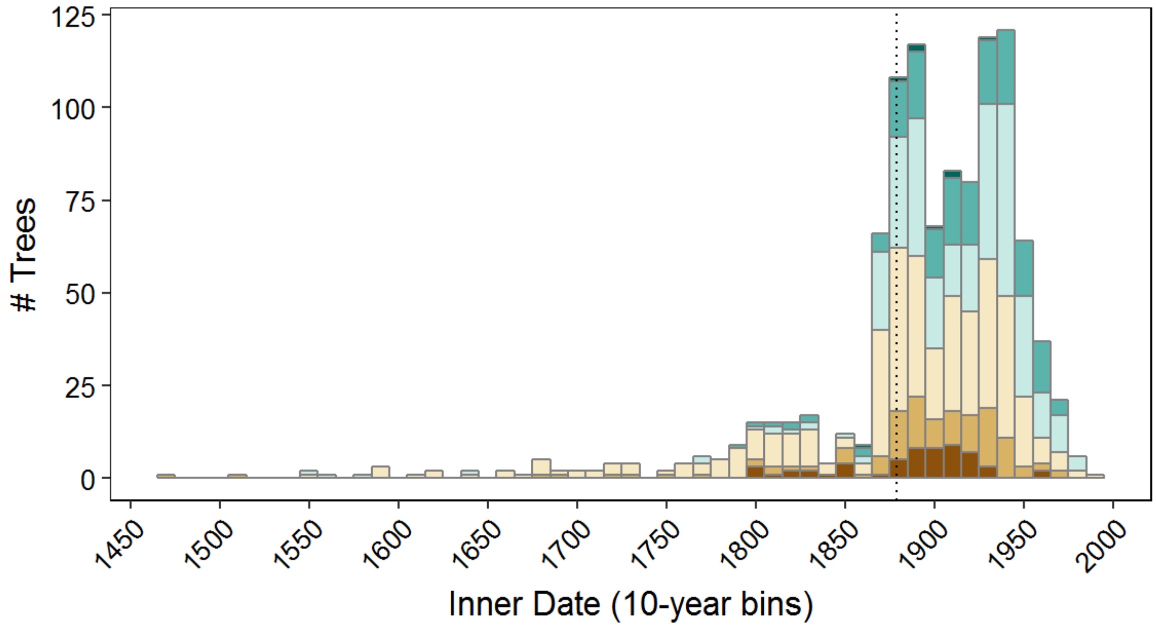
Figures

Figure FRD-1



This figure presents the project design framework used for interpreting tree-scale processes across broader scales. For each appendix (A-C) and scale, the primary climate and disturbance drivers, response functions, and key factors for investigation are indicated. Sections a. and b. are comprised of original artwork by the author, and c. is derived from USGS DEM data in QGIS.

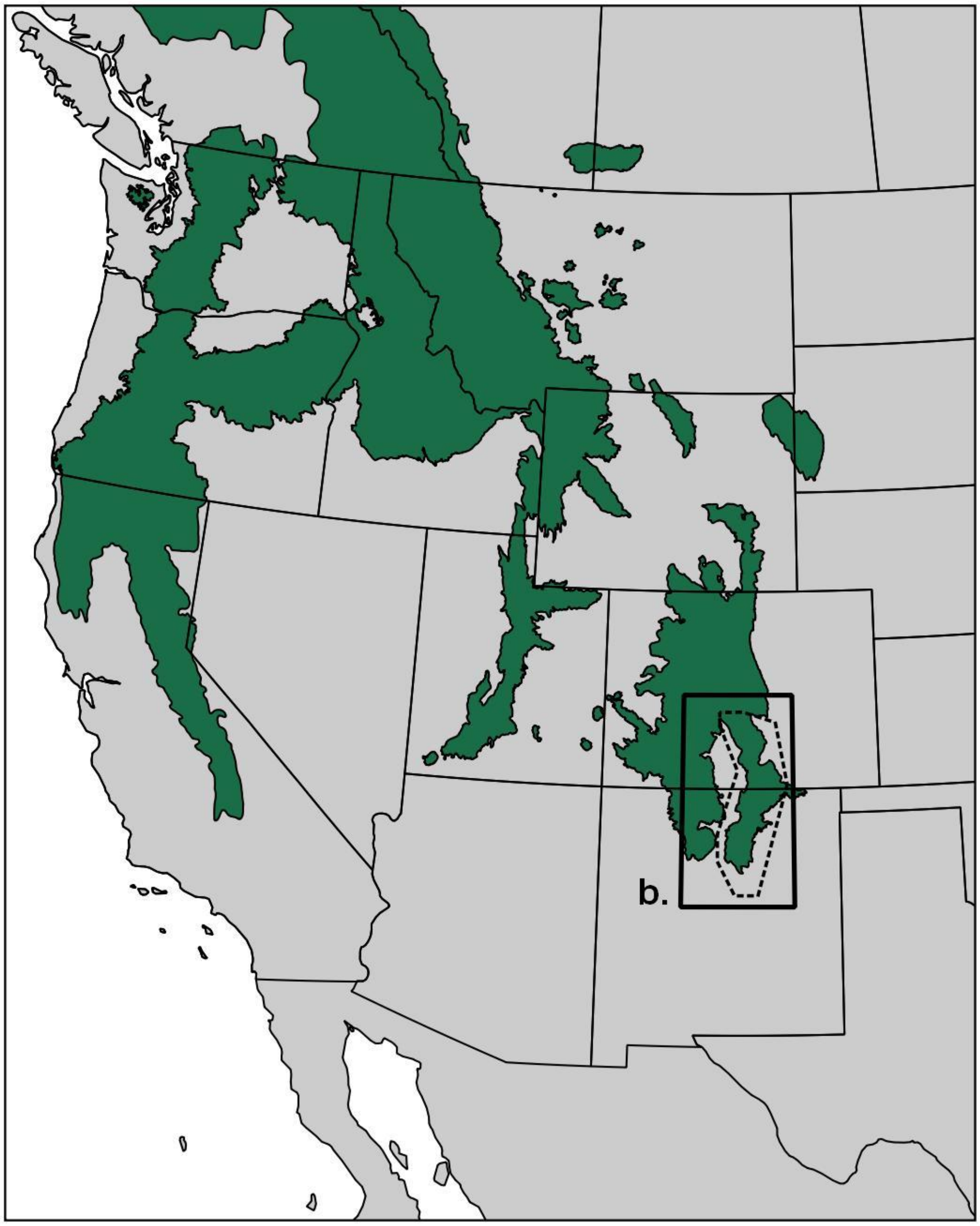
Figure FRD-2



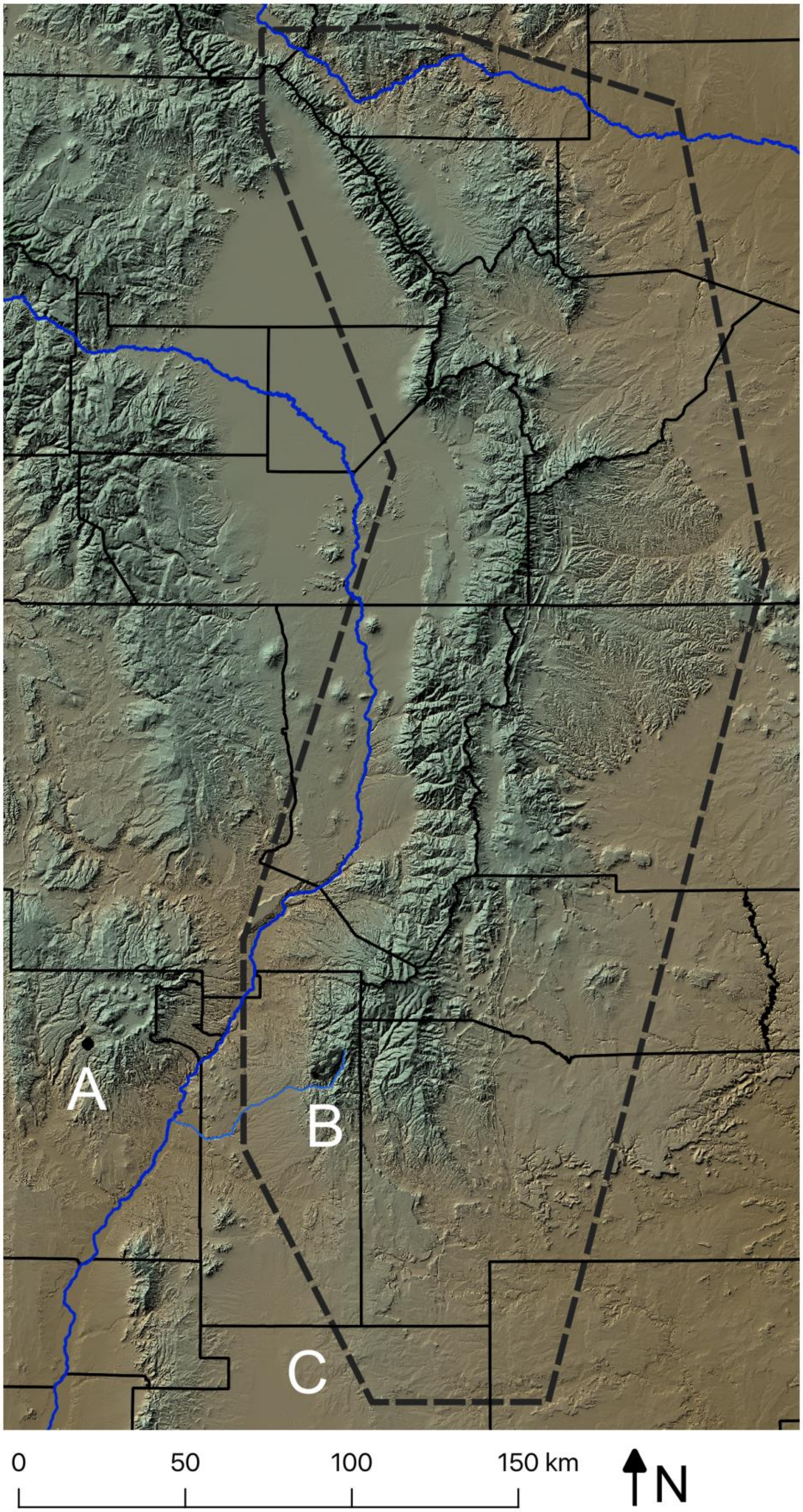
Time series of inner date of trees sampled for Appendix B study. Color scale is tree species graded from most (brown) to least (dark green) drought tolerant. Vertical line is at 1879, the date of the last widespread fire in the watershed.

See Appendix B Supplemental Information Figure S-1 for additional details.

Figure FRD-3



a. Overview of study areas for dissertation work, northern New Mexico and southern Colorado, USA. The green areas are the forested mountains of the western USA and a portion of Canada. The square indicated by b. is enlarged below, with dotted line surrounding the portion of the southern Rocky Mountains studied in Appendix C.


A
B
C
0
50
100
150 km
N

b. Study areas corresponding to Appendix A, B and C (white letters adjacent to black point, white-filled polygon, and within the dashed line, respectively), showing the increase in scale considered between each appendix. The blue lines are the major rivers of northern New Mexico and southern Colorado adjacent to the study areas, with state counties indicated by solid black lines.

Appendix A:

Nitrogen Can Limit Overstory Tree Growth Following Extreme Stand Density Increase in a Ponderosa Pine Forest

Nitrogen Can Limit Overstory Tree Growth Following Extreme Stand Density Increase in a Ponderosa Pine Forest

L.A. Marshall[a,b], Donald A. Falk[a,b], Nate G. McDowell[c]

[a]School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721-0045, USA

[b]Laboratory of Tree-ring Research, The University of Arizona, Tucson, AZ 85721-0045, USA

[c]Pacific Northwest National Laboratory, Richland, WA 99352, USA

Abstract

Extreme stand density increases have occurred in ponderosa pine forests throughout the western U.S. since the early 20th Century, with adverse implications for growth, physiological functioning, and mortality risk. Identifying primary stressors on large, old overstory trees in dense forests can inform management decisions to promote resilience and survival. We tested the impact of stand density increase on overstory tree-ring growth, and the relative influence of water and nitrogen, in an old-growth ponderosa pine forest subject to variable density increase. We measured annual tree-ring growth and carbon discrimination in trees before stand density increased, in a climatically-similar period post-density increase, and in recent transition to drought. We expected density-driven water stress to drive reduced tree-ring growth in overstory trees in dense stands. We found reduced growth and higher mortality in dense stands, but nitrogen rather than water constrained growth, as determined by carbon isotope discrimination in tree rings, leaf nitrogen concentration, and soil nitrogen supply. In dense stands, less available nitrogen limited photosynthetic rate, leading to reduced assimilation of intracellular ^{13}C and higher discrimination with low tree-ring growth and a reduced relationship with climate. This unexpected result illustrates that a variety of limiting factors can influence forest dynamics, as density-driven nitrogen limitation interacts with water stress to influence tree growth and physiological functioning.

Keywords: dendroecology; tree-ring width; limiting factors; stable carbon isotopes; stand density; water stress; soil nitrogen; soil types; growth limitation.

Introduction

Fire exclusion followed by an increase in forest stand density is a common natural history progression for many areas of the contemporary western United States, with serious implications for forest management and the perpetuation of ecologically valuable large, old trees (Kolb et al. 2007; Hurteau et al. 2014). Before fire exclusion, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forests burned frequently. Low-severity fires removed smaller trees, resulting in low stand densities with spatial variation in forest structure (Allen et al. 2002; Moore et al. 2004). Recruitment in ponderosa pine forests is episodic, concentrated in wetter periods with lower fire frequency (Brown and Wu 2005; Meunier et al. 2014). Fire exclusion led to higher tree density as recruitment occurred without thinning by frequent fire. Greater tree density in turn increased fuel load and the risk of high-severity fire (Fulé et al. 1997; Moore et al. 2004). Large, old trees are particularly affected by increased density in multiple ways. Competitive interactions, a greater risk of extreme fire behavior and bark beetle attack, and drought effects interact with other factors to increase the chance of overstory tree mortality (Kolb et al. 2007; Allen et al. 2010; van Mantgem et al. 2018).

Higher stand density results from conditions favoring recruitment and survivorship over time. Soil characteristics including soil depth, water availability, and parent material can increase water and nutrient availability to seedlings, such that higher survivorship and establishment occurs in certain areas (Abella et al. 2014). Stand density drives competition-mediated changes to water and nutrient availability, so greater stand density can indicate a greater number of trees sharing a limited resource pool. Trees in dense stands tend to have reduced growth, lower leaf area, and may show physiological impacts including reduced gas exchange (McDowell et al. 2003; Sala et al. 2005).

Competition-driven water stress leads to stomatal closure, limits carbon acquisition and constrains tree growth. A reduced ability to photosynthesize puts a tree at risk of death through carbon starvation and/or hydraulic failure in the event of prolonged drought stress (McDowell 2011). Competition is a contributing factor to tree mortality in dense stands, but is difficult to disentangle from other factors such as direct drought effects and vulnerability to insect attack (Allen et al. 2010; Das et al. 2011).

Stable-carbon isotope discrimination ($\Delta^{13}C$) in trees reflects water limitation in arid and semiarid ecosystems. Discrimination is correlated negatively with water stress, as fractionation of lighter and heavier isotopes is influenced by the rate of stomatal conductance (McCarroll and Loader 2004). Tree-ring cellulose discrimination is a reliable measure of relative water stress over time, because it tracks the influence of environmental variation on tree-water relations utilizing temporally-stable components of wood, such as cellulose and hemicellulose (McCarroll and Loader 2004). However, nitrogen availability can complicate the use of discrimination as a measure of water stress.

Nitrogen is an important factor in C_3 plant carbon assimilation. It makes up a substantial portion of proteins found in leaves, notably the Rubisco enzyme (ribulose-1,5-bisphosphate carboxylase/oxygenase), which catalyzes carboxylation during photosynthesis. When there is higher leaf nitrogen per unit area, more nitrogen goes to proteins active in the Calvin cycle, and CO_2 assimilation is higher (Evans 1989). Net photosynthesis is correlated positively with leaf nitrogen concentration, and thus with greater growth and tree-ring widths (Lupi et al. 2013). Stand density can also influence nitrogen cycling. High stand density leads to reduced belowground resource uptake per individual, constraining nitrogen acquisition and thus photosynthetic rate. This can lead to a disjunction between discrimination and water stress by trees in dense stands (De Boeck et al. 2006; Rennenberg et al. 2009).

Here we consider the impacts of density-driven resource limitation on overstory ponderosa pine, as a legacy of fire exclusion. We examined the physiological responses to stand density-mediated water and nitrogen availability, leading to growth and mortality changes in overstory trees in a relatively intact natural landscape. Our null hypothesis (H_0) was that overstory trees in dense stands would show reduced tree-ring growth and reduced carbon isotope discrimination, when compared to trees in open stands. Here the primary mechanism would be competition-driven water stress. Our alternate hypothesis (H_1) was that decreased availability of nitrogen in dense stands would constrain photosynthetic rates, leading to reduced growth in dense stands while discrimination rates remained equal or greater than that of overstory trees in open stands. In this condition, water stress would be secondary to nitrogen limitation reducing trees' capacity to assimilate carbon. Understanding the effects of high stand density on these forests facilitates a deeper knowledge of how increased stand density affects the physiological functioning of overstory ponderosa pine.

Materials and Methods

The study area is the 256-ha Monument Canyon Research Natural Area (MCRNA), located in the Jemez Mountains (35.805556°N, -106.627222°W; mean elevation 2469 m a.s.l.), in northern New Mexico, USA (Figure 1). MCRNA was established in 1932 and protected from logging, although not from fire exclusion (Allen 1998). MCRNA is predominantly old-growth ponderosa pine forest, covering portions of San Juan and Cat Mesa. Substrates are of volcanic origin, primarily Lower Bandelier tuff (Otowi member) (QBO) and El Cajete pumice (QEC), with Holocene alluvium in drainages (Kelley et al. 2003; Goff et al. 2005). High tree density closely aligns with QEC substrate origin on San Juan and portions of Cat Mesa (Figure 1). Mesa-level differences were controlled by analyzing trees in open and dense stands across mesas. Frequent low-severity surface fire was common from the 1500s to the late 1800s (Falk et al. 2007; Swetnam et al. 2016). Fire exclusion around 1900 was followed by a massive increase in stand density across parts of MCRNA during the first half of the 20th Century.

Climate and Periods of Study

We identified three periods for analysis: (1) prior to stand densification (1897-1907, hereafter “Pre”), (2) post-densification with similar climate (1971-1980, hereafter “Post”), and (3) the shift to sustained regional drought (1990-2007, hereafter “Recent”). We used 1875-2007 to review longer-term growth changes relative to climate.

For climate response we used PRISM reconstructions and Palmer Drought Severity Index (PDSI). Selected climate variable means and standard deviation are summarized by period in Table 1. Growing-season PDSI (March–September) was calculated from the closest gridpoint, 119 (Cook et al. 2008). In southwestern North America, PDSI is correlated strongly with previous winter precipitation, and generally well correlated with tree-ring width (St. George et al. 2010). Growing season (March–September) mean temperature (ºC), VPD (hPa), and water-year precipitation (mm, previous October–current September) were calculated using monthly PRISM values from the 4-km cell encompassing MCRNA at 35.8040°N, -106.6192°W (PRISM Climate Group 2018). Climate variables were correlated with mean annual tree response variables for each time period and density class using Pearson's *r*, and significance tested using two-tailed t-tests.

Sampling and Variables

We used three response variables: tree-ring carbon isotope discrimination ($\Delta^{13}C$), foliar and soil nitrogen (leaf %, soil net supply $\mu g/10cm^2$), and basal area increment (BAI cm^2). We selected dominant overstory ponderosa pine trees in currently dense and open natural communities across MCRNA with similar substrate conditions, but differing tree densities. Data analysis was performed and figures produced using R *tidyverse* and *ggthemes* packages (Arnold 2018; R Core Team 2016; Wickham 2017). We used the fire history package FHAES for fire interval analysis (Brewer et al. 2016).

We considered a site dense if it fell above the median density across all sites (2300 stems ha^{-1}), and open if density was less than the median (Figure 1). Dense stands averaged 6717 stems ha^{-1} (range 2929-15,839), whereas open stands averaged 776 stems ha^{-1} (range 186-2128) across all size classes. Open stands were dominated by clusters of 2-5 large overstory trees with herbaceous understory. Dense stands were characterized by numerous small diameter (<15 cm DBH) ponderosa pine stems with interlocking canopies and low light reaching the forest floor. Understory plants were scarce or absent, with deep needle litter. The density increase at MCRNA dates primarily to a recruitment pulse in the early 20th Century combined with decades of fire exclusion that reduced small tree mortality (Allen 1998; Falk 2004). Over the period 1600-1900 at MCRNA, a fire exceedance interval longer than 11.98 years had a $p << 0.001$ (minimum 2 scarred trees and 5 recorders active), yet by 1971, 70 years had passed without fire, and forest structure had undergone extensive changes.

We used a gridded plot design to compare stand density with fire history and geologic features across MCRNA (Figure 1), with twenty-eight 0.01 ha square plots adjacent to a gridpoint, where all trees ≥ 2.5 cm DBH were counted and measured, and nearby fire scar samples were collected by Falk (2004). We calculated mean stand density and standard error (stems ha^{-1}) and tested for significance between variables using two sample t-tests assuming unequal variance, by mesa landform and geologic unit (El Cajete Pumice versus others) (Kelley et al. 2003; Goff et al. 2005).

Thirty living overstory trees, "target trees", all ≥40 cm diameter at breast height (DBH, 1.4 m) and mature by 1900, were selected randomly from the set of gridded plots (15 trees per dense/open condition). For leaf nitrogen, additional understory ponderosa pines were selected randomly for sampling within the same stands. We prepared and crossdated tree cores using standard dendrochronological techniques (Speer 2010). Cores were initially collected in 2004. Additional cores were collected in 2008 to capture the recent drought period, and to minimize potential confounding effects of substrate on density by sampling in dense and open areas across each mesa in MCRNA. Trees were cored with 12-mm borers at *ca*. 140 cm for carbon isotope analysis and *ca*. 10 cm above the root crown with 5-mm borers for ring-width analyses. All cores were dried, 5-mm cores were mounted to plywood with glue, and then sanded and crossdated to annual resolution. The 12-mm cores for isotopic analysis were surfaced with a razor to provide a dateable surface and not mounted to avoid contamination.

Stem Growth, Mortality, Water and Nitrogen

We measured annual tree-ring growth increment from target tree cores using a Velmex measuring system (Velmex, Inc, Bloomfield, NY, USA) to a precision of 0.001 mm. To correct for age-growth trends while retaining interdecadal variation, we used basal area increment (BAI, cm^3), calculated from measured tree-ring widths assuming a circular tree bole, for the length of each series (Biondi and Qeadan 2008). Mean annual BAI chronologies and cumulative mean basal area (BA) were calculated for the period 1875-2007 for dense and open stands. We tested for significant differences using a two tailed t-test assuming unequal variance in mean annual BAI between and within stands and time periods.

We calculated mortality in target trees using counts of live and dead trees within 0.1 ha plots around a subset of gridpoints, over the period 2000-2006. We compared the proportion of dead trees in 2006 to 2000 in dense and open stands, and tested for significance using a two tailed t-test.

We used carbon isotope discrimination (Δ, $^{13}C/^{12}C$ ‰) in tree-ring cellulose to test the physiological impacts of increased stand density. After cores for isotopic analysis were dated, the complete annual rings (earlywood and latewood) for each of the three analysis periods were separated and milled individually. Each sample was processed into α-cellulose using chemical treatment to remove extractives and lignin (McCarroll and Loader 2004).

Cellulose was isolated in order to minimize the potential for mobile carbon to influence results, as the earlier analysis periods in some cores crossed the sapwood–heartwood boundary (McCarroll and Loader 2004; Leavitt 2010).

Cellulose was analyzed in a Micromass IsoPrime continuous-flow isotope ratio mass spectrometer to measure annual $\delta^{13}C$ (McCarroll and Loader 2004). Discrimination values for each tree-year were calculated with adjustments for the atmospheric trend in $\delta^{13}C$ using ice core atmospheric records (Keeling et al. 2005). Mean Δ and standard error were calculated for each year sampled, for dense and open stands. We used squared Pearson's correlation coefficients (r^2) to determine the degree to which reconstructed climate variables explained variation in Δ, and Δ explained BAI, by stand density and sampling period. Two sample t-tests for significance were conducted between stand densities and across sampling periods.

We collected soil nitrogen data over a 9-week period during June–August 2008. We used Plant Root Simulator (PRS) probes (Western Ag, Saskatoon, Canada) set in dense and open stands to find soil nitrogen net supply (total available nitrogen, NH_4, and NO_3, $\mu g/10cm^2$) for a 9-week burial period. Probes were placed at a 10 cm depth among roots, at cardinal points around the focal overstory trees within the radius of the tree crown. Some dense stands in MCRNA were thinned during the winter of 2006-7 as part of an ongoing restoration project, so additional dense stands (< 150 m from boundary of MCRNA) were sampled outside the thinning treatment area for soil N comparison, along with remaining dense stands within MCRNA (Figure 1). We calculated the mean and standard error in N for soils in dense and open stand conditions, and tested for significant differences using a two sample t-test assuming equal variance.

We sampled foliage in winter 2006 from the sunlit canopy of 11 overstory and 7-10 understory trees in dense and open stands. Foliage was harvested using a shotgun from high on the south side of the crown to maximize leaf sun exposure and minimize the potential confounding effect of shading (Bond et al. 1999). Leaf samples were dried and homogenized by tree before analysis of nitrogen (%), carbon (%), and C:N ratio per leaf weight in grams, using a dry mass analyzer at Los Alamos National Laboratory. We found the mean and standard error of %N in overstory and understory tree leaves in dense and open stand conditions and tested for significant differences using a two-sample t-test assuming equal variance.

Stand Density, Soils, and Fire

Fire-scar dating indicates the cessation of widespread fire in MCRNA by 1900, with no subsequent fire scarring more than 10% of samples (Falk 2004). We tested for significant differences in mean fire interval and years since fire for events from 1801-1981, by density (dense versus open), soils, and mesas using two tailed t-test assuming unequal variance. We found mean years since fire (YSF) intervals in 50-year segments covering *ca.* one century before and after fire exclusion: 1800-1849, 1850-1899, 1900-1949, and 1950-1981. We tested for significance between these periods using a single-factor ANOVA.

Inter-tree competition was quantified as an index of competitor basal area within an allometrically-determined radius around each overstory tree. Within a search radius of 40×DBH (m), we measured distance to the target overstory tree, and DBH of each competitor tree taller than 1.4 m. Basal area of competitors was summed for trees in dense and open stands by distance. We used the distance-weighted competition equation sum ((diameter competitor cm/diameter target cm)/distance cm) as an index of competition in dense and open stands (Lorimer 1983; Burkhart and Tomé 2012). From this we calculated competitor tree density surrounding target trees (stems ha^{-1}). In one case of extreme density and limited resources, we surveyed 2/3 of the surrounding area (1585 competitor stems), and extrapolated to the full area.

Results

Stem Growth, Mortality, Water and Nitrogen

Mean BAI (cm^2) was significantly different between dense and open stands in the Post ($p = 0.003$) and Recent ($p < 0.001$) period, whereas mean discrimination (Δ ‰) between dense and open stands was significant only in the Post period ($p < 0.001$) (Table 1). Lower growth yet higher discrimination in dense stands means H_0 is rejected in the Post period. In the Recent period discrimination was not different between stands, but BAI in dense stands was much lower, suggesting a disconnect between radial growth and discrimination (Table 1).

From 1875-2007 growth was lower in open stands than dense stands in only four years (1891, 1918, 1946, and 2004) (Figure 2c). The mean annual BAI of target trees (mean ± se cm^2) for 1875-2007 was 6.84 ± 0.29 in dense stands, and 10.68 ± 0.37 in open stands ($p < 0.001$). Cumulative basal area increment (cm^2) diverged between stands over time, with dense stands accumulating less wood, at a slower rate (Figure 2d). As stand density increased, the rebound in mean ring growth following a severe event (such as drought in 1956 or 1996) became reduced in dense stands, suggesting a longer time to recover from climate stress. Tree mortality tended to be higher in dense stands from 2000-2006, although because of high variance the difference was not statistically significant. In dense stands, the mean proportion of dead trees increased by 5.7%, whereas in open stands, dead trees increased by 0.9% over this time period. At the densest site sampled, 88% of trees > 25 cm DBH were recorded dead in 2006.

Discrimination (Δ ‰) was similar between dense and open stands in the Pre period, significantly different and higher in dense stands in the Post period, and similarly high in the Recent period (Figure 2a). During the Pre period, the similarity in Δ and BAI between dense and open stands suggests similar access to water and resources, and similar effects of top-down controlling mechanisms, such as fire, across MCRNA. Over time, we observed an increasing trend in Δ for all stands, even after correcting for drift in atmospheric □ ^{13}C (Figure 2b).

Reconstructed summer PDSI predicted BAI best in open stands in all periods, and in dense stands during the Pre period (Table 2). Over time, PDSI predicted Δ less well with a declining r^2 for all stand densities. Climate correlations with BAI and Δ tended to be lower in dense than open stands in the Recent period compared to the Pre period, when climate correlations tended to be similar across stand densities (Table 2). During the Post period, most climate variables were non-significantly correlated with response variables across stand types, and the few significant findings were more strongly correlated with open stand variables than dense (Table 2).

There were small differences in soil nitrogen between dense and open stand conditions with marginally significant greater net supply in dense stands ($p = 0.10$) (Figure 3a). The difference was driven by NO_3^-, which was significantly higher in dense stands ($p = 0.01$). There was no significant difference in NH_4^+ between stands. Dense stands had a slightly higher mean nitrogen net supply (measure of available nitrogen in soils) of 17.1 (2.1 standard error) N (μg/10 cm²/9 weeks) whereas open stands had 13.1 (0.9) N. This was partitioned into 10.6 (1.3) NO_3^- and 6.4 (1.1) NH_4^+, in dense stands, and 6.1 (0.8) NO_3^- and 6.9 (0.7) NH_4^+ in open stands.

Trees in dense stands had marginally lower leaf nitrogen (Figure 3b). Leaf nitrogen (mean % ± standard error) was significantly lower in dense (0.92% ± 0.05) versus open (1.07% ± 0.03) stands in understory trees ($p = 0.01$) (Figure 3b). Percent leaf nitrogen was not statistically different in overstory trees in dense (1.04% ± 0.02) compared to open (1.09% ± 0.03) stands (Figure 3b), consistent with the finding of similar discrimination rates among stands in the Recent period (Figure 2b). Within stands, leaf nitrogen was significantly lower in understory than overstory trees in dense stands ($p = 0.04$), but not in open stands.

Leaf carbon was significantly different between overstory and understory trees within both dense (0.74%, $p = 0.04$) and open (0.70%, $p = 0.03$) stands. No difference was found between stand densities for overstory or understory trees. Leaf C:N ratio was significantly different between overstory and understory trees in dense stands (5.67, $p = 0.04$), and in understory trees between stand densities (7.77, $p = 0.01$). No difference in C:N was found between overstory and understory trees in open stands (0.11, $p = 0.90$), or in overstory trees between stand densities (2.21, $p = 0.45$).

Stand Density, Soils, and Fire

Over the 20th Century, stand density increased in some areas of MCRNA, most notably on El Cajete Pumice (QEC) soils where the highest densities were found (Figure 1). Tree density (mean ± s.e. stems ha^{-1}) was significantly higher on QEC soils (5600 ± 1537) compared to other soil types across MCRNA (1767 ± 280) ($p = 0.05$). Tree density (mean ±

s.e. stems ha^{-1}) across mesas was significantly different between San Juan Mesa (4142 ± 1030) and Cat Mesa (1638 ± 340) ($p = 0.04$).

Prior to the early 1900s, fire is thought to have limited density across the entire study area (Falk 2004; Swetnam et al. 2016). The mean fire interval (MFI) was significantly different between Cat (16 years) and San Juan (11 years) Mesas ($p = 0.03$). However, we found no significant difference in MFI between dense (11 years) and open stands (16 years), or between QEC (12 years) and other soil types (14 years).

Years since fire (YSF) was relatively consistent and low across the study area in the 19th Century (mean YSF 1800-1849 = 17 years, 1850-1899 = 10 years). It then increased dramatically over the 20th Century (mean YSF 1900-1949 = 27 years, mean YSF 1950-1981 = 54 years). YSF was significantly different between 1950-1981 and 1800-1942 ($p < 0.001$). Across mesas, the only significant difference ($p < 0.05$) in time since fire from 1801-1981 was in 1892 ($p = 0.03$) and 1893 ($p = 0.03$), when much of San Juan Mesa experienced fire but Cat Mesa did not. YSF across dense and open stands, for events from 1801-1981, differed significantly in only two years, 1897 ($p = 0.03$) and 1899 ($p = 0.04$).

Discussion

Mechanisms of Reduced Growth: Water and Nitrogen

Annual tree radial growth can be regulated by any of several time-varying limiting factors (Fritts 1976). In dry forests of the interior U.S. Southwest, water availability is generally expected to serve as the principal limiting factor. However, in this study of very dense forests we found that a combination of nitrogen limitation plus variable water stress produced the result of high ^{13}C discrimination with low radial growth in overstory ponderosa pine in dense stands.

Changes over time in correlation between climate and the response variables, discrimination and BAI, show a trend towards weaker connection between tree growth and climate, especially in very dense stands. The disconnection is particularly notable in the Post period, when few climate variables are correlated significantly with growth across stand densities or variables. In the Recent period, covering a transition to drought conditions, all climate variables are correlated significantly with growth and discrimination, but generally to a lesser degree than before fire exclusion implying other important factors are affecting the trees. Beyond water availability and climate trends, nitrogen resources are likely to limit and impact tree growth and physiological functioning, as we found in exceptionally dense stands (Rennenberg et al. 2009). This is notable as generally drought is the primary factor of interest affecting ponderosa pine forests, and different management choices might be appropriate if nitrogen is as important or moreso at some places and times (Hurteau et al. 2014; Allen et al. 2015).

These observations suggest that decadal-scale shifts between nitrogen and water limitation can affect carbon assimilation in dense stands following fire exclusion. The lack of nitrogen data from earlier decades adds unavoidable uncertainty to this conclusion, but the trends in tree-ring growth and discrimination, combined with known stand structure changes, strongly imply a nitrogen limitation effect on photosynthesis. In the Recent period, significantly lower radial growth in dense stands, while discrimination remains high, demonstrates ongoing physiological impact of stand density.

Reduced or less available leaf nitrogen in dense stands leads to lower concentrations of the nitrogen-intensive Rubisco enzyme, a decrease in gross photosynthesis, and thus reduced growth. Higher soil nitrogen and reduced leaf nitrogen in dense stands could be a consequence of less available nitrogen, with more going to microbial activity than in open stands. Differences in carbon isotopic response might then originate more from soil microbiota and geology than from density (Rennenberg et al. 2009). Trees could adapt to less available nitrogen through reorganization of hydraulic architecture, decreasing leaf area in nutrient-limited trees (McDowell et al. 2008). In this case density would drive the relative decrease in growth, while indirectly contributing to the discrimination response through impacts to resource allocation.

Extreme density-driven impacts to tree growth and physiological functioning will be exacerbated under climate change, with a trend towards hot and dry drought conditions that put forests at increased risk of widespread mortality (Allen et al. 2015). A trend of increasing nitrogen limitation, resulting from stand density changes in the absence of fire, could be an additional stressor contributing to tree mortality. Recent, large-scale forest mortality events show the impacts that drought and climate change have on forests (Allen et al. 2010, 2015). Underlying nutrient limitation issues could reduce trees' resilience and contribute to the severity of these events. Over time, a tradeoff of limitations on growth may be occurring, driven by interactions between stand conditions, climate and disturbance.

Stand Density, Soils, and Fire

Tree growth findings generally aligned with expectations. Overstory trees in dense stands had slower stem growth, with dense stands accumulating 509.8 cm^2 less basal area per tree over 1875-2007. Mortality was not different across stand densities, but was highly variable across sites with highest mortality in the densest stand. This likely resulted from greater intraspecific competition for resources, compounded by environmental stress.

Interactions between climate-driven variation in water stress and density-related chronic nitrogen limitation led to the forest present on the landscape today.

At MCRNA, the underlying patterns of stand density are explained primarily by substrate differences, as there is no significant variation in fire history. El Cajete Pumice is linked to high tree density, and historically, to Puebloan farming locations with highly productive soils (Gauthier et al. 2007; Swetnam et al. 2016). The superior water-retention and mulching abilities of QEC soils led to high seedling recruitment, and in the absence of fire, to extreme tree density.

Conclusions

Fire exclusion beginning in the early 20th Century removed an important constraint on ponderosa pine seedling and sapling survival. In the absence of landscape fire, mass tree establishment (driven by pluvial periods and soil characteristics) resulted in extremely high tree density compared to other reference ponderosa pine forests (Abella et al. 2014; Meunier et al. 2014). Environmental stress and density-driven growth effects compound mortality risk from fire (van Mantgem et al. 2018).

Increasing tree density over time combined with climate perturbations and underlying soil variation resulted in differential stress impacts on trees in dense stands. Nitrogen likely limited photosynthetic uptake after stand density increased, resulting in overstory trees in dense stands with unexpectedly high ^{13}C discrimination yet low growth relative to trees in open stands, and continued low growth with high discrimination during recent drought. Ongoing and climate-change exacerbated drought is likely to cause increased stress to forests, further impacting growth, physiological functioning, and increasing mortality in dense stands.

Chronic nitrogen limitation in dense ponderosa pine forests is a stressor that could lead to reduced resiliency under current and projected future drought. Multiple lines of inquiry may be required for accurate analysis of ecosystem conditions in dense modern forests, as demonstrated by the discrimination-nitrogen interaction. We can draw a direct line between fire exclusion, increasing stand density, reduced BAI, and the emergence of joint control on tree growth by available nitrogen and water. Trees can be highly adaptive to environmental stresses and constraints, although observed physiological responses may vary in unexpected ways where forests are pushed beyond their historical variation in density, fire regime, or climate.

Acknowledgments

For support and help with fieldwork and in the lab, thanks to Alex Arizpe, Tyson Swetnam, Faith Campbell, Ellis Margolis, and Samantha Stutz. Thanks to Craig Allen, Ellis Margolis, and Tom Swetnam who contributed thoughts and ideas to the project. This work was supported by the US Forest Service, Collaborative Forest Restoration Program (CFRP) and Rocky Mountain Research Station [02-DG-11031000-001, 00-JV-11221615], the Joint Fire Science Program [99-1-3-08], the New Mexico Forest and Woodlands Restoration Institute, and the US Department of Energy Global Change Education Program. NGM was supported by the Department of Energy-Office of Biological and Environmental Research.

References Cited

Abella, S. R., Crouse, J. E., Covington, W. W., & Springer, J. D. (2014). Diverse responses across soil parent materials during ecological restoration. *Restoration Ecology, 23,* 113–121.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere, 6,* 1–55.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. T., & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management, 259*, 660–684.

Allen, C. D., Savage, M., Falk, D. A., Suckling, K. F., Swetnam, T. W., Schulke, T., Stacey, P. B., Morgan, P., Hoffman, M., & Klingel, J. T. (2002). Ecological restoration of southwestern ponderosa pine ecosystems: A broad framework. *Ecological Applications, 12,* 1418–1433.

Allen, C. D. (1998). A ponderosa pine natural area reveals its secrets. In *Status and Trends of the Nation's Biological Resources*, edited by Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran, (pp. 551–552). U.S. Department of the Interior, U.S. Geological Survey, Reston, VA, USA.

Arnold, J. B. (2018). *ggthemes: Extra Themes, Scales and Geoms for 'ggplot2'.* R package version 3.4.2. https://CRAN.R-project.org/package=ggthemes

Biondi, F., & Qeadan, F. (2008). A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research, 64,* 81–96.

Bond, B. J., Farnsworth, B. T., Coulombe, R. A., & Winner, W. E. (1999). Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia, 120*, 183–192.

Brewer, P. W., Velásquez, M. E., Sutherland, E. K., & Falk, D. A. (2016). *Fire History Analysis and Exploration System (FHAES) version 2.0.2* [computer software]. http://www.fhaes.org

Brown, P. M., & Wu, R. (2005). Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology, 86,* 3030–3038.

Burkhart, H. E., & Tomé, M. (2012). *Modeling Forest Trees and Stands.* Springer Netherlands, Dordrecht.

Cook, E. R., Woodhouse, C. A., Eakin, C. M., Meko, D. M., & Stahle, D. W. (2008). *North American Summer PDSI Reconstructions, Version 2a.* Archived at IGBP PAGES/World

Data Center for Paleoclimatology, Data Contribution Series # 2008-046. http://www.ncdc.noaa.gov/paleo/pdsi.html

Das, A., Battles, J., Stephenson, N. L., & van Mantgem, P. J. (2011). The contribution of competition to tree mortality in old-growth coniferous forests. *Forest Ecology and Management, 261*, 1203–1213.

De Boeck, H. J., Nijs, I., Lemmens, C. M., & Ceulemans, R. (2006). Underlying effects of spatial aggregation (clumping) in relationships between plant diversity and resource uptake. *Oikos, 113,* 269–278.

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia*, *78*, 9–19.

Falk, D. A. (2004). Scaling rules for fire regimes. PhD Dissertation. University of Arizona, Tucson, AZ, USA.

Falk, D., Miller, C., McKenzie, D., & Black, A. (2007). Cross-scale analysis of fire regimes. *Ecosystems, 10,* 809–823.

Fritts, H. C. (1976). *Tree Rings and Climate*. Academic Press, Elsevier. London, UK.

Fulé, P. Z., Covington, W. W., & Moore, M. M. (1997). Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications, 7,* 895–908.

Gauthier, R., Powers, R., Herhahn, C., Bremer, M., & Goff, F. (2007). Dry farming El Cajete Pumice: Pueblo farming strategies in the Jemez Mountains, New Mexico. In *Geology of the Jemez Mountain Region II*, pp. 469–474. New Mexico Geological Society, 58th Field Conference Guidebook, Socorro, NM.

Goff, F., Gardner, J. N., Reneau, S. L., & Goff, C. J. (2005). *Preliminary Geologic Map of the Redondo Peak Quadrangle, Sandoval County, New Mexico.* NM Bureau Geology & Mineral Resources, Open-file Geologic Map OF-GM-111, scale 1:24,000. Available at http://geoinfo.nmt.edu/index.html

Hurteau, M. D., Bradford, J. B., Fulé, P. Z., Taylor, A. H., & Martin, K. L. (2014). Climate change, fire management, and ecological services in the southwestern US. *Forest Ecology and Management, 327,* 280–289.

Keeling, C. D., Piper, S. C., Bollenbacher, A. F., & Waker, S. J. (2005). *Monthly Atmospheric* $^{13}C/^{12}C$ *Isotopic Ratios for 10 SIO Stations.* Archived at Trends: a compendium of data on global change. http://cdiac.ornl.gov/trends/trends.htm

Keeling, E. G., Sala, A., & DeLuca, T. H. (2006). Effects of fire exclusion on forest structure and composition in unlogged ponderosa pine/Douglas-fir forests. *Forest Ecology and Management, 237*, 418–428.

Kelley, S., Kempter, K. A., Goff, F., Rampey, M., Osburn, G. R., & Ferguson, C. A. (2003). *Geology of the Jemez Springs 7.5-Minute Quadrangle, Sandoval County, New Mexico*. NM Bureau Geology & Mineral Resources, Socorro, NM. Available at http://geoinfo.nmt.edu/index.html

Kolb, T. E., Agee, J. K., Fulé, P. Z., McDowell, N. G., Pearson, K., Sala, A., & Waring, R. H. (2007). Perpetuating old ponderosa pine. *Forest Ecology and Management, 249*, 141–157.

Leavitt, S. W. (2010). Tree-ring C–H–O isotope variability and sampling. *Science of the Total Environment, 408*, 5244–5253.

Lorimer, C. G. (1983). Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management, 6,* 343–360.

Lupi, C., Morin, H., Deslauriers, A., Rossi, S., & Houle, D. (2013). Role of soil nitrogen for the conifers of the boreal forest: a critical review. *International Journal of Plant and Soil Science, 2,* 155–189.

McCarroll, D., & Loader, N. J. (2004). Stable isotopes in tree rings. *Quaternary Science Reviews, 23,* 771–801.

McDowell, N., Brooks, J. R., Fitzgerald, S. A., & Bond, B. J. (2003). Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell & Environment, 26,* 631–644.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist, 178,* 719–739.

McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology, 155,* 1051–1059.

Meunier, J., Brown, P. M., & Romme, W. H. (2014). Tree recruitment in relation to climate and fire in northern Mexico. *Ecology, 95,* 197–209.

Moore, M. M., Huffman, D. W., Fulé, P. Z., Covington, W. W., & Crouse, J. E. (2004). Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science, 50,* 162–176.

New Mexico Geospatial Data Acquisition Coordination Committee (GDACC), State of New Mexico, (2005). *Jemez Springs 7.5 Minute Quad 35106, 10M Enhanced DEM,*

DEM GeoTIFF. Albuquerque, NM: GDACC, EDAC, 2010-10-13. Available at http://rgis.unm.edu/

New Mexico Geospatial Data Acquisition Coordination Committee (GDACC), State of New Mexico, (2009). *Redondo Peak 7.5 Minute Quad 35106, 10M Enhanced DEM Hillshade*, 2005. Albuquerque, NM: GDACC, EDAC, 2009-07-24. Available at http://rgis.unm.edu/

PRISM Climate Group (2018). *Prism Climate Data*. Oregon State University, http://prism.oregonstate.edu, created 11 June 2018.

Rennenberg, H., Dannenmann, M., Gessler, A., Kreuzwieser, J., Simon, J., & Papen, H. (2009). Nitrogen balance in forest soils: Nutritional limitation of plants under climate change stresses. *Plant Biology, 11,* 4–23.

QGIS Development Team (2016). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Sala, A., Peters, G. D., McIntyre, L. R., & Harrington, M. G. (2005). Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Physiology, 25,* 339–348.

Speer, J. H. (2010). *Fundamentals of Tree-Ring Research.* University of Arizona Press, Tucson.

St. George, S., Meko, D. M., & Cook, E. R. (2010). The seasonality of precipitation signals embedded within the North American Drought Atlas. *The Holocene, 20,* 983−988.

Swetnam, T. W., Farella, J., Roos, C. I., Liebmann, M. J., Falk, D. A., & Allen, C. D. (2016). Multi-scale perspectives of fire, climate and humans in Western North America and the Jemez Mountains, U.S.A. *Philosophical Transactions of the Royal Society* B*: Biological Sciences*, *371*(1696), 20150168.

USGS National Gap Analysis Program (GAP) (2009). *Protected Area Database of the United States (PAD-US_v1).* Edition 1.0. Moscow: ID, 2009-04-06. Available at http://gapanalysis.usgs.gov/PADUS/

van Mantgem, P. J., Falk, D. A., Williams, E. C., Das, A. J., & Stephenson, N. L. (2018). Pre-fire drought and competition mediate post-fire conifer mortality in western US National Parks. *Ecological Applications*, *28*(7), 1730-1739.

Wickham, H. (2017). *tidyverse: Easily Install and Load the 'Tidyverse'.* R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse.

Table and Figure Captions

Table 1. Variable means and standard deviations. Climate (left) and response variable (right) means with standard deviation in parentheses, by time period and stand density class. Growing season (GS, March–September) mean temperature (°C), maximum VPD (hPa), PDSI, and water year (WY, previous October–current September) precipitation (mm) are the climate variables presented. Temperature, VPD, and precipitation variables are derived from PRISM climate reconstruction at 4-km resolution around the study area. Asterisks indicate significant difference between stand density classes within the given time period.

Table 2. Significant ($p < 0.05$) Pearson's r correlations between reconstructed climate variables and annual tree response variables across stand densities. Climate variables are growing season (GS, March–September) mean temperature (°C), maximum VPD (hPa), PDSI, and water year (WY, previous October–current September) precipitation (mm). Response variables are basal area increment (BAI, cm^2) and carbon isotope discrimination (Δ, $^{13}C/^{12}C$ ‰). NS indicates non-significant relationships.

Figure 1. Sampling sites, soil geologic origin and tree density. Monument Canyon Research Natural Area (MCRNA) (at right), located in the Santa Fe National Forest in northern New Mexico (at left, national forest lands shaded in gray), with 50-m elevation contours derived from DEM (NM GDACC 2009; USGS GAP 2009). Black circles indicate isotope-sampled target trees in dense stands, white circles indicate target trees in open stands, and grayscale diamonds are gridded sampling points used for fire history and density analysis, with darker

shades indicating denser stands (range 186-15839 trees ha^{-1}). The thick dashed line indicates median stem density (2300 stems ha^{-1}), used as a cutoff for open/dense sites. Dotted lines are one and two standard deviations above the mean (6093 and 9327 stems ha^{-1}, respectively), derived from an inverse distance weighted interpolation of sampled point stem density. Maximum density is found at the lower right of the study area. Shaded gray areas at right indicate El Cajete pumice (QEC), where the densest stands occur (Goff et al. 2005; Kelley et al. 2003).

Figure 2. Time series of discrimination and growth. Solid black points and lines indicates dense stands; white points and dotted lines indicates open stands throughout. Gray boxes indicate isotope sampling periods. White dot-dash line at 1900 indicates cessation of frequent fire, and gray dot-dash line at 1919 indicates the pluvial event linked to dense stand seedling establishment. (a) Carbon isotope discrimination (Δ ‰) in dense (black circles) and open (white circles) stands in Pre (1887-1907) where Δ is similar across stands, Post (1971-1980) where Δ is unexpectedly lower in open stands, and Recent (1990-2007) periods where Δ is variable and responsive to drought onset. All but one core was missing the 2002 ring. (b) Boxplots of carbon isotope discrimination (Δ ‰) across the three periods, with dense in gray and open in white. (c) Mean basal area increment (BAI cm^2) time series for trees in dense and open conditions. (d) Mean cumulative basal area (cm^2) for dense and open trees, as categorized by density surrounding individual trees.

Figure 3. Soil and leaf nitrogen. Available nutrient surplus over the 9-week sampling period (μg/10cm^2) (a) and mean % leaf nitrogen (b) in overstory and understory tree leaves, in open and dense stands. Asterisks indicate significant difference ($p < 0.05$) between open and dense stands. Marginally more total N was present in dense soils (black square, p = 0.10), driven by a significant difference in NO_3^- ($p = 0.01$). Percent leaf nitrogen was significantly different between overstory and understory trees in dense ($p = 0.01$), but not in open stands.

Tables

Table 1.

Period	Climate		Period	Response		
	Variable	Mean (SD)		Stand - Variable	Mean (SD)	
Pre	PDSI (GS)	-0.32 (2.83)	Pre	Open - BAI	7.16 (3.89)	
	PPT (WY)	43.8 (9.3)		Dense - BAI	6.50 (4.25)	
	Tmean (GS)	13.1 (0.8)		Open - Δ	14.45 (0.71)	
	VPDmax (GS)	18.8 (1.5)		Dense - Δ	14.75 (0.67)	
Post	PDSI (GS)	-0.36 (2.37)	Post	Open - BAI	6.69 (2.33)	*
	PPT (WY)	42.5 (9.4)		Dense - BAI	3.45 (1.70)	
	Tmean (GS)	13.0 (0.8)		Open - Δ	14.84 (0.28)	*
	VPDmax (GS)	19.2 (1.5)		Dense - Δ	15.59 (0.17)	
Recent	PDSI (GS)	-0.47(1.81)	Recent	Open - BAI	8.14 (4.44)	*
	PPT (WY)	45.6 (12.1)		Dense - BAI	3.42 (1.69)	
	Tmean (GS)	13.5 (0.8)		Open - Δ	16.50 (0.60)	
	VPDmax (GS)	19.5 (2.2)		Dense - Δ	16.24 (0.50)	

Table 2.

Period	**Stand - Variable**	**PDSI (GS)**	**PPT (WY)**	**Tmean (GS)**	**VPDmax (GS)**
Pre	**Open - BAI**	**0.78**	**0.80**	**-0.75**	**-0.89**
	Dense - BAI	**0.92**	**0.71**	**-0.77**	**-0.84**
	Open - Δ	**0.95**	**0.71**	**-0.65**	**-0.69**
	Dense - Δ	**0.93**	**0.71**	**-0.72**	**-0.68**
Post	**Open - BAI**	**0.75**	NS	NS	NS
	Dense - BAI	**0.63**	NS	NS	NS
	Open - Δ	NS	NS	**-0.82**	NS
	Dense - Δ	NS	**0.63**	NS	NS
Recent	**Open - BAI**	**0.55**	**0.87**	**-0.76**	**-0.73**
	Dense - BAI	**0.46**	**0.78**	**-0.68**	**-0.69**
	Open - Δ	**0.49**	**0.63**	**-0.69**	**-0.79**
	Dense - Δ	**0.49**	**0.44**	**-0.44**	**-0.56**

Figures

Figure 1.

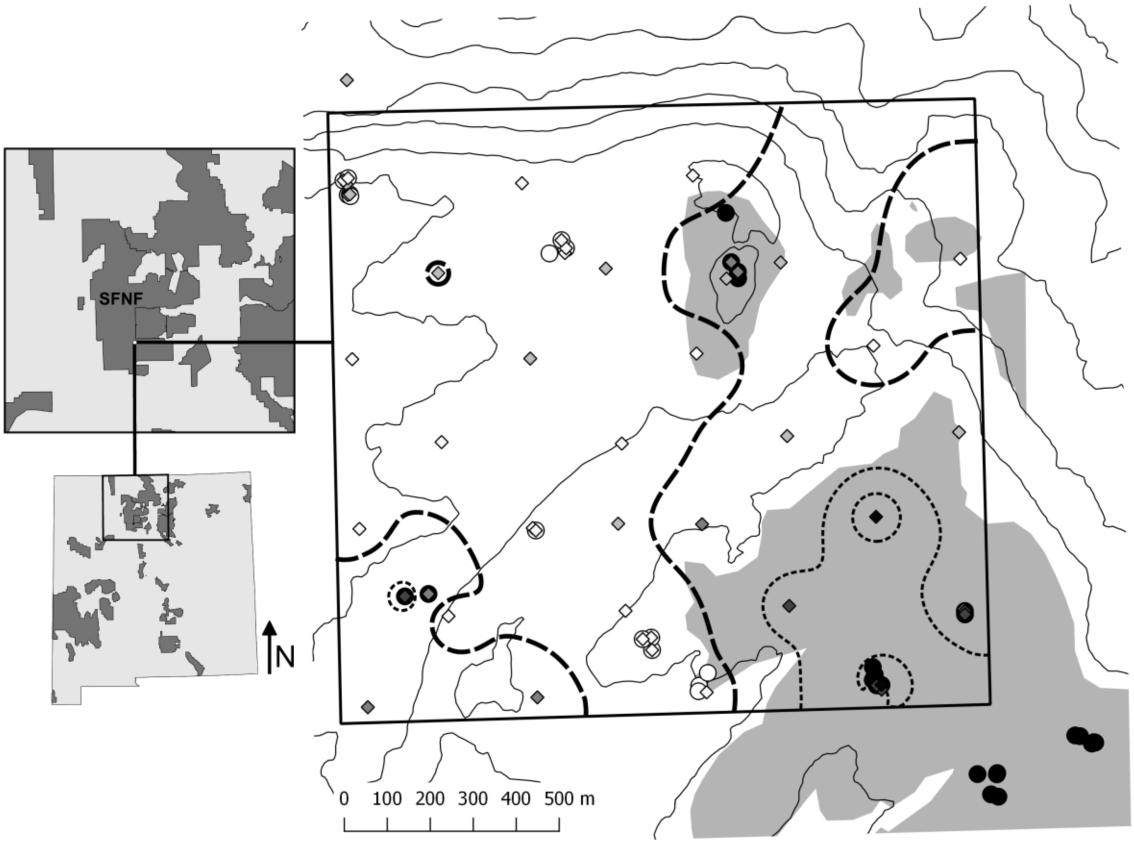


Figure 2.

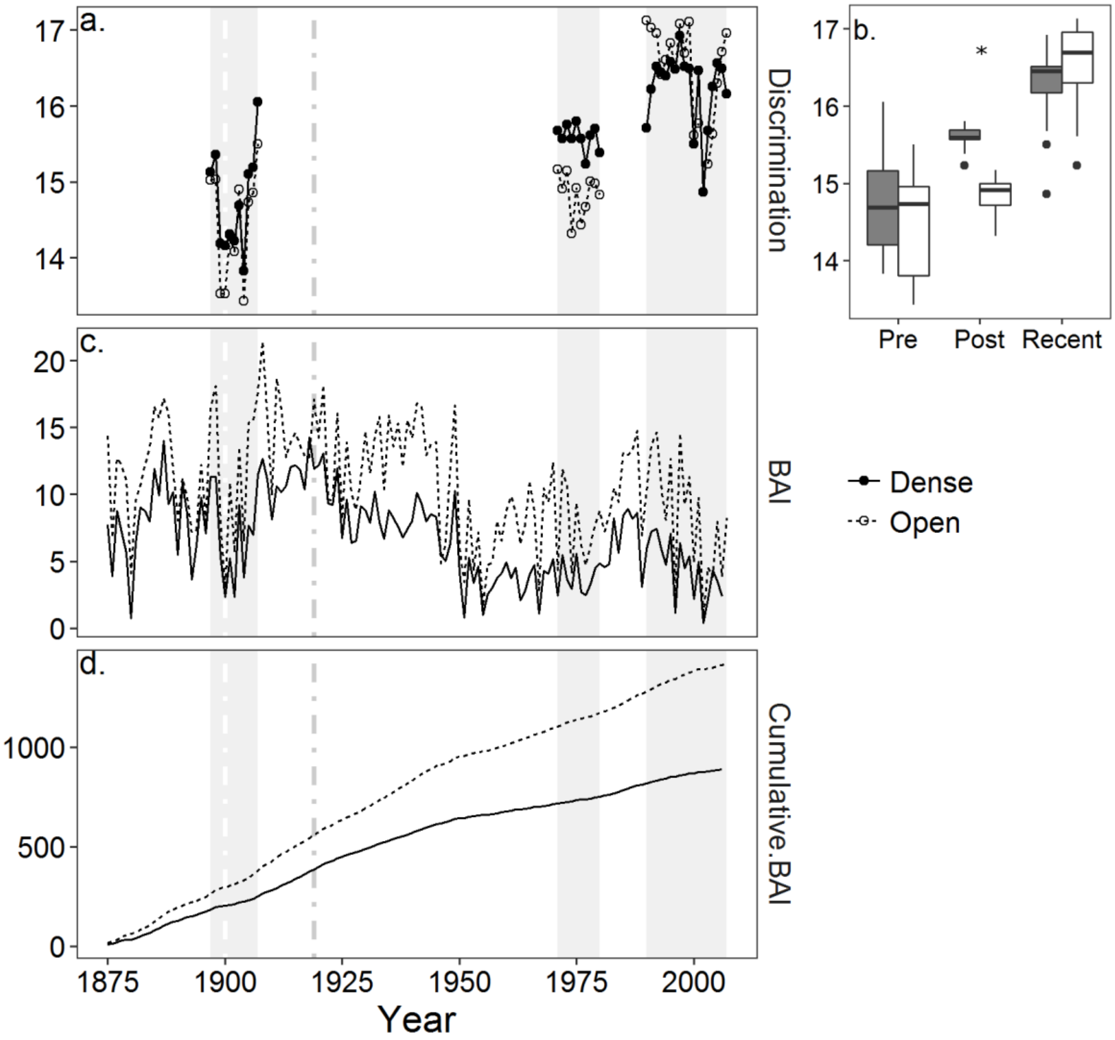
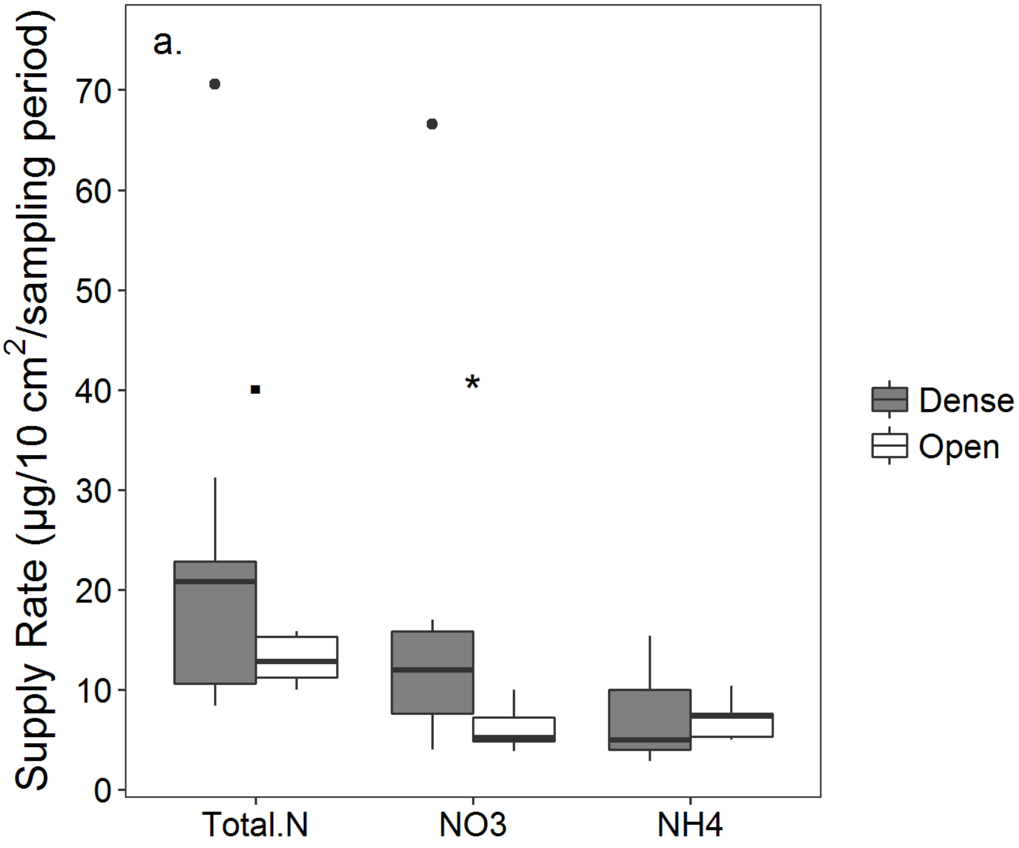
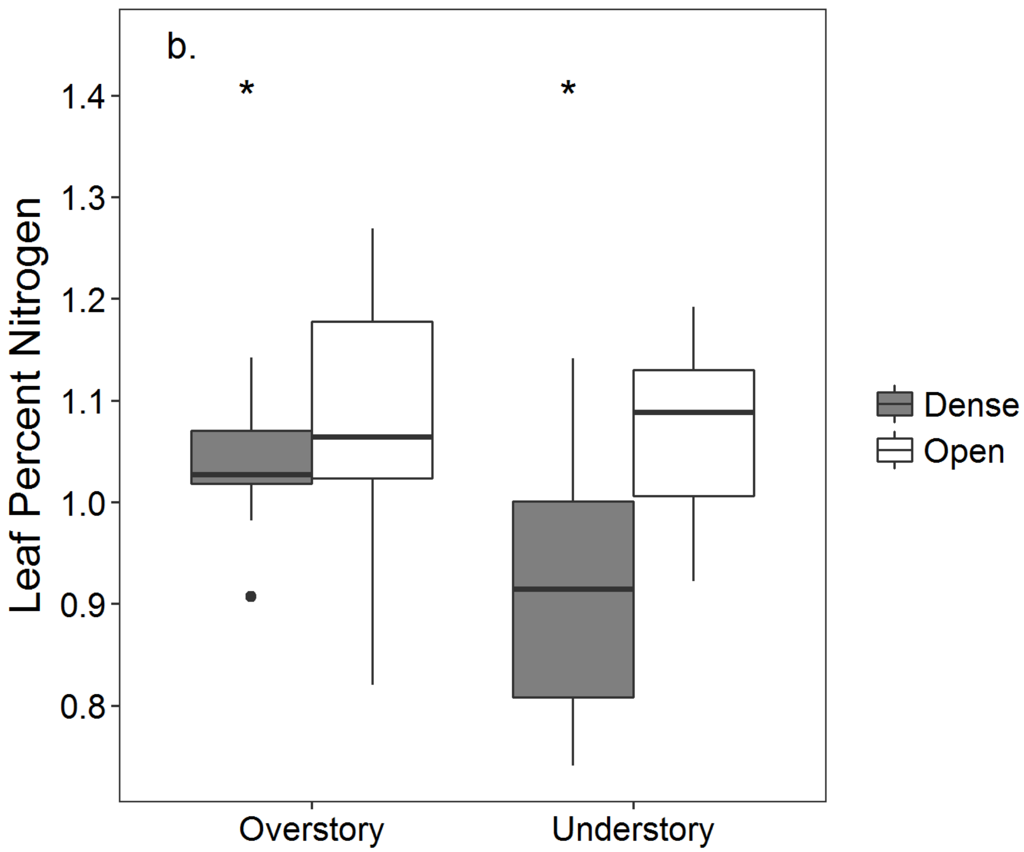

a.
17
16
15
14
Discrimination
b.
17
16
15
14
*
Pre
Post
Recent
c.
20
15
10
5
0
BAI
Dense
Open
d.
1000
500
0
Cumulative.BAI
1875
1900
1925
1950
1975
2000
Year

Figure 3.


a.
Supply Rate (µg/10 cm²/sampling period)
0
10
20
30
40
50
60
70
*
Total.N
NO3
NH4
Dense
Open


b.
Leaf Percent Nitrogen
1.4
1.3
1.2
1.1
1.0
0.9
0.8
*
*
Overstory
Understory
Dense
Open

Appendix B:

Modeled Climate-Growth Relationship and Topographic Influence on Changing Species Distributions

Modeled Climate-Growth Relationship and Topographic Influence on Changing Species Distributions

LA Marshall[a.,b.], DA Falk [a.,b.]

[a]School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721-0045, USA

[b]Laboratory of Tree-ring Research, The University of Arizona, Tucson, AZ 85721-0045, USA

Abstract

Resilience and the potential for species distribution shifts under the effects of climate change is a pressing concern for forested ecosystems. Increasing temperature and changing precipitation patterns drive changes to plant water balance and are compounded by the legacy of altered disturbance regimes across much of the western USA. Cumulatively, these interacting stressors are shaping both the forest present on the landscape today and the trajectory of future changes. At the watershed scale, climate and disturbance are major contributors to demographic patterns of recruitment and mortality.

We examined how climate variation influences tree growth and recruitment in a mixed-conifer forest in northern New Mexico, USA. We studied tree growth responses along a biophysical gradient in a watershed that spans from near the lower to upper elevation range for two widespread species, ponderosa pine (*Pinus ponderosa* var. scopulorum Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). We compared the growth response with stand dynamics and regeneration patterns of the six major tree species found in the study area, allowing us to track shifts in species community composition and dominance within the watershed. We used AICc model selection to identify which temperature and precipitation variables were most influential on species-specific mean tree growth series, and used spatial modeling to identify the best climate-growth relationships across groups defined by elevation and aspect.

Differences in modeled climatic drivers indicate species-specific drought effects on tree growth at the lower limits of species distribution. Generally, precipitation best fit ring growth patterns in ponderosa pine across all groups, while Douglas-fir ring growth was best modeled by precipitation except in low elevation southwest aspect plots, where temperature was selected as a covariate. We found significant changes in species distribution between mature trees, and seedlings and saplings across elevation-aspect groups in several species. Notably we found increasing community dominance of pinyon pine (*Pinus edulis* Engelm.) at low elevations and white fir *(Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) at high elevations, while ponderosa pine and Douglas-fir had reduced regeneration across the study area. Drought stress drove patterns of tree growth and species composition shifts at low elevations, while at higher elevations fire exclusion and increased stand density led to success of shade tolerant species. This combination reveals how altered growth and demographic trends derived from drought and fire exclusion vary across a mixed-conifer forest gradient.

Key words: tree-rings, species composition, demography, gradient studies, range shifts

Introduction

Resilience and the potential for species distribution shifts under the effects of climate change is a pressing concern for forest managers and researchers. Increasing temperature and changing precipitation patterns are compounded by the legacy of disturbance and altered fire regimes, which interact to give us the forest of today and the likelihood and magnitude of possible future changes (Allen et al. 2010; Williams et al. 2010).

Fire exclusion occurred in many areas of southwestern North America, first as a result of extensive livestock grazing in the late 1800s and early 1900s, followed by active suppression. This led to very limited fire activity in the study area over the 20th century. Across the southwest this led to increased stand density in the mixed-conifer and ponderosa pine-dominant forests where frequent, low-severity ground fire was formerly common (Covington and Moore 1994; Margolis and Balmat 2009). The lack of fire significantly affected forest structure in ponderosa pine- and Douglas-fir-dominated mixed-conifer forests (O'Connor et al. 2014). In the absence of fire, there tends to be a substantial increase in tree density with a shift towards shade-tolerant species and corresponding decrease in ponderosa pine and other disturbance-adapted species (Heinlein et al. 2005; O'Connor et al. 2017; Battaglia et al. 2018).

Along with disturbance history, climate and its variation along environmental gradients is another major factor influencing tree growth, demography, and species distribution (Lomolino 2001; Babst et al. 2013; Levine et al. 2016). Climate change, especially hotter droughts, will therefore lead to changes in tree establishment, growth, and mortality, and drive shifts in species distribution, sometimes in unanticipated directions (Allen et al. 2010; Lenoir and Svenning 2015). Climate change is expected to drive increasing drought stress, affecting the survival of individual plants. Over time, patterns of mortality and regeneration will lead to shifts in species distribution, where dispersal allows species to follow suitable climates for regeneration and persistence (Williams et al. 2010).

In response to recent climate change, species composition shifts moving the center of distribution uphill have been reported, and sometimes in other directions by latitude and altitude, depending on local stresses including stand disturbance history (Breshears et al. 2008; Lenoir and Svenning 2015). Tracking changes in species composition and dominance through time or across demographic groups can indicate places where range shifts are likely, before extirpation or expansion occurs.

The concept of extinction debt and immigration credit is useful for interpreting the effects of climate change on range and demographic shifts. Extinction debt occurs in an area that has experienced a change pushing it outside the envelope of suitable habitat for all life stages of a species, but where extirpation has not yet occurred due to persistence of mature individuals (Jackson and Sax 2010). Immigration credit balances extinction debt, and occurs when an area has become suitable habitat but dispersal into the area has not yet happened, generally due to a mismatch between the speed of change and the dispersal rate (Jackson and Sax 2010). In both cases demographic change potentially leading to species range shifts is built into the system but not yet fully expressed.

In plants, areas and species subject to extinction debt will lack or have a reduced regenerative presence when considering species composition, and be at risk for mortality events in drought when unsuitably hot/dry conditions are driving the shift. Where lag between extinction debt and immigration credit is high and dispersal low, climate change driven extinction of the species is a risk (Urban 2015). Evidence for such lag in plant species has been found in surveys and modeling, showing species range shifts are occurring, but not keeping up with the pace of climate change (Bertrand et al. 2011; Talluto et al. 2017). Lags between climate change and the developing species response might be recognized first by changing patterns of species recruitment.

Understanding species demography and how drivers and responses might change across age groups is important when considering how climate and disturbance alters the forest. The demographics of tree reproduction, seedling recruitment and survival over time are subject to pressures from species-level tolerances and competition, stand dynamics resulting from past disturbance, and broad-scale climate and environmental factors (Brown and Wu 2005; Del Río et al. 2016; Andrus et al. 2018). Over time, changing patterns of recruitment, mortality, and species dominance in response to climate and disturbance can result in changes to the composition of the forest. Notably, more fir and less pine has been found in some mixed-conifer forests subject to fire exclusion, while areas with more frequent fire tend to retain pine dominance (Fulé et al. 2002; Levine et al. 2016).

Seedling establishment and survival are dependent on viable seed availability and a suitable climate for regeneration, which is often species-specific with high year-to-year variability (Shepperd et al. 2006; Lutz et al. 2012). In gap dynamics, initial establishment of individual seedlings of one species or another is thought to be due to chance (Brokaw and Busing 2000). Survival and growth then relies on stand dynamics, access to resources, and environmental conditions (Lutz et al. 2012; Goodrich and Waring 2016). Conifer species tend towards mass establishment of seedlings, with high thinning rates in the first few years. A negative exponential relationship is common in conifer species, between numbers of individuals and diameter or age, with a small fraction of individuals surviving beyond a few years of age (Shepperd et al. 2006; Lutz et al. 2012). Saplings are somewhat older individuals whose physiological and morphological attributes allowed them to survive that first winnowing period. The species composition of seedlings and saplings reflects the trends in recent pressures on survival (Grossnickle 2012).

The suitable climate niche for seedlings tends to be similar to, but narrower than, that of mature trees, meaning seedlings will struggle to survive weather extremes that mature trees survive (Bell et al. 2013; Dobrowski et al. 2015). Canopy cover can provide a measure of protection against weather extremes, and restrict seedling survival for less shade-tolerant species (Bell et al. 2013). Modeled projections of climate change, applied to climate envelopes for conspecific seedlings and trees, can identify places likely to face extinction debt as conditions become increasingly unlikely to support seedling survival (Bell et al. 2013; Dobrowski et al. 2015).

Vegetation surveys considering demographics of trees and regeneration can be used to detect ongoing shifts and the sum of past change on forests (Franklin et al. 2016). By comparing relative species composition of seedlings and saplings (regeneration) and mature tree groups, we can track changes in stand dynamics and the species-level response to ongoing disturbance and climate influences (Bell et al. 2013; Dobrowski et al. 2015; Serra-Diaz et al. 2016). Seedlings and saplings reflect the conditions under which they established, at the annual to decadal scale. Mature tree species composition reflects a longer period, from decades to centuries depending on stand age. In the Southwest, mixed-conifer stand age often reflects the time since the last widespread fire, as the cessation of fire removed an important control on seedling establishment (Levine et al. 2016). Changes in relative species composition among demographic groups and across environmental gradients can predict trends in stand dynamics and changing species dominance; whether under certain conditions a species is increasing in dominance, stable, or decreasing and at risk of extirpation.

We combined past climate-tree growth relations with stand dynamics and regeneration patterns to find shifts in growth drivers and species composition across an elevation-aspect gradient encompassing the elevational range of the two dominant tree species, ponderosa pine and Douglas-fir. Gradient studies are useful for the investigation of factors that vary across a species' elevational and/or latitudinal range (Whittaker 1967; Fukami 2005; De Frenne 2013). Spatial variation tends to correspond with variation in environmental factors, with concomitant effects on forest structure, tree species distribution and growth (Fritts et al. 1965; Lomolino 2001; Homeier et al. 2010). Differences in climate-growth relationships and species composition are driven primarily by these other environmental factors (temperature and precipitation, plus disturbance history) rather than changes in elevation itself, as noted by Körner (2007). Trends in growth and demography across elevational gradients in mountain systems can reveal a large amount of change in a relatively small area of study.

Tree rings integrate climate and limited resources into growth time series that can reflect multiple factors influencing forest dynamics. Simplified models of ring growth can be useful for describing varying climate-growth response across a study space (Babst et al. 2013). Comparisons of climate drivers across multiple species can provide insight into species-specific drivers of forest dynamics (Carrer 2011; Rollinson et al. 2016). Given a suite of significant climate drivers, model selection allows discriminating among variables to determine which are most important (Nakawatase and Peterson 2006). Tree-ring growth has long been known to be more climate-sensitive at the lower forest boundary, and less so at inner forest locations (Fritts et al. 1965). Here we use growth-climate model selection to find if mature trees are approaching their climatic limits at low elevations and southwestern aspects.

This study addresses the central question: how do forest stands evolve over time to reflect changing environmental conditions? We used two lines of evidence to show how species populations change in response to variation over space and time. First, we asked whether precipitation or temperature variables are better predictors of growth across the species ranges encompassing different elevation-aspect conditions for the 1895-2010 period. We hypothesized that growth at lower elevations and more southwesterly aspects would be driven predominantly by temperature, while growth at higher elevations and more northerly aspects, where temperatures are more moderate, would be driven by precipitation. We expected species differences in drought tolerance and climate response to be more apparent at lower elevation range boundaries, where the effects of drought are stronger (Fritts 1965).

Second, we evaluated relative species dominance in conspecific overstory tree and regeneration (seedling and sapling) populations as a way to identify indicators of future forest species distribution. We compared species composition across broad demographic groups among and between elevation-aspect groups to identify the potential for shifts in species dominance along their current elevational range. Here we asked: are species re-centering their distribution to begin moving uphill and/or to north slopes following recent drought? We hypothesized that if climate is the primary driver, across climate-sensitive species we will find positive recruitment trends (species making up a greater proportion of the community of seedlings and saplings compared to mature trees) at higher elevations and/or on northeastern aspects for each species' range. If disturbance (as fire exclusion) is the primary driver, we hypothesized that trends in recruitment will vary depending on species shade tolerance, with more shade tolerant species having positive recruitment trends across all elevations and less shade tolerant species having reduced . We expected to find recruitment trends that vary depending on the primary factor driving tree growth by elevation-aspect group, interacting with relative species tolerance of drought and shading. At lower elevations, we expected a stronger climate-response favoring the increased dominance of drought-tolerant species, while at mid-forest and higher elevations we expected recruitment to favor shade-tolerant species.

Methods

Study Area

We studied tree growth—climate responses along a biophysical gradient in the Little Tesuque Watershed, Sangre de Cristo Mountains, New Mexico, USA (Figure 1a). The gradient spans from near the lower to the upper elevation range for two species, ponderosa pine (*Pinus ponderosa* var. scopulorum Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). These two species make up a majority of tree composition in the mixed-conifer forest present in the watershed, while other species made up a smaller portion of the trees sampled (Table 1). Other tree species present in the mixed-conifer forest and included in this study as major components of the ecosystem are: pinyon pine (*Pinus edulis* Engelm.), limber pine (*Pinus flexilis* E. James), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and quaking aspen (*Populus tremuloides* Michx.). Ponderosa pine and Douglas-fir were the species with best replication across the study area and so were the species used in the growth-climate modeling portion of the study.

This area was affected by fire exclusion from the late 19th century and through much of the 20th century, as was much of the intermountain west. The last widespread fire affecting the area occurred in 1879, after which large even-age aspen stands established in the upper reaches of the Little Tesuque Watershed (Margolis et al. 2007). The results of the cessation of frequent fire is evident in the stand age structure of trees sampled, which shows the forest is largely made up of trees established after fire exclusion (Figure S-1). Human impact continued beyond fire exclusion, as logging and mining occurred in the area following the expansion of the railroad in the late 19th century (DeBuys 1985).

Information is limited for seedling age-growth relationships specific to Southern Rockies mixed-conifer species growing without recent disturbance. Ponderosa pine height-age relationships suggest approximately 20 years for seedlings to reach 1.4 m in height in the intermountain west (Shepperd et al. 2006; Puhlick et al. 2013). In suppressed understory individuals growing into dense stands, seedlings can be 30 years or older (Thomas and Waring 2014). Limber pine in mixed-conifer has a very slow growth rate, such that seedlings <1.4 m range from 47-115 years (Veblen 1986). Published growth rates for Douglas-fir and white fir are generally from the coastal Pacific Northwest and less applicable to the Southern Rockies. Pinyon pine has a comparatively short stature, and is reported to take 42-87 years to reach a height of 3.3 m (Diersing et al. 1987).

Field Sampling

We conducted field sampling during the summers 2007 to 2010. Sampling locations (plots) were selected using stratified random sampling across elevation (200 m blocks from 2400 m to 3200 m). This elevation range covered the full extent of mixed-conifer forest type in the study area with some plots in predominantly pinyon-juniper woodland at the lowest elevations and spruce-fir forest mixed with aspen stands at the highest plots. We used a stratified random sampling plot design and sampled all trees at the plot (up to a set number) to ensure that samples would be representative of the entire mixed-conifer forest in the watershed (Nehrbass-Ahles 2014).

At 58 plots, we sampled the nearest 30 (sampled from 2007 to 2009) or 15 (2010 sampling) live trees greater than 2.5 cm dbh, plus any dead trees within the bounds of the live trees sampled including stumps and remnant wood. The number of trees sampled was reduced in 2010 as we found 15 sufficient to capture the stand structure at a plot, and were prioritizing adding plots to less sampled elevation-aspect conditions. We sampled all trees but analyzed only the six species investigated, which were the majority of all trees sampled in the mixed-conifer forest (Table 1). Codes, and common names used to refer to the six species are: PIPO (ponderosa pine), PSME (Douglas-fir), PIED (pinyon pine), PIFL (limber pine), ABCO (white fir), and POTR (quaking aspen).

Up to four large, old ponderosa pine and/or Douglas-fir trees nearest the plot center point were added to the trees sampled to capture longer growth chronologies. Additional fire-scarred remnants (approximately 100 trees) were sampled opportunistically across the study area to determine the fire history within the watershed and extend the tree-ring chronology by multiple centuries. We collected demography data, including tree diameter in cm at 1.4 m (dbh, diameter at breast height), species, and tree condition (Thomas 1979). Up to three increment cores were extracted per tree, approximately 10 cm above the root collar perpendicular to the ground slope.

We considered “trees” plants with arboreal life form and greater than 2.5 cm dbh, and classified woody plants smaller than 2.5 cm dbh or shorter than 1.4 m as “seedlings”, including individuals a few years old with larger saplings into a regeneration group. We used the term “seedlings” broadly and included individuals potentially several decades old in order to reduce the high interannual variation in true seedling recruitment and survival (Shepperd et al. 2006; Lutz et al. 2012). Live and dead trees were graded by condition (live) and decay class (dead) in accordance with Thomas (1979).Within the radius of trees sampled at each plot, we counted seedlings by species. For analysis all seedling and saplings were grouped and referred to as "seedlings". A total of 1463 trees and 1406 seedlings of the six species of interest were surveyed across the 58 plots.

Given the age distribution of trees dated (Figure S-1), the "tree" category generally reflects forest establishment and survival over the 1800-1950 CE period when the majority of trees were established. The majority of individuals in the "seedling" category (seedlings and saplings < 1.4 m, including small trees with suppressed growth) likely established after 1960 CE, and reflect the suitability of conditions in recent decades for tree reproduction.

We applied standard dendrochronological techniques to prepare cores and sections for dating and measuring (Speer 2010; Minor and Arizpe 2015). Cores and sections from 1040 ponderosa pine and Douglas-fir trees were crossdated visually, then measured using a Velmex stage measuring system (Velmex Inc., Bloomfield, New York) with data recording in Tellervo (Brewer et al. 2016). Nearly half of the trees dated were younger than 1895, so we used a negative exponential detrending method on measured ring-width series. The negative exponential detrending method was chosen to conservatively remove age trend, while retaining more of the higher-frequency variation that tends to derive from stand ecological processes and so contributes to differences across the stratified study groups (Cook and Peters 1997; Speer 2010).

We then built standardized species-specific elevation-aspect group (EAG) index chronologies with dplR, using Tukey's biweight robust mean (Bunn et al. 2018). As reconstructing stand establishment was not the focus, we used core inner dates for analysis regardless of whether pith was obtained, as core inner dates were generally within 5-10 years of pith date based on pith estimation of a subsample of cores.

Climate Variables for Modeling

We developed climate variables using 4 km-grid cell PRISM reconstructions from the three grid cells overlapping the study area (PRISM Climate Group 2018). The "low" grid cell (elevation 2472 m) was centered at 35.7131 N, -105.8826 W; the "mid" grid cell (elevation 2665 m) was centered at 35.7232 N, -105.8400 W, and the "high" grid cell (elevation 2778 m) was centered at 35.7571 N, -105.8261 W. PRISM data from each grid cell were not interpolated among adjacent cells. Selecting between variables from multiple grid cells was done in order to provide potentially better matches to the elevation-aspect groups, which fit into three elevation bands roughly equivalent to each PRISM grid cell. Same-variable series across grid cells were similar, with expected similar fits to growth, The analysis took into consideration that model selection between similar series led to reduced AICc weight where multiple similar series were the best fit for tree growth (Table 2).

PRISM variables used from each grid cell were maximum and minimum temperature and precipitation. For temperature series we used annual means and extremes (ºC), and growing season (ºC, March-September) means and extremes. For precipitation series we used water year sum precipitation (mm, previous October-current September). The growing season interval (March-September) was chosen for temperature variables and based on regional dendrometer band measurements, to include maximum potential growing season at the lowest elevation sites sampled (McDowell et al. 2010). Water year rather than annual or current-season precipitation was preferred, as southwest conifer tree-ring growth tends to correlate strongly with previous winter precipitation (Fritts 1976; St. George et al. 2010). The Standardized Precipitation Evapotranspiration Index (SPEI) was also included as an option for general drought-growth response incorporating evapotranspiration, calculated as an annual value from the mid-point PRISM variables (Vicente-Serrano et al. 2010).

Data Analysis

All data analysis took place in R version 3.5.0 (R Core Team 2018). Data were manipulated and graphics created in R using the packages *reshape2*, *tidyverse*, and *ggthemes* (Arnold 2018; R Core Team 2018; Wickham 2007; Wickham 2017). Using the package *rpart*, plots were grouped into elevation-aspect groups (EAGs) using a regression tree model driven by elevation (m) and aspect (deviation from 45º) to find useful break points (Therneau and Atkinson 2018). Five groups were created, across three elevation splits, and two aspect splits for the lower and middle elevation group (Table 1). Aspect was transformed to deviation from 45°, as ridgelines in the study area tend to run along a southeast-northwest line and thus plots tended to fall on either a northeasterly or southwesterly aspect. In QGIS (QGIS Development Team 2016), aspect and elevation groups were applied to the study area by splitting a DEM into polygons based on the rules derived from the regression tree model (Figure 1a).

We used Akaike Information Criterion with correction (AICc) to select between generalized linear models (gamma family, log link) using either precipitation or temperature variables to model mean standardized chronologies for ponderosa pine and Douglas-fir from 1895-2010. AICc was used as the model factors are autocorrelative time series (Hurvitch and Tsai 1989). AICc model selection was performed using the R packages *AICcmodavg*, *lme4*, and *MASS* (Bates et al. 2015; Mazerolle 2017; Venables and Ripley 2002).

We examined whether species-specific mean tree-ring series by group, for ponderosa pine and Douglas-fir, were better modeled by PRISM-derived temperature or precipitation metrics, and we applied the findings using GIS to show the areas across the watershed that fit each climate-growth model. We used the R package *HMisc* to find correlations and significance between EAG mean chronologies and climate variables (Harrell et al. 2018).

To find the potential for near-future species distribution changes across the study area, we tested the plot mean relative percentage change by species (% seedlings – % trees), by EAG. Here trees are defined as all arboreal plants >2.5 cm dbh, and seedlings (regeneration) were counted in three categories (small <5 cm, medium 5 cm to 1.4 m, and large >1.4 m but <2.5 cm dbh). Seedlings were summed together across size classes for analysis, capturing tree regeneration and recruitment from recent decades.

We examined variation in relative percentages of species between all seedlings and trees counted at plots, within and across EAGs to determine the degree to which recent seedling recruitment reflects the distribution of the longer-established tree demographic class across the study area (Table 1). Where the difference in species proportion (% seedlings - % trees) is near 0, we find similar trends in tree presence and recruitment across the study area, such that the patterns of seedling recruitment are similar to the current forest community. Where the difference in percent is positive, we find a greater proportion of seedlings of a given species such that the species is becoming increasingly prevalent. Where the difference is negative, that species makes up a lesser proportion among the seedling class and so is declining in prevalence among the forest community. For species-percentage comparisons within EAGs, we used all plots regardless of whether seedlings were present to find overall species dynamics within each group. For comparing across EAGs we used only plots with seedlings to focus on the species distribution trend in areas where regeneration is occurring.

We tested for statistical significance of increases or decreases by species and EAG among the seedling class using a one-way two-sided *t* test on mean percent difference (% seedlings – % trees) assuming a null of 0, following testing for normality using a Shapiro-

Wilk test as sample sizes tended to be small. To test for significant difference across EAGs, species, and topographic variables, we used a two-way ANOVA with Tukey HSD to address the specific questions.

Using a series of one-sample *t* tests to compare the mean to a null of 0, we found the difference in species proportion between tree and seedling classes, such that significantly higher values indicate species with increased recruitment in a given EAG while significantly lower values indicate a decline in recruitment relative to the species proportion within the tree class or mature forest stands.

Results

Modeled Growth-Climate Relationships

For past tree growth – climate relationships, we found differences in models selected between species and some but not all elevation-aspect groups among climate model options (Figure 1b). Generally, we found precipitation to be the best predictor of tree-ring growth across species and EAGs. Across all EAGs, ponderosa pine growth was modeled best by total precipitation (water year). However, Douglas-fir growth was best modeled by temperature at low- and mid-elevation southwest aspects (EAG 1 and EAG 3) while elsewhere precipitation was a better fit. The selected EAG 1 and EAG 3 Douglas-fir growth model encompassed the summer climate extremes (growth $\propto$ mean growing season maximum temperature + minimum temperature). This finding was consistent with our hypothesis that species-level differences in climate-growth relationships would be strongest near the species' lower elevational range limits.

Table 2 summarizes the first two to three models selected, chosen to minimize Δ AICc and maximize model weight. Either precipitation or temperature series tended to be preferred across the first few models. Using multiple nearby climate series, which are by nature similar, enhanced this tendency. When only one PRISM point was used for climate comparison, the tendency to select either temperature or precipitation persisted, although the elevational spread of the study area resulted in a poorer fit. Crossover between temperature and precipitation as selected variables was evident only where AICc weight was generally low, as in the EAG 2-PIPO (ponderosa pine) model (Table 2).

In ponderosa pine, correlation between mean tree-ring chronologies and model-selected climate variables was strongest at low elevations and lower higher up the gradient (Table 2). This supports the expectation of stronger correlation between tree-ring growth and climate drivers at lower elevations, and indicates climate is a stronger driver of tree growth in those conditions. In Douglas-fir, correlation between mean tree-ring chronologies and model-selected climate variables was similar across the groups, though interpretation was complicated by a multivariate model being selected for the low- and mid-elevation southwest EAGs where we expected to find stronger correlation.

Trends in Species Recruitment

To identify the species and areas with notably high or low recruitment, we found trends in the species % difference between tree and seedling groups, in and between EAGs. Differences between groups suggest incipient changes in the species makeup of the forest community in a given group with specific topographic characteristics (Figure 2), and across the species range studied (Figure 3). We first addressed difference in species proportion (% seedlings - % trees) within EAGs (Figure 2), by testing species means individually against a difference of 0 (i.e., no difference between overstory and recruitment age classes). We found consistent increases in pinyon pine at lower elevations and white fir at higher elevations. Ponderosa pine and Douglas-fir made up a smaller percentage of seedlings relative to mature trees across the EAGs both absolutely and relative to other species.

Testing individually against a null mean of 0 difference, pinyon pine difference (% seedlings - % trees) was significantly positive only in EAG 1, indicating an increased presence among the regenerative seedling group at low elevations ($p = 0.021$) (Figure 2). EAG 3 had a high proportion of pinyon but a low number of plots with pinyon seedlings and so the difference was not significant. White fir seedling difference was significantly positive in EAG 5 only, indicating an increased presence in the seedling group at high elevations ($p = 0.004$). Ponderosa pine had a significantly negative difference across all EAGs, indicating a substantially reduced presence in the regenerative seedling group (EAG 1 ($p = 0.018$), EAG 2 ($p = 0.009$), EAG 3 ($p = 0.003$), EAG 4 ($p = 0.044$), EAG 5 ($p = 0.009$)). Douglas-fir had a significantly negative difference indicating reduced seedling presence only at mid and high elevations, in EAG 3 ($p = 0.019$) and EAG 5 ($p = 0.007$). Aspen and limber pine differences were not significant, indicating that those species had similar proportions among the tree and seedling class and so can be considered demographically stable.

Testing by ANOVA across mean species proportion difference (% seedlings - % trees) within EAGs, white fir was found to have the largest and most positive differences (Figure 2). In EAG 3, white fir % difference was positive and significantly larger than ponderosa pine ($p = 0.019$) and Douglas-fir ($p = 0.022$). In EAG 5, white fir % difference was positive and significantly larger than Douglas-fir ($p < 0.001$) and aspen ($p = 0.017$). Other comparisons among species within the same EAG were not significant.

To find where species are having substantial regeneration success or failure across the full range sampled, we compared trends in species percentage across elevation aspect groups (% seedlings in one EAG - % trees in each EAG) in plots with seedlings present to find trends in species-level regeneration across the study area (Figure 3). Testing by ANOVA within individual EAGs, we identified species with significantly higher difference in species proportions, thus indicating which species are tending towards increased demographic dominance in the seedling group. Generally, drought-tolerant pinyon at low and mid elevations and southwest aspects had greater recruitment than other species, while at high elevations shade-tolerant white fir and mesic aspen recruitment was proportionally larger. These elevation and aspect trends in regeneration held when testing across or between EAGs and species.

In EAG 1, we found significantly larger and positive recruitment % difference in pinyon, when compared to all other species ($p < 0.001$ for each, except white fir where $p = 0.008$), indicating pinyon had the greatest regenerative success in EAG 1 of the species analyzed (Figure 3). Species differences in EAG 2 were not significant. In EAG 3, pinyon recruitment % difference was significantly larger than ponderosa pine or Douglas-fir ($p < 0.001$ for each). In EAG 4, aspen recruitment % difference was significantly larger than ponderosa pine ($p = 0.003$) or Douglas-fir ($p = 0.048$). And in EAG 5, white fir recruitment % difference was significantly larger than limber pine, ponderosa pine, or Douglas-fir recruitment % difference, and aspen recruitment % difference was significantly larger than ponderosa recruitment % difference ($p < 0.001$ for each).

Testing by species and EAG across the study area for overall difference in plots with seedlings present identified which species were recruiting disproportionately compared to the overstory in each EAG (Figure 3). For pinyon, proportional difference (% seedling - %

tree) in EAG 1 was significantly positive and larger than in EAG 2 or 4 ($p < 0.001$ for each), and pinyon % difference in EAG 3 was significantly positive and larger than in EAG 4 ($p = 0.002$). Only a few adult pinyon and no seedlings were found in EAG 4, at the upper extent of the species elevational distribution in the watershed and on northeast aspects (Table 1). This indicates pinyon recruitment in EAG 1 and EAG 3 is proportionally higher than any other species in the study area. For white fir, proportional difference in EAG 5 was positive and larger than in EAG 2 ($p = 0.032$). For aspen, proportional difference in EAG 4 was positive and larger than in EAG 1 ($p = 0.006$). Proportional difference in other species and EAGs were not significantly different from 0.

Seedling recruitment in general was highest in mid-elevation southwest plots (EAG 3), encompassing 36.6% of all seedlings tallied, and averaging 38 seedlings per plot, although the per-plot value was not significantly larger than other EAGs (Table 1). Recruitment was lowest in low-elevation northeast plots (EAG 2), where 70% of plots lacked seedlings, although where seedlings were present the number per plot was not significantly different from other groups.

Discussion

Growth-Climate Response: Implications for the Hotter, Drier Future

Tree species vary in their tolerance of moisture and temperatures stress, and tree growth is more sensitive to stressors and at risk of climate-induced mortality near the lower limits of their elevational species distribution (Fritts et al. 1965; Williams et al. 2010; McDowell et al. 2010; King et al. 2013). Temperature and drought stress are increasing over time due to anthropogenic climate change. Increasing climate stress at lower forested elevations leads to elevational trends in mortality depending on species tolerances, as was seen regionally in pinyon in the early 2000s (Breshears et al. 2005; Williams et al. 2010). The demographic balance of mortality, recruitment, and growth among species creates the potential for demographic shifts, and results in altered future species composition and forest structure.

In these ecosystem, differences in modeled climatic drivers across low- and mid-elevation southwest aspect plots (EAG 1 and EAG 3) indicate a divergence in species-specific climate stressors on tree growth for ponderosa pine and Douglas-fir, aligning with their relative tolerance for drought (Niinemets and Valladares 2006). This modeled difference occurs near the lower elevational limit of each species, where we might expect to see effects of climate change to be most strongly expressed, including possible mortality events in the near future (Williams et al. 2010). Higher correlation between growth and climate variables at low elevation in EAG 1 supports the idea that climate is a stronger influence on growth in areas at lower elevation and with a southwest aspect. As we also found changes in seedling composition favoring drought-tolerant pinyon pine over all other species in EAG 1, it follows that climate is more likely to drive species demographic shifts at low elevations.

Compared to the tree group, ponderosa pine and Douglas-fir were less dominant among the seedling group across the watershed. The net result of climate-driven drought-related mortality, and reduced recruitment in the more climate-sensitive lower elevations of the watershed, is substantially reduced populations of ponderosa pine and Douglas-fir over time (Allen et al. 2010). Lower elevation mature trees on the landscape at present, near the lower elevational limits for their species, likely established in relatively mesic sites and with increasing climate stress will be at greater risk of reduced regenerative success, and eventually mortality. A mixed-conifer forest with a different species composition may thus be emerging.

However, it must be noted that climate sensitivity model conclusions are highly responsive to choices made in standardizing chronologies. In testing, different standardization processes led to different climate variables selected, though the general increased climate sensitivity at lower elevations held throughout. We chose a moderately conservative method of detrending ring series in an attempt to minimize methodological influences skewing the conclusions.

If elevational trends in climate sensitivity continue, some low-elevation southwest-aspect areas may shift to pinyon-juniper woodland as individuals of less drought tolerant species have reduced success at regeneration, and eventually die as the landscape moves from extinction debt to extirpation of certain species in climate change-exacerbated drought. Analyzing species composition shifts in seedling regeneration is more revealing of areas of extinction debt than where species might succeed but have not yet dispersed, which requires climate analysis based on known species tolerances (Jackson and Sax 2010; Urban 2015).

Climate and Disturbance as Drivers of Species Distribution Shifts

Changes in species distributions and community composition have been noted globally, by altitude and latitude, in response to changing climate and other disturbance factors, though movement is not always directly upwards or northward. Direct movement upslope or leaning to center distribution at a higher elevation is a common finding (Kelly and Goulden 2008; Breshears et al. 2008; Feeley et al. 2011). In other cases communities may instead re-organize and change in composition, or move in other directions in accordance with local effects (Walther 2010; Lenoir and Svenning 2015). Climate and species niche requirements are largely thought to drive distribution and range shifts at large scales; within a single watershed, stand dynamics, disturbance, and chance incidents also contribute to observed demographic compositional shifts (Bell et al. 2013; Dobrowski et al. 2015; Savage and Vellend 2015).

When seedling percent difference was positive, we found a general tendency for relative species proportional difference to be larger in the seedling class across the upper portions of their elevational range. This reflects the findings from our summarized growth-climate model (Figure 1b), which suggests a correspondence of climate drivers and the potential for movement upslope. However, this correspondence was not reflected universally in relative seedling recruitment—we found greater regeneration of pinyon and white fir at higher elevations but not always on northeast aspects.

Drivers of demographic change were likely not the same across all species where significant increase or decrease in dominance was found. At low elevations where we found higher climate correlation with tree growth and increasing pinyon pine dominance, climate seems to be a stronger component in observed changes. At all elevations, stand-level disturbance factors (fire exclusion followed by stand density increase) likely affect the composition of the regenerative seedling demographic group, favoring shade-tolerant white fir at high elevations and resulting in reduced dominance everywhere of the less shade-tolerant but relatively drought-tolerant ponderosa pine. In California, similar trends of reductions in pine and increases in fir were found in mixed-conifer forests following fire exclusion (Levine et al. 2016). Local effects were also important controls on species demographic composition and regeneration trends in a broader survey of California forests (Serra-Diaz et al. 2016).

Species Distribution Shifts: Regeneration and Mortality

We found changes in the relative proportions of species between mature trees and seedlings, within and across the elevation-aspect groups. At low- to mid-elevation plots on southwest aspects (EAG 1 and 3), pinyon pine dominated recruitment. Despite recent regional-scale pinyon mortality (Breshears et al. 2005), we found numerous pinyon seedlings and saplings on southwest aspect plots near the upper elevational limit of the species' range in this watershed. Mortality events, plus regeneration at higher elevations, indicate that the pinyon species regenerative niche, or "center of mass" of its range where conditions are most suitable for reproduction and growth, may be leaning uphill.

We also found an increase in the relative presence of white fir in seedlings at higher elevations. The success of white fir at high elevations may be linked to its shade-tolerant growth habits, filling in available gaps without the recruitment-limiting effects of frequent fire, although white fir can also express drought tolerance (O'Connor et al. 2017; North et al. 2019). Pinyon regeneration success may also be linked to fire exclusion. Pinyon is not very fire resistant, with fire intervals of approximately 300 years (Romme et al. 2003). At upper elevation pinyon ecotones mixing with ponderosa pine and mixed-conifer forests, patch dynamics are important to regeneration, and severe fire is most limiting on recruitment (Huffman et al. 2008). As a result, regeneration was likely limited by the recurrence of widespread fire in the lower, warmer mixed-conifer sites by frequent mixed-severity fire (mean fire interval 12.4 years, widespread fire interval 31.6 years) that characterized the fire regime in the area until the cessation of frequent fire (Margolis and Balmat 2009).

The broadest change in species proportional distribution found was the reduction in ponderosa pine and Douglas-fir across the entire elevation-aspect gradient. These two species were codominant in the mature tree group, yet made up a substantially reduced proportion of the seedling group (Table 1). Changing regeneration patterns correspond to the changes taking place in the ecosystem following fire exclusion, with fewer patches opening up after fire suitable for recruitment, compounded by the variability in factors affecting successful tree reproduction and recruitment.

We found seedling presence to be highly variable across the study area. Many factors contribute to successful seedling recruitment resulting in survival of the individual to later life stages, including a local seed source, sufficient resources (water, nutrients, and space), and lack of disturbance (fire or predation) (Kitajima and Fenner 2000; North et al. 2019). Certain conifers, including ponderosa pine, are masting species with pulses of mass reproduction, and successful recruitment often corresponds to a persistent wet, moderate climatic period following a masting event (Brown and Wu 2005; Keyes and Gonzales 2015). Masting events occur only occasionally, and so even though we found a low percentage of ponderosa pine seedlings, this could correspond to recent conditions not supporting reproduction. If precipitation patterns result in a wet period, a pulse of ponderosa establishment might then occur.

Overall seedling density was particularly sparse at low elevation, northeast aspect plots (EAG 2). Here, seedling recruitment may be limited by the tendency for seeds to roll and disperse further, as plots in EAG 2 tended to be steeper on average, or by cold air drainage from higher elevations suppressing regeneration. Steep slopes and incised mountain orography, above more open valleys, tend to encourage cold air drainage overnight, leading to cooler temperatures (Zardi and Whiteman 2013). Ponderosa seedlings in particular are temperature-sensitive and so limited by conditions to a small range of suitable climate conditions (Petrie et al. 2016). We found the highest rates of regeneration across species at mid elevation, southwest aspect plots (EAG 3), likely reflecting a combination of microclimatic optima and available resources, plus an element of stochasticity inherent in the variable regeneration found across the state space.

Fire exclusion across the study area has resulted in a century of recruitment with increasing stand density, favoring the infill of shade-tolerant and fire-intolerant species. As time without fire has increased, the forest may have become progressively less suitable for ponderosa pine and Douglas-fire recruitment compared to other species already present. The net result of these differences may be an emerging shift in species composition across the watershed away from ponderosa pine and toward pinyon pine and white fir. These changes in relative abundance are the net result of demographic processes driven by disturbance and shifting climate, processes that may continue to operate at large scales in coming decades.

Acknowledgements

Thanks to Alex Arizpe, Mark Betancourt, Jacquie Dewar, Alicia Durnin, Josh Farella, Ali Jaffery, Sarah Jorgensen, Kyle Miller, Jesse Minor, Rebecca Minor, Christopher O'Connor, Anastasia Rabin, Ben Schippers, and Tyson Swetnam for help in the field and lab. Thanks to Erica Newman for modeling and R help, and to Steven Leavitt, Valerie Trouet, David Moore, Nathan McDowell for comments.

References Cited

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. T., & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660-684.

Andrus, R., Harvey, B. J., Chai, R. K., & Veblen, T. T. (2018). Different vital rates of Engelmann spruce and subalpine fir explain discordance in understory/overstory dominance. *Canadian Journal of Forest Research*. *48*(12), 1554-1562.

Arnold, J. B. (2018). ggthemes: Extra Themes, Scales and Geoms for 'ggplot2'. R package version 3.5.0. https://CRAN.R-project.org/package=ggthemes

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., & Panayotov, M. (2013). Site‐and species‐specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography, 22*(6), 706-717.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1-48.

Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, *23*(2), 168-180.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., Pierrat, J. C., & Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., & Anderson, J. J. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, *102*(42), 15144-15148.

Breshears, D. D., Huxman, T. E., Adams, H. D., Zou, C. B., & Davison, J. E. (2008). Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences*, *105*(33), 11591-11592.

Brewer, P. W. (2016). Tellervo: A Guide for Users and Developers, 10.5281/zenodo.51329, www.tellervo.org

Brokaw, N., & Busing, R. T. (2000). Niche versus chance and tree diversity in forest gaps. *Trends in Ecology & Evolution*, *15*(5), 183-188.

Brown, P. M., & Wu, R. (2005). Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*, *86*(11), 3030-3038.

Bunn, A., Korpela, M., Biondi, F., Campelo, F. Mérian, P., Qeadan, F., Zang, C., Pucha-Cofrep, D., & Wernicke, J. (2018). dplR: Dendrochronology Program Library in R. R package version 1.6.8. https://CRAN.R-project.org/package=dplR

Carrer, M. (2011). Individualistic and time-varying tree-ring growth to climate sensitivity. *PLoS One*, *6*(7), e22813.

Cook, E. R., & Peters, K. (1997). Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene*, *7*(3), 361-370.

Covington, W. W., & Moore, M. M. (1994). Postsettlement changes in natural fire regimes: ecological restoration of old-growth ponderosa pine forests. *J. Sustain. Forest, 2*, 153-181

DeBuys, W. E. (1985). *Enchantment and exploitation: The life and hard times of a New Mexico mountain range*. UNM Press.

De Frenne, P., Graae, B. J., Rodríguez‐Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., & Gruwez, R. (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, *101*(3), 784-795.

Del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Condés, S., Ducey, M. J., Fonseca, T., von Lüpke, N., & Pach, M. (2016). Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *European Journal of Forest Research*, *135*(1), 23-49.

Diersing, V. E., Tazik, D. J., & Novak, E. W. (1987). *Growth Rate of Pinyon Pine (*Pinus edulis*) on Fort Carson and Pinyon Canyon Maneuver Site, Colorado* (No. CERL-TR-N-87/20). CONSTRUCTION ENGINEERING RESEARCH LAB (ARMY) CHAMPAIGN IL.

Dobrowski, S. Z., Swanson, A. K., Abatzoglou, J. T., Holden, Z. A., Safford, H. D., Schwartz, M. K., & Gavin, D. G. (2015). Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography*, *24*(8), 917-927.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R., & Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, *38*(4), 783-791.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, *113*(14), 3725-3734.

Fritts, H. C. (1976). *Tree rings and climate.* Elsevier.

Fritts, H. C., Smith, D. G., Cardis, J. W., & Budelsky, C. A. (1965). Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology*, *46*(4), 393-401.

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*(1577), 2105-2115.

Fulé, P. Z., Covington, W. W., Moore, M. M., Heinlein, T. A., & Waltz, A. E. (2002). Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography, 29*(1), 31-47.

Goodrich, B. A., & Waring, K. M. (2016). *Pinus strobiformis* seedling growth in southwestern US mixed conifer forests in managed and non-managed stands. *Forestry: An International Journal of Forest Research*, *90*(3), 393-403.

Grossnickle, S. C. (2012). Why seedlings survive: influence of plant attributes. *New Forests*, *43*(5-6), 711-738.

Harrell Jr., F. E., with contributions from Charles Dupont and many others. (2018). Hmisc: Harrell Miscellaneous. R package version 4.1-1. https://CRAN.R-project.org/package=Hmisc

Heinlein, T. A., Moore, M. M., Fulé, P. Z., & Covington, W. W. (2005). Fire history and stand structure of two ponderosa pine–mixed conifer sites: San Francisco Peaks, Arizona, USA. *International Journal of Wildland Fire*, *14*(3), 307-320.

Homeier, J., Breckle, S. W., Günter, S., Rollenbeck, R. T., & Leuschner, C. (2010). Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica*, *42*(2), 140-148.

Huffman, D. W., Fulé, P. Z., Pearson, K. M., & Crouse, J. E. (2008). Fire history of pinyon–juniper woodlands at upper ecotones with ponderosa pine forests in Arizona and New Mexico. *Canadian Journal of Forest Research*, *38*(8), 2097-2108.

Hurvich, C. M., & Tsai, C. L. (1989). Regression and time series model selection in small samples. *Biometrika*, *76*(2), 297-307.

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153-160.

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences*, *105*(33), 11823-11826.

Keyes, C. R., & González, R. M. (2015). Climate-influenced ponderosa pine (Pinus ponderosa) seed masting trends in western Montana, USA. *Forest Systems*, *24*(1), 21.

King, G. M., Gugerli, F., Fonti, P., & Frank, D. C. (2013). Tree growth response along an elevational gradient: climate or genetics?. *Oecologia*, *173*(4), 1587-1600.

Kitajima, K., & Fenner, M. (2000). Ecology of seedling regeneration. *Seeds: The Ecology of Regeneration in Plant Communities*, *2*, 331-359.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569-574.

Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts–a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15-28.

Levine, C. R., Krivak-Tetley, F., van Doorn, N. S., Ansley, J. A. S., & Battles, J. J. (2016). Long-term demographic trends in a fire-suppressed mixed-conifer forest. *Canadian Journal of Forest Research*, *46*(5), 745-752.

Lomolino, M. V. (2001). Elevation gradients of species-density: historical and prospective views. *Global Ecology and biogeography*, *10*(1), 3-13.

Lutz J. A., Larson A. J., Swanson M. E., & Freund J. A. (2012). Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS ONE,* 7(5): e36131. https://doi.org/10.1371/journal.pone.0036131

Margolis, E. Q., Swetnam, T. W., & Allen, C. D. (2007). A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research*, *37*(11), 2227-2241.

Margolis, E. Q., & Balmat, J. (2009). Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecology and Management*, *258*(11), 2416-2430.

Mazerolle, M. J. (2017) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. https://cran.r-project.org/package=AICcmodavg.

McDowell, N. G., Allen, C. D., & Marshall, L. (2010). Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. *Global Change Biology*, *16*(1), 399-415.

Minor, J. J., & Arizpe, A. H. (2015). Trimming and planing rough-cut wood for efficient dendrochronological sample preparation and storage. *Tree-Ring Research*, *71*(2), 130-134.

Nakawatase, J. M., & Peterson, D. L. (2006). Spatial variability in forest growth–climate relationships in the Olympic Mountains, Washington. *Canadian Journal of Forest Research*, *36*(1), 77-91.

Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M., & Frank, D. (2014). The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology*, *20*(9), 2867-2885.

Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs*, *76*(4), 521-547.

North, M. P., Stevens, J. T., Greene, D. F., Coppoletta, M., Knapp, E. E., Latimer, A. M., Restaino, C. M., Tompkins, R. E., Welch, K. R., York, R. A., & Young, D. J. (2019). Tamm Review: Reforestation for resilience in dry western US forests. *Forest Ecology and Management*, *432*, 209-224.

O'Connor C. D., Falk, D. A., Lynch, A. M., Swetnam, T. W., & Wilcox, C. (2017). Disturbance and productivity interactions mediate stability of forest composition and structure. *Ecological Applications, 27*(3), 900–915.

O'Connor, C. D., Falk, D. A., Lynch, A. M., & Swetnam, T. W. (2014). Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient of the Pinaleño Mountains, Arizona, U.S.A. *Forest Ecology and Management, 329*, 264–278.

Ohsawa, T., Tsuda, Y., Saito, Y., Sawada, H., & Lde, Y. (2007). Steep slopes promote downhill dispersal of *Quercus crispula* seeds and weaken the fine-scale genetic structure of seedling populations. *Annals of forest science*, *64*(4), 405-412.

Petrie, M. D., Wildeman, A. M., Bradford, J. B., Hubbard, R. M., & Lauenroth, W. K. (2016). A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *Forest Ecology and Management*, *361*, 328-338.

Puhlick, J. J., Moore, M. M., & Weiskittel, A. R. (2013). Factors influencing height-age relationships and recruitment of ponderosa pine regeneration in northern Arizona. *Western Journal of Applied Forestry*, *28*(3), 91-96.

QGIS Development Team (2016). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

PRISM Climate Group (2016). *Prism Climate Data*. Oregon State University, http://prism.oregonstate.edu, created 3-24-2016.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rollinson, C. R., Kaye, M. W., & Canham, C. D. (2016). Interspecific variation in growth responses to climate and competition of five eastern tree species. *Ecology*, *97*(4), 1003-1011.

Romme, W. H., Floyd-Hanna, L., & Hanna, D. (2003). Ancient pinyon–juniper forests of Mesa Verde and the West: a cautionary note for forest restoration programs. In 'Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings', 16–19 April 2002, Fort Collins, CO.(Eds P Omi, L Joyce) USDA Forest Service, Rocky Mountain Research Station. *Proceedings RMRS-PO-29. (Fort Collins, CO).*

Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, *38*(6), 546-555.

Serra-Diaz, J. M., Franklin, J., Dillon, W. W., Syphard, A. D., Davis, F. W., & Meentemeyer, R. K. (2016). California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography*, *25*(2), 164-175.

Speer, J. H., (2010). Fundamentals of Tree-Ring Research. University of Arizona Press, Tucson.

St. George, S., Meko, D. M., & Cook. E. R. (2010). The seasonality of precipitation signals encoded within the North American Drought Atlas. *Holocene*, *20,* 983–988

Shepperd, W. D., Edminster, C. B., & Mata, S. A. (2006). Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. *Western Journal of Applied Forestry*, *21*(1), 19-26.

Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution, 1*(7), 0182.

Therneau, T., & Atkinson, B. (2018). rpart: Recursive partitioning and regression trees. R package version 4.1-13. https://CRAN.R-project.org/package=rpart

Thomas, J. W. (1979). Wildlife habitats in managed forests--the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553, USDA Forest Service.

Thomas, Z., & Waring, K. M. (2014). Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in northern New Mexico, USA. *Forest Science*, *61*(1), 93-104.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571-573.

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S.* Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vicente-Serrano S. M., Beguería, S., & López-Moreno, J. I. (2010). A Multi-scalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index - SPEI. *Journal of Climate* 23, 1696-1718.

Walther, G. R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1549), 2019-2024.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews*, *42*(2), 207-264.

Wickham, H. (2017). tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse

Wickham, H. (2007). Reshaping data with the reshape package. *Journal of Statistical Software,* *21*(12), 1-20. URL http://www.jstatsoft.org/v21/i12/.

Williams, A. P., Allen, C. D., Millar, C. I., Swetnam, T. W., Michaelsen, J., Still, C. J., & Leavitt, S. W. (2010). Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*, *107*(50), 21289-21294.

Zardi, D., & Whiteman, C. D. (2013). Diurnal mountain wind systems. In *Mountain Weather Research and Forecasting* (pp. 35-119). Springer, Dordrecht.

Table and Figure Captions

Table 1. Sampling Descriptions

Description of plots sampled, split into Elevation-Aspect Groups (EAGs) by classification tree model, and grouped by plot elevation (m) and aspect (deviation from 45°). # Plots is the number of plots that fell in each EAG, and the number of plots with seedlings (*italics*). Species distribution (% of total per EAG) for trees and seedlings (italics) of the six species that make up the majority of individuals present follow. EAG 5 included the upper extremes of ponderosa pine, so numbers sampled were low. Species codes are: PIPO (*Pinus ponderosa,* ponderosa pine), PSME (*Pseudotsuga menziesii,* Douglas-fir), PIED (*Pinus edulis* var. Engelm., pinyon pine), PIFL (*Pinus flexilis*, limber pine), ABCO (*Abies concolor*, white fir), POTR (*Populus tremuloides*, quaking aspen).

Table 2. Model Summary

Summary of variables selected by AICc for glm models of the form (EAG species-specific mean tree-ring chronology~glm(climate variable), gamma family, log link). Species codes are as in Table 1. Multiple models were included (a, b, c) where Δ AICc was low. Model name prefixes indicate which of the three PRISM cells covering the study area was used, ranked from low to high elevation (l = low, m = mid, h = high). Climate variables selected were water year precipitation (PPT.wyr, mm sum previous October to current September), mean growing season maximum temperature (Tmax.gsm °C, March-September), and mean growing season minimum temperature (Tmin.gsm °C, March-September). The null deviance was 14.9, null degrees of freedom (df) 115, and residual df for PIPO was 114 for all EAG, and for PSME 113 for EAG.1 (two years had missing rings in the chronology) and 114 for

EAG.2 through EAG.5. Series-model correlation coefficient uses Pearson's *r* except for two NA rows (1-PSME and 3-PSME) for which *r* cannot be calculated. Negative correlations occur when maximum temperature is a selected variable, as growth is reduced in hotter periods.

Figure 1. Study Area and Growth-Climate Variable Summary

(a.) Location of study area in northern New Mexico, USA (top left, forest service lands shown in medium gray), with inset box showing watershed units including the study area in Little Tesuque watershed (shaded darker gray), Santa Fe National Forest (shaded medium gray). Lower/right shows the study area with site sampling locations and GIS-derived Elevation-Aspect Group (EAG) polygons, with gray shading for EAG.1 through EAG.5, with general northeast aspect indicated by diagonal lines. EAG.5 ends at 3150 m, with a 50 m buffer above the highest sampled site, at the upper extent of mixed-conifer forest in the watershed.

(b.) Summarized results of growth-climate model selection by species (PIPO: ponderosa pine, PSME: Douglas-fir) and Elevation-Aspect Group (EAG) on the sampling space of aspect (x-axis) and elevation (y-axis). Linking between EAGs, solid lines indicate the same primary climate variable selected (temperature or precipitation), while dotted lines with a slash indicate a different climate variable selected, indicating potential movement between EAGs might be easier or harder respectively. For ease of interpretation, the gradient of gray shading indicates elevation with darker corresponding to higher areas. Species names are separated vertically for visual comparison of climate variables selected.

Figure 2. Mean Species Shift in Distribution within EAG

Boxplot of the mean of relative species dominance between the seedling and tree groups (% plot difference seedling – tree) within Elevation-Aspect Groups (EAG), Values greater than 0 indicate seedlings of that species makes up a greater proportion of individuals than trees across plots in the EAG, and values lower than 0 indicate seedlings make up a smaller proportion than trees, with significant difference from 0 starred. Includes the six predominant species sampled in the watershed by species code: PIPO (*Pinus ponderosa,* ponderosa pine), PSME (*Pseudotsuga menziesii,* Douglas-fir), PIED (*Pinus edulis* var. Engelm., pinyon pine), PIFL (*Pinus flexilis*, limber pine), ABCO (*Abies concolor*, white fir), POTR (*Populus tremuloides*, quaking aspen). All plots sampled were included in the data regardless of whether they have seedlings present in order to find overall forest composition trends. Within EAG.1, PIED was significantly higher ($p = 0.021$) than other species indicating increasing dominance, and within EAG.5 ABCO was significantly higher ($p = 0.004$). PIPO difference was significantly lower than 0 across all groups (EAG 1 ($p = 0.018$), EAG 2 ($p = 0.009$), EAG 3 ($p = 0.003$), EAG 4 ($p = 0.044$), EAG 5 ($p = 0.009$)). PSME was significantly lower in EAG 3 ($p = 0.019$) and EAG 5 ($p = 0.007$) only.

Figure 3. Mean Difference Across EAGs for Plots with Seedlings

Boxplot of mean % difference (seedling – tree) across EAGs by species, where seedling values are from a single EAG (EAG.*n*s) while tree value from each EAG are used. This allows for a comparison of seedling % to tree % by species, across EAGs, to find species and areas with substantially more seedlings than trees. Significance comparisons are within each EAG between species (low solid line, starred are significantly different from all crosses, and crosses are not different among themselves), and by species across EAGs (high dotted line, starred are significantly different from all crosses, and crosses are not different among themselves). Plots without seedlings are excluded in this figure in order to test regeneration patterns rather than whole forest-community patterns. See Table 1 for numbers of included plots, with seedlings present. Species codes are: PIPO (*Pinus ponderosa,* ponderosa pine), PSME (*Pseudotsuga menziesii,* Douglas-fir), PIED (*Pinus edulis* var. Engelm., pinyon pine), PIFL (*Pinus flexilis*, limber pine), ABCO (*Abies concolor*, white fir), POTR (*Populus tremuloides*, quaking aspen).

Tables

Table 1. Sampling Descriptions

EAG	**Elevation (m)**	**Aspect (dev. from 45°)**	**Summary**	**# Plots**	**# All Trees *Seedlings***	**% PIPO**	**% PSME**	**% PIED**	**% PIFL**	**% ABCO**	**% POTR**
1	2400 - 2678	≥ 126	Low elevation, SW	10 *7*	202 *240*	**36** *10*	9 *8*	28 ***62***	3 *5*	17 *10*	3 *0*
2	2400 - 2678	< 126	Low elevation, NE	21 *8*	420 *188*	**35** *8*	20 *26*	9 *24*	10 *11*	27 ***31***	0 *0*
3	2679 - 2908	≥ 85	Mid elevation, SW	22 *13*	446 *495*	**28** *16*	**36** *13*	1 ***23***	12 *17*	13 ***25***	9 *5*
4	2679 - 2908	< 85	Mid elevation, NE	15 *9*	258 *188*	**33** *8*	**32** ***34***	3 *0*	18 *27*	9 *17*	5 *13*
5	2909 - 3150	All	High elevation, All aspects	11 *9*	137 *240*	6 0	**42** ***36***	0 *0*	5 *1*	12 ***43***	**35** 20

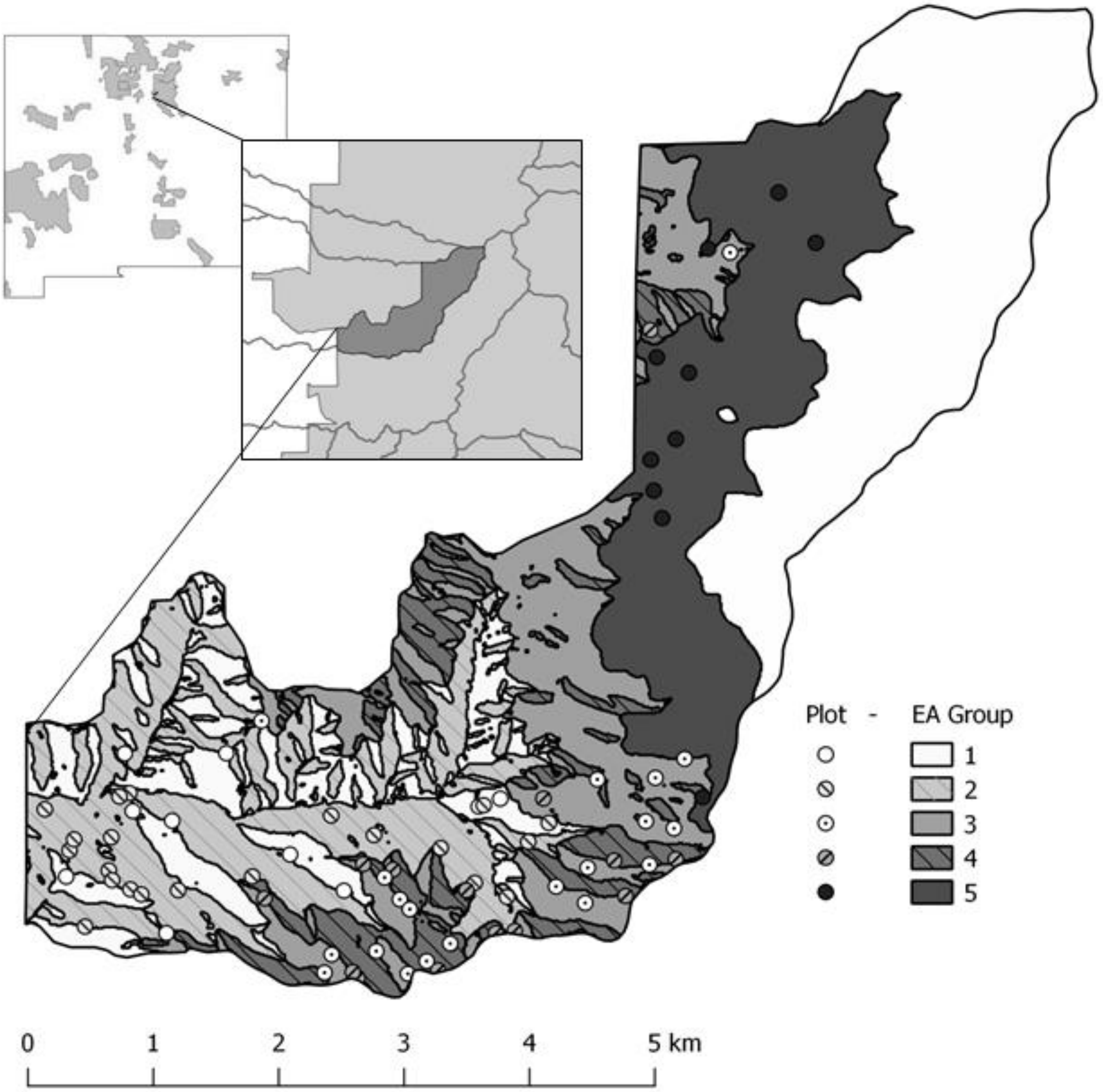
Table 2. Model Summary

EAG	Species		Model formula	AICc weight	Δ AICc	Residual deviance	Series correlation
1	PIPO	a	y ~ m.PPT.wyr	0.4	0.0	9.0	0.72
		b	y ~ u.PPT.wyr	0.4	0.1	9.2	0.72
2	PIPO	a	y ~ m.PPT.wyr	0.2	0.0	9.0	0.65
		b	y ~ u.PPT.wyr	0.2	0.3	9.2	0.65
		c	y ~ m.Tmax.gsm	0.1	0.3	10.7	-0.64
3	PIPO	a	y ~ m.PPT.wyr	0.4	0.0	9.0	0.68
		b	y ~ u.PPT.wyr	0.4	0.2	9.2	0.68
4	PIPO	a	y ~ m.PPT.wyr	0.5	0.0	9.0	0.69
		b	y ~ l.PPT.wyr	0.4	0.6	9.1	0.68
5	PIPO	a	y ~ m.PPT.wyr	0.6	0.0	9.0	0.47
		b	y ~ u.PPT.wyr	0.2	1.8	9.2	0.46
1	PSME	a	y ~ u.Tmax.gsm + u.Tmin.gsm	0.5	0.0	10.3	NA
		b	y ~ l.PPT.wyr	0.3	1.4	9.1	0.59
2	PSME	a	y ~ m.PPT.wyr	0.5	0.0	9.0	0.60
		b	y ~ l.PPT.wyr	0.4	0.1	9.1	0.60
3	PSME	a	y ~ u.Tmax.gsm + u.Tmin.gsm	0.3	0.0	10.3	NA
		b	y ~ u.Tmax.gsm	0.3	0.2	10.5	-0.53
		c	y ~ m.Tmax.gsm	0.2	1.4	10.7	-0.53
4	PSME	a	y ~ l.PPT.wyr	0.5	0.0	9.1	0.59
		b	y ~ m.PPT.wyr	0.4	0.1	9.0	0.58
5	PSME	a	y ~ u.PPT.wyr	0.4	0.0	9.2	0.59
		b	y ~ m.PPT.wyr	0.3	0.1	9.0	0.58

Figures

Figure 1. Study Area and Growth-Climate Variable Summary

a. Study Area



b. Summary of Growth Model

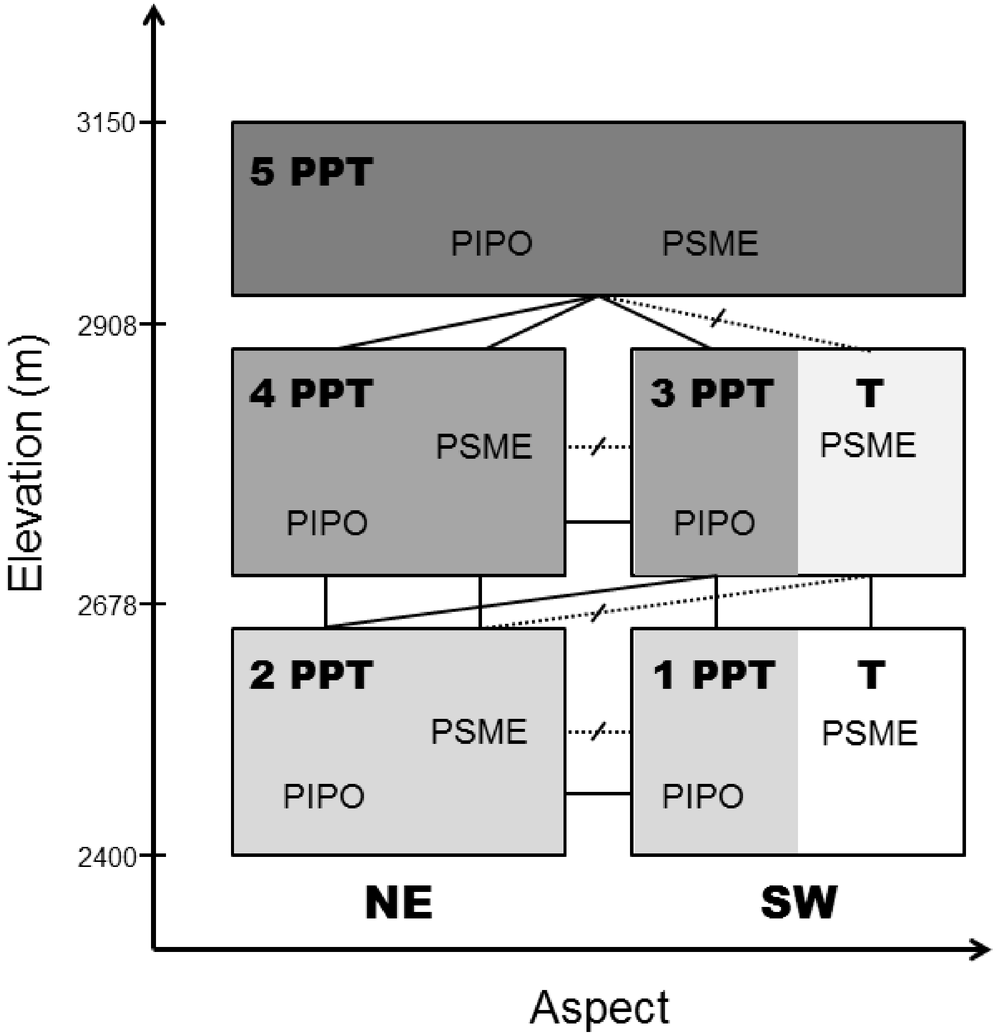


Figure 2. Mean Species Shift in Distribution within EAG

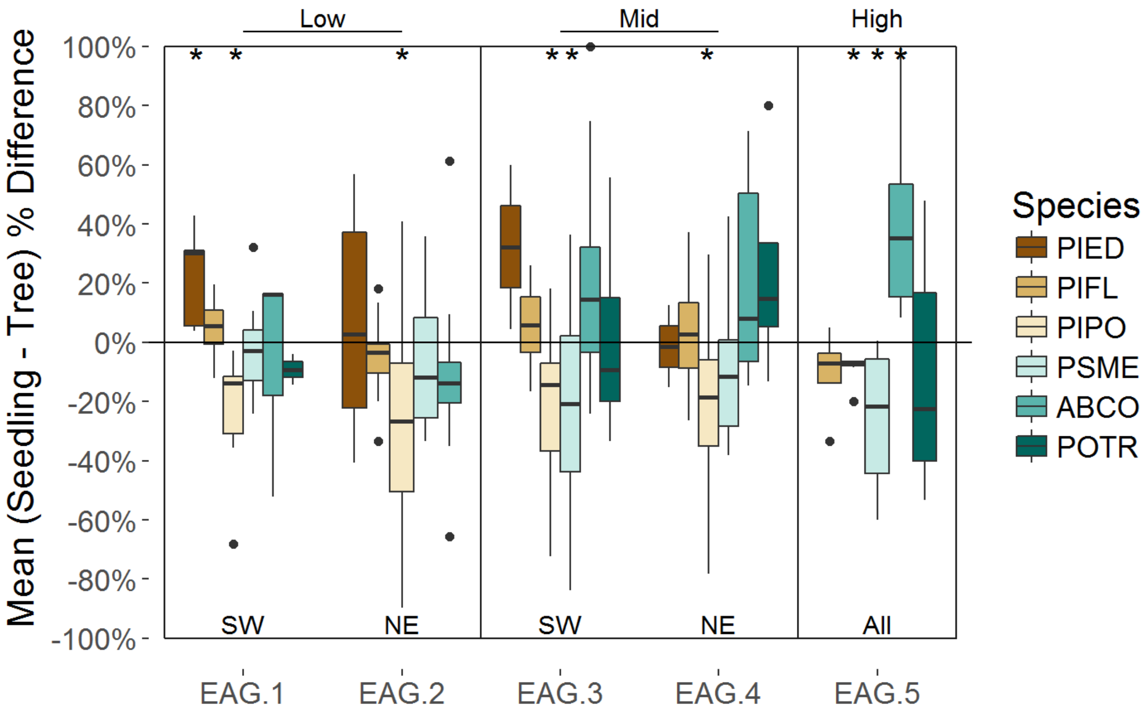
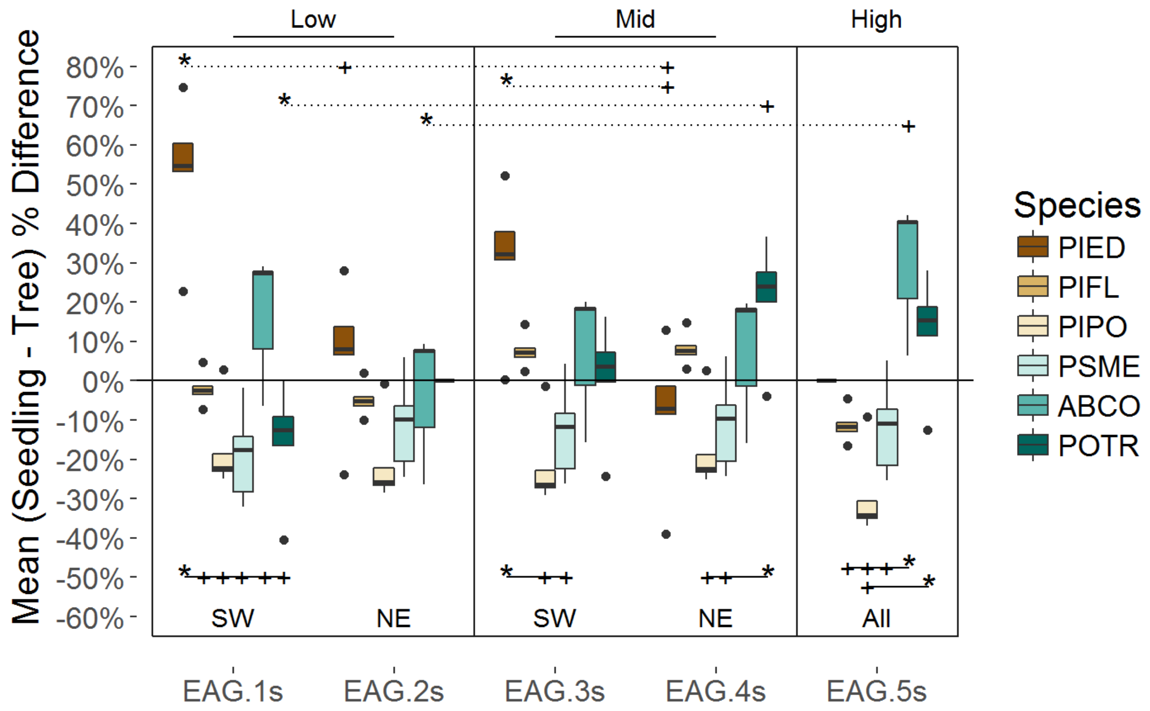
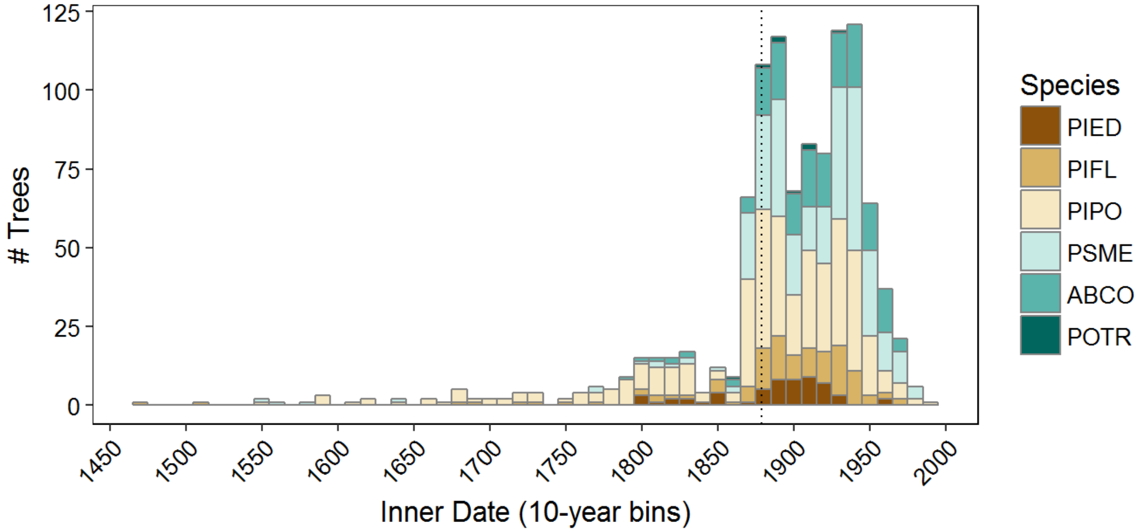


Figure 3. Mean Difference Across EAGs for Plots with Seedlings



Supplemental Information

Figure S-1. Southwest Mixed-Conifer Stand Age Structure



Stand-age structure for live and dead trees from the six dominant species at 58 randomly sampled plots stratified by elevation, in the Little Tesuque Watershed, SFNF, NM, USA. Also included are fire scar samples and remnant wood from non-plot locations, collected to extend the chronology, resulting in the long tail of the histogram. This demonstrates the increase in tree establishment following the exclusion of fire in late 1800s. Vertical dotted line is at 1879, the year of the last widespread fire in the watershed (Margolis et al. 2007). Inner date is pith date when available or within 5-10 rings, at approximately 10 cm above ground level, so is not the exact date of tree establishment, but generally within a decade and so the histogram is grouped into 10-year bins.

Margolis, E. Q., Swetnam, T. W., & Allen, C. D. (2007). A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research*, *37*(11), 2227-2241.

Appendix C:

Demographic Trends in Community Functional Tolerance Reflects Tree Responses to Climate and Disturbance

Demographic Trends in Community Functional Tolerance Reflects Tree Responses to Climate and Disturbance

L.A. Marshall[a,b], D.A. Falk[a,b]

[a]School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721-0045, USA

[b]Laboratory of Tree-Ring Research, The University of Arizona, Tucson, AZ 85721-0045, USA

Abstract

Forests of the western U.S. are undergoing substantial stress from fire exclusion and increasing effects of climate change altering ecosystem functions and processes. Shifts in broad-scale drivers of forest community composition become apparent in their effect on regeneration, driving demographic shifts. Here we take a community functional approach to tracking forest demography changes driven by drought and fire regime shifts, by investigating mean community assemblages shifts framed by species drought and shade tolerance. We created the novel Community Mean Tolerance Index (CMTI), a response metric utilizing drought/shade tolerance tradeoffs to identify communities undergoing demographic change from a functional trait perspective. We applied the CMTI to Forest Inventory and Analysis data to investigate demographic trends in drought and shade tolerance across the southern Rocky Mountains. We predicted greater shifts in drought tolerance would occur at lower forest type ecotones where climate stress is limiting, and that shifts in shade tolerance would correspond to excursions from the historic fire regime

leading to greater changes in forest types adapted to frequent, low-intensity fire. To find the major drivers of change in community tolerance within and across forest types, we compared index trends to climate and fire exclusion-driven disturbance, and identified where demographic change was greatest. The CMTI was applied spatially to find sites likely to transition to oak shrubfield, where disturbance history combined with a species-driven demographic shift towards drought tolerance.

Within forest types, lower elevations trended towards increased drought tolerance, while higher elevations trended towards increased shade tolerance. Across forest types, CMTI difference peaked in mid-elevation ponderosa pine and mixed-conifer forests, where fire exclusion and autecology drove demographic changes. The CMTI demographic tolerance difference across forest types was correlated significantly with elevation and climate variables, but the relationship varied across the elevation transect. Peak CMTI difference was associated with fire exclusion in forest types adapted to frequent fire. At higher elevations, site-level stand dynamics appeared to influence demographic tolerance trends more than broad climate drivers.

Through a community demographic approach to functional traits, the CMTI highlights areas and forest types where ecosystem function is in the process of changing, before absolute vegetation type change occurs. Applied to regional plot networks, the CMTI provides an early warning of shifts in community functional processes as climate change pressures continue.

Key words: drought tolerance, shade tolerance, functional traits, Southern Rockies ecoregion, Rocky Mountains, community mean index, forest inventory analysis, vegetation type change

Introduction

Variation in abiotic and biotic stressors over space and time drives species adaptation, and results in species-specific tolerance to factors such as drought and shading appropriate to their niche. In vascular plant species, physical and physiological traits can be arrayed into common functional trait groups along axes defined by trade-offs (Díaz et al. 2016). Stressors and tolerance response occur across an interactive multivariate space, leading to gradients in species functional traits following stress gradients (Díaz et al. 2013; Violle et al. 2014). The spatial distribution of tree species is strongly dependent on individual species tolerance and response to stressors including drought, disturbance, and fire, along with an element of stochastic variability (Barton 1993; Adams 2005; Thuiller et al. 2007; Anderegg and HilleRisLambers 2016). Over time, species functional traits interacting with the environment contribute to the demographic patterns of mortality and regeneration that determine species presence or absence at a particular site, modified by biotic interactions and disturbance history (Adler et al. 2014; Violle et al. 2014; Normand et al. 2014). Community tolerance can be considered as a state factor model (Amundson and Jenny 1997) through the sum of key drivers (climate, topography) affecting regeneration success over time with the influence of interactive stand-level controls of fire regime and disturbance history.

Tree species adapt to their environment in ways definable through distinct physical and physiological traits, which in sum demonstrate a species-level tradeoff between drought and shade tolerance (Niinemets and Valladares 2006). Numerous physiological and functional traits contribute to individual species' tolerance response. For evergreen coniferous species, drought or shade tolerance is favored by variance in foliage traits including leaf age and dry mass per unit area, and physiological traits like photosynthetic capacity, which inversely favor drought or shade tolerance (Hallik et al. 2009; Niinemets 2010). Although stresses and tolerance responses are multivariate, species tend to align based on tradeoffs in tolerance, driven by species life history and environmental setting interacting to favor certain traits that support either drought or shade tolerance (Smith and Huston 1989; Niinemets 2010; Díaz et al. 2016). The tradeoff in tolerances driven by plant functional traits and environmental interactions creates a functional response vector for conifers between drought and shading; applied to the community level, this life-history tradeoff can reveal a gradient between species assemblies responding to climate stress and those responding to stand-level disturbance and biotic interactions.

Plant functional traits such as drought and shade tolerance affect the local and regional distribution of species (Violle et al. 2014; Anderegg and HilleRisLambers 2016). Functional traits are distinct metrics of species-environment interactions, and useful for investigating community species diversity and ecosystem-plant interactions (Kunstler et al. 2012; Reichstein et al. 2014). Plant functional traits interpreted through a community mean index can describe how traits of interest vary in response to biotic and abiotic influences across a sample space encompassing multiple ecosystems and environments (Garnier et al. 2004; Ricotta 2005; Garnier and Navas 2012). Interactions between plants and their environment are a particular focus of comparative functional ecology, as plant traits and environmental factors vary across gradients in concert (Albert et al. 2010; Garnier and Navas 2012; Díaz et al. 2013; Reichstein et al. 2014). Some intraspecific variation in traits occurs across stress gradients, with stronger drought tolerance occurring at lower species ecotones where individuals are subject to greater stress (Kolb et al. 2016). Tracking the overall ecosystem response allows for broader interpretation of ecosystem processes and response to changes like climate change, fire, or land-use change (Mokany et al. 2008; Moretti and

Legg 2009; Vandewalle et al. 2010). Functional traits in particular are useful in bridging the gap between individual, species, and community responses to environmental gradients and changes over time (Violle et al. 2014).

Increasing stand density is a major ecological concern across many forests of the western U.S., resulting from decades of fire suppression and centuries of grazing, together known as fire exclusion (Fulé et al. 2002; McIntyre et al. 2015; O'Connor et al. 2017). Increasing stand density has led to substantial changes to ecosystem processes in forest types adapted to frequent fire, such as ponderosa pine and mixed-conifer forests (Heyerdahl et al. 2001; Falk et al. 2011). Fire exclusion in frequent-fire forests alters successional pathways, resulting in changing species assemblies in ponderosa pine and mixed-conifer forests (Odion et al. 2014; O'Connor et al. 2017). When fires returns to these forests, they tend to be larger and more severe than before the period of fire exclusion and lead to greater tree mortality, a tendency exacerbated by climate change (Falk et al. 2011; Abatzoglou and Williams 2016; Kitzberger et al. 2017; Hood et al. 2018). Post-fire recovery following extreme events, and without further restoration efforts, tends to either reinforce ecosystem changes or else promotes a transition to a grass or shrub-dominated system (Savage and Mast 2005; Falk et al. 2011; Pausas and Keely 2014; Enright et al. 2015).

In forest types adapted to longer fire return intervals, fire exclusion may not push stand density conditions outside the historic norm. When combined with ongoing climate change, fire exclusion has led to increased fire severity and ecological changes across many forest types with varying fire regimes (Schoennagel et al. 2004; O'Connor et al. 2014; Hessburg et al. 2016). Higher elevation spruce-fir has a stand-replacing fire regime with fire return intervals on the order of hundreds of years, while mixed-conifer fire regimes can range from frequent, low-severity to infrequent and stand-replacing depending on local stand controls and broad-scale climate drivers (Falk et al. 2011; Margolis et al. 2011; Cansler and McKenzie 2014; Heyerdahl et al. 2019). Depending on forest type and local stand history, fire exclusion may or may not have pushed conditions outside the historic range of variability. The effects of fire exclusion on community composition, functional traits and ecosystem processes appear to be greatest in forest types adapted to frequent fire, though changes are also seen in forests with longer fire intervals (Odion et al. 2014; O'Connor et al. 2017).

Climate stress is a dominant interacting factor affecting forests, with drought a notable driver of sudden demographic change through widespread forest mortality (Allen et al. 2015; Millar and Stephenson 2015). Climate variability also drives fuel load and continuity, resulting in larger and more severe fires (O'Connor et al. 2014; Cansler and McKenzie 2014). In the southern Rocky Mountains, the number of fires and area burned has increased substantially since 1970, and climate change is expected to drive further increases (Westerling et al. 2006; Litschert et al. 2012; Kitzberger et al. 2017). Forest fire activity has increased in recent decades, and climate change is expected to exacerbate the frequency and extent of wildfire in the western United States (Abatzoglou and Williams 2016). Interactions of fire and climate with other disturbance factors such as insect outbreaks are also likely to drive forest changes (Veblen 2000; Millar and Stephenson 2015; Liang et al. 2016). Insect outbreaks may become more common with warmer weather, and dense forests contribute to spreading outbreaks, although responses are species-specific (Bentz et al. 2010).

Disturbance, including altered fire regimes, affects forests across many scales. Identifying drivers of changing species composition can be difficult due to sampling constraints and stabilizing processes inherent in resilient forest ecosystems (Lloret et al. 2012). Forest resilience is a factor of concern where climate change and disturbance may push ecosystems past tipping points, resulting in vegetation-type conversion to new or novel assemblages, and often losses of ecosystem functions (Reyer et al. 2015; Enright et al. 2015; Falk 2017). At forest interior sites, shade tolerance may increase in areas lacking recent disturbance, where fire exclusion has lengthened the time between fires.

The relative balance of climate and disturbance drivers on a forest stand will push community species composition towards drought or shade tolerance. Species composition and functional tolerance varies across elevation and climatic gradients (Albert et al. 2010; Vandewalle et al. 2010; Brusca et al. 2013; Wieczynski et al. 2018). Climate stress gradients are likely to correspond to site mean drought tolerance, as they do with drought-related mortality and species composition in general (Gitlin et al. 2006; Brusca et al. 2013). With ongoing changes, drought tolerance is likely to increase at lower elevation ecotones among forest types, reflecting the strong effects of climate limitation (Clark et al. 2016; Kolb et al. 2016). Climate change compounded with extended drought and land-use changes is increasingly likely to contribute to reduced growth, increased mortality, and vegetation type conversion (Allen et al. 2015; Clark et al. 2016; Gleason et al. 2017; Guo et al. 2018). Changes in species assemblages along montane gradients indicate that species have begun to indicate range shifts, and more are expected in response to climate change (Breshears et al. 2008; Crimmins et al. 2009; Brusca et al. 2013; Bell et al. 2014). Trees must grow where they establish, and can move only so far and fast as dispersal permits, which introduces lag between species distribution and climate and results in areas of extinction debt (Jackson and Sax 2010; Clark et al. 2016). Climate change, particularly through extreme drought related mortality, is likely to outpace dispersal (Allen et al. 2015; Clark et al. 2016). Species composition changes across demographic groups can provide an early indication of change.

Understanding demography, or plant population changes over time driven by recruitment, dispersal, and mortality, is critical to understanding species distribution dynamics (Normand et al. 2014; Evans et al. 2016). Changes in species composition across demographic age groups can suggest changing top-down controls and bottom-up limitations on regeneration and growth over time and as trees grow (Jackson et al. 2009; Bell et al. 2014; Law et al. 2019). Climate, past disturbance, and biotic interactions all influence species composition and dominance patterns across demographic groups (Jackson et al. 2009; Arx et al. 2013; Allen et al. 2015; Liang et al. 2016). Seedlings have a narrower window of climate requirements for establishment and survival than mature trees, and varying tolerance for drought and shading (Grubb 1977; Arx et al. 2013; Law et al. 2019). Shifts in seedling communities represent current regeneration success and, through successional pathways, the potential future forest species composition (Bell et al. 2014; Clark et al. 2016). Demographic approaches using difference across age classes or groups, including observed changes in regeneration composition relative to other groups, can indicate the potential for species shifts in response to past and current ecosystem influences like fire, drought, and disturbance history (Arx et al. 2013; Martínez-Vilalta and Lloret 2016; Evans et al. 2017; O'Connor et al. 2017).

Study Goals and Hypotheses

To address the question of how functional traits vary across demographic groups in a broad array of southern Rocky Mountain forests, we developed a novel community functional index, the Community Mean Tolerance Index (CMTI; described below). The index interprets species composition at a site in terms of mean drought- and shade- tolerance within and among demographic groups (such as trees *cf.* seedlings, or more broadly the regeneration group), to determine how recent climate and disturbance are contributing to trends in functional traits at the community level. We used the CMTI difference across demographic groups to investigate changes and current trajectories in community functional traits relating to drought and shade stress tolerance across and within multiple forest types.

We applied the index across a broad area within the southern Rocky Mountains, using Forest Inventory and Analysis data (USDA Forest Service 2018 (1)). We related functional trait CMTI difference values to key spatial and climate factors, to find specific drivers of demographic trends in drought and shade tolerance. Taking species life history into account, we noted areas where regeneration species composition and CMTI difference aligned to suggest the potential for vegetation type change following severe fire in forests adapted to frequent fire and subject to fire exclusion.

The balance of site-level changes in drought and shade tolerance between demographic groups (mature trees compared to regeneration) based on relative species dominance provides a window into possible trajectories of community change. Given that differential tree species regeneration is subject to many influencing factors, we expect mean regeneration drought and shade tolerance to reflect forest recruitment in recent decades. At lower elevations, within and across forest types, we expect increasing drought tolerance among regeneration (positive drought CMTI difference), as drought has been a regional influence for two decades. We expect the drought index to be correlated significantly with climate and elevation variables, and to be higher at lower elevations and arid sites. We expect drought effects to decrease with elevation, and thus expect greater shade tolerance at higher elevations in accordance with the established drought-shade tolerance tradeoff. At higher elevations, we expect drought to have less of an effect than fire exclusion resulting in an overall increase in forest density among shade-tolerant species (positive shade CMTI difference). We expect that greater shade tolerance among the regeneration group is being driven by increasing stand density in the absence of recent fire.

Methods

Study Area

We located our study within the Sangre de Cristo Mountains, New Mexico and Colorado, USA (Figure 1). Forested area within this range is approximately 150 km by 420 km, a measured area of 4,620,000 ha bounded by 34.85° to 38.45° N latitude, -104.43° to -106.00° W longitude. This includes the areas east of Poncha Pass and south of the Arkansas River, CO, incorporating numerous sub-ranges south to the Santa Fe, NM, area, generally to the east of the Rio Grande River. Elevations range from approximately 2000 m in the fringing pinyon-juniper woodland to 4374 m at Blanca Peak. With increasing elevation, forest types range from pinyon-juniper woodland and ponderosa pine, through mixed-conifer and spruce-fir, with occasional stands of lodgepole pine (*Pinus contorta* Douglas ex Loudon) and more frequent Rocky Mountain bristlecone pine (*Pinus aristata Engelm.*), and high peaks above treeline (Allen and Peet 1990). Forest types are determined by the dominant species present at plot sampling (USDA Forest Service 2018 (2)). This area is the southeastern-most part of the Southern Rockies ecoregion (Bailey et al. 1994). It has undergone fire exclusion, leading to changing fire regimes and in some areas other recent disturbance including wind-driven blowdown and insect-driven mortality events (Veblen et al. 2000; Litschert et al. 2012). Tree ring demography work within the study area demonstrates the effects of fire exclusion on the mixed-conifer forest, with substantial recruitment following the last widespread fire (Supplementary Figure S-1). In the near future, this area is expected experience hotter, drier conditions from climate change (McDowell et al. 2015). Summaries of climate, elevation, and fire history variables by forest type are available in Table 1.

Constraining the analysis to this portion of the southern Rocky Mountains allows for a more precise interpretation of the utility of the index we developed. Limiting the forest types and ecosystems under investigation reduces the complexity of interpreting variation across space within forest types. Focusing on mixed-conifer dynamics further allows for a close look at climate-disturbance interactions in a forest type subject to substantial anthropogenic effects from fire exclusion (Falk et al. 2011; O'Connor et al. 2017). Results of this study are broadly applicable across western US interior forests with similar forest types.

Forest Inventory and Analysis

We used data from the Forest Inventory and Analysis National Program (FIA), a US federal program that surveys all forested land in the United States using standardized protocols (USDA Forest Service 2018 (2)). We used FIA plot, condition, tree, and seedling/regeneration data from Colorado and New Mexico encompassing eleven forest types (Burrill et al. 2017; USDA Forest Service 2018 (1)). Using QGIS (QGIS Development Team 2016), we selected plots within the study area encompassing the New Mexico-Colorado Sangre de Cristo range and associated pinyon-juniper woodland. In R (R Core

Team 2018), we extracted all relevant data for this set of plots. We used data from the first sampling of plots starting in 2003 (CO) or 2005 (NM), through 2017 for analysis. We excluded plot data sampled prior to implementation of total seedling counts, as well as plot re-measurements. A limited number of re-measured plots were available after the change to seedling sampling protocols; we used the first sampling instance from these plots and excluded the later sampling.

According to FIA protocols, trees of ≥ 12.7 cm (5 in) diameter (at breast height or root crown, DBH or DRC) are recorded at four 7.3 m (24 ft) diameter subplots near each plot point sampled. We compared trees with regeneration, the set of small young stems as defined by individuals comprising the FIA seedling data set. Seedlings per the FIA are conifer stems at least 15.2 cm (6 in) in length and less than < 2.5 cm (1 in) diameter and hardwood stems at least 30.5 (12 in) in length and less than < 2.5 cm (1 in) in diameter, were recorded within a 2.1 m (6.8 ft) diameter microplot in each of the four subplots (Burrill et al. 2017). Woodland species (including Gambel oak (*Quercus gambelii* Nutt.) were counted as one individual seeding where stems emerged from one point.

We refer to products derived from the FIA seedling data as 'regeneration' or 'regeneration group', as seedling tends to refer to very young individuals only, and in Rocky Mountain conifers a stem may take decades to reach 40 cm in height (Mast et al. 1998; Nigh and Everett 2007). Following a release event clearing space these stems may emerge from the understory and so may be considered a potential future of the stand.

A total of 30,359 individual trees and 20,815 seedling stems were surveyed across all plots included in the study (Table 2). The smaller area for seedling sampling combined with trees tending towards a mass-reproduction strategy means that recorded seedlings tend to consist of fewer species in greater numbers than recorded trees, with high variance across the study space (Koenig and Knops 2000). Normalizing the CMTI by individuals recorded for each demographic group reduces the influence of variable reproduction by focusing on the community-level functional tolerance of recent recruitment.

The unique unit of analysis is the FIA plot-condition: an area with consistent forest type and other condition data within which sub-plot sampling of species composition occurs. Forest type is an assigned value based on species presence and dominance at a plot, and can vary across sub-plots at a sampling site. Location and elevation is tied to the plot level, and exact locations are not available due to site protection and privacy concerns. On federal lands, plot locations are adjusted by a random factor up to 1.6 km (1 mi) from their actual location; up to 20% of private land locations may be "swapped" within the county between ecologically-similar plots (Burrill et al. 2017). Within the study area, approximately 50% of plots were federal, and 50% private or Native American tribal land, and potentially subject to swapping. As a result explicitly mapped findings are accurate only to ±1.6 km, and up to 10% of all sites are accurate to within-county distances. Forest type and other data values used for analysis are retained for swapped sites. No significant difference in index value by forest type was found based on land ownership (public vs. private/tribal lands) despite FIA swapping of plot locations, and so all plots were included in the analysis.

Community Mean Tolerance Index

We developed the novel Community Mean Tolerance Index (CMTI), which is applied across demographic groups to find mean site values depending on the community composition of species functional tolerances. Using trait-based species-level relative tolerance for drought and shading, the CMTI can track ecosystem trends driving regeneration success.

Drought and shade tolerance align with specific climate or disturbance drivers, notably precipitation and temperature for drought tolerance and time since fire for shade tolerance (Niinemets and Vallardes 2006; Clark et al. 2016; O'Connor et al. 2017). The CMTI reflects the recent site-specific growing conditions, and the relative ability for species reproduction, seedling survival and recruitment into the regeneration group under those conditions. Species composition shifts are quantifiable and become apparent when analyzed as a vector of summed tolerances sampled across time, or in the absence of repeated measures, across demographic groups at a given site.

The CMTI is a weighted average of the functional tolerance of all individuals of all species within a plot or site. It is calculated as a sum of species tolerance values times the number of each species, normalized by the total number of individuals, with an individual index value derived for each demographic group (mature trees and regeneration groups), and tolerance type (drought or shade). The relative proportion of species was used rather than basal area or other metrics of dominance as the primary concern was shifting patterns of regeneration and for seedlings, tally data are more available and meaningful than basal area.

The CMTI is described by the following equation, as derived from species-specific drought (Tol_D) or shade (Tol_S) tolerance values, the sum across species of the relative proportional influence of the number of individuals of each species by demographic group at a unique plot ($n\ Species_{site\text{-}group}$), times the individual species-specific tolerance value, and divided by the total number of individuals by demographic group at a unique plot ($n\ Total_{site\text{-}group}$). For drought tolerance the equation is as follows:

$$\textbf{Community Mean Tolerance Index}_{\mathbf{D}} = \frac{\sum(n\,Species_{site-group} \times\ Tol_D)}{n\,Total_{site-group}}$$

and for shade tolerance:

$$\textbf{Community Mean Tolerance Index}_{\mathbf{S}} = \frac{\sum(n\,Species_{site-group} \times\ Tol_S)}{n\,Total_{site-group}}$$

For investigating drought and shade tolerance tradeoffs, we computed two CMTI index values for each site, one each for drought and one for shade tolerance. For investigating demographic trends in tolerance, four CMTI index values were calculated, a drought value for regeneration and for trees, and a shade value for regeneration and for trees. Each of the four values was plotted on a trait space, showing the drought-shade tradeoff across tree and regeneration demographic groups (Figure 2). The index difference between demographic groups indicates the directionality of trend toward either increasing drought tolerance or shade tolerance. Given changing species assortments, movement within the drought-shade sample space is possible in directions other than a single linear tradeoff, and so individual index values are calculated for drought and shade.

Species tolerance values used in developing the index were established in Niinemets and Vallardes (2006), which summarizes species-level drought, shade, and waterlogging tolerances for northern hemisphere trees and shrubs on a scale from 0-5 for each tolerance variable by species. Tree species present in the southern Rocky Mountains plant communities surveyed were extracted from FIA data and checked for error based on known species presence using SEINet county-level records and the USDA PLANTS database (USDA Forest Service 2018 (1); SEINet Portal Network 2019; USDA, NRCS 2019). Individual species-level shade and drought tolerance values used to compute the CMTI were extracted from the appendix provided in Niinemets and Vallardes (2006), with specific values used summarized in Table 2.

Certain species found in the study area were not included in Niinemets and Vallardes (2006), and so required special treatment for assigning tolerance values. Arizona pinyon pine (*Pinus monophylla* Torr. & Frém. var. *fallax* (Little) Silba) was reported at one plot (1 seedling), and was excluded as the species is not known to be present within hundreds of miles of that range and was likely a twoneedle pinyon (*Pinus edulis* Engelm.) (Cole et al. 2008). Two oak species without established tolerance values present at low numbers were also excluded from analysis (*Quercus arizonica* Sarg., 6 trees and 6 seedlings, and *Quercus grisea* Liebm., 1 tree). Corkbark fir (*Abies lasiocarpa* (Hook.) Nutt. var. *arizonica* (Merriam) Lemmon) does not have tolerance values established in Niinemets and Vallarades (2006); however, it intergrades with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) across the study area and has known similar drought tolerance responses (Burns and Honkala 1990; Adams 2005). Given the similarities, corkbark fir was assigned the same tolerance values as subalpine fir, which was included in Niinemets and Vallardes (2006).

Recorded seedlings of *Quercus gambelii* Nutt. (Gambel oak) occurred with a frequency 10× greater than any other species, in accordance with its clonal root-sprouting tendency and growth habits as an understory shrub across this region (Guiterman et al. 2018). Dense growth habits of Gambel oak and the species' high drought tolerance skewed index values at sites with oak-dominant understory towards a higher drought CMTI value for the regeneration class. To address this, plots that contained >30% oak seedlings and <10% oak trees were classified as oak-dominant understory plots (equal to and less than the median species % for each group, respectively) (Supplementary Figure S-2). These plots were analyzed separately by forest type as "[forest type] - oak", when the separation of oak-dominant understory plots led to a significant difference between mean regeneration index values by forest type (two-sample t test, $p < 0.05$).

Mixed-conifer plots dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are referred to as the Douglas-fir forest type, while mixed-conifer dominated by white fir are included in the spruce/fir category, in accordance with FIA forest type assignments. All mixed-conifer plots with oak – dominated regeneration group were classed separately as mixed-conifer – oak regardless of dominant tree type.

Questions Addressed

We posed the following specific questions:

1. Does the shade and/or drought CMTI differ significantly between tree and regeneration groups by forest type (CMTI difference value)? What is the directionality of change between demographic groups, if any, and is it consistent with a drought-shade tradeoff? Where is the CMTI difference maximized?

In mountain systems climatology is correlated strongly with elevation, and also with forest type depending on species habitat suitability, here interpreted through species drought and shade tolerances. The null hypothesis assumes no significant difference in functional tolerance across demographic groups, by forest type. As an alternative, we predict significant

CMTI difference values where conditions affecting regeneration group recruitment and survival are trending away from historic norms towards either increased drought tolerance (at lower forest type ecotones), or increased shade tolerance (driven by increasing density in frequent-fire-adapted forest types lacking recent fire).

2. How are drought and shade index differences across demographic groups (adult trees and regeneration) associated with variation in elevation and recent climate across the study space?

We expect stronger correlations between drought CMTI difference and elevation-climate variables among forest type in lower forest ecotones, where climate is the primary driver of regeneration group recruitment and survival (Law et al. 2019). We expect past disturbance (fire exclusion) to be reflected in the shade CMTI difference. In frequent-fire forest types with an interrupted fire regime, more shade-tolerant species will have greater recruitment success, and the index will have lower correlation with elevation-climate variables. We expect low or no correlation between shade CMTI difference and climate variables at high elevations with longer natural fire regimes. The null expectation is similar CMTI difference and CMTI-climate correlation across forest types regardless of disturbance history or elevation.

3. Can we use the tree-regeneration difference index to identify areas undergoing or likely to undergo vegetation type conversion?

Forest types with substantially different mean functional tolerances across demographic groups should be identifiable by large differences in index values by group. In areas where disturbance or climate is contributing to changing species assemblage, autecology and life history adaptations related to stress tolerance are expected to drive a greater change in index value between tree and regeneration groups. If true, forest types undergoing the greatest divergence from past conditions in terms of disturbance and climate should show the greatest index difference. We expect the greatest difference to be found in ponderosa pine and mixed-conifer forest types where fire exclusion has had a substantial effect. The null expectation would be similar difference across forest types.

Analysis

All data were analyzed in R version 3.5.0 (R Core Team 2018). Data manipulation and graphics creation in R used the packages reshape2, tidyverse, ggthemes, and ggrepel (Slowikowski 2018; Wickham 2007; Wickham 2017). We used forest type (COND-FORTYPCD, as determined by dominant species presence) as the primary grouping factor for analysis, with an added factor where regeneration was dominated by oak (Burrill et al. 2017).

Regeneration Cluster and Mapping

To interpret general community tolerance trends across forest types, we grouped plots using regeneration CMTI values. We performed K means cluster analysis on regeneration CMTI values for drought and shade, by unique plot condition, in R with the cluster and factoextra packages (Euclidean distance, three clusters) (Kassambara and Mundt 2017; Maechler et al. 2018; R Core Team 2018). The NbClust package was used in R to pick the appropriate number of cluster groups based on the greatest agreement across a set of 30 indices (Charrad et al. 2014; R Core Team 2018). Due to patterns of seedling recruitment, tolerance values clustered strongly into three groups, referred to as "drought", "shade", and "low/aspen" by their primary tolerance characteristic (Supplementary Figure S-2). After calculating tolerance values, we excluded the "Cottonwood/ash" forest type from analysis as it had five or fewer unique plot conditions across the forest type-regeneration cluster classifications.

We used QGIS to map the interpolated drought (Figure 1a) and shade (Figure 1b) CMTI difference (regeneration mean minus adult tree mean) (QGIS Development Team 2016). We employed inverse distance weighting on CMTI difference values from plots with regeneration to map gradients of drought tolerance across the landscape. The interpolation was categorized with five even intervals from the mean ± 2 × standard deviation, from low to high tolerance difference.

Along with interpolated CMTI values, we included some plot-based data most contributory to the main conclusions drawn. Plots with oak-dominated regeneration groups were flagged in Figure 1a as locations with high potential to convert to oak shrubfield following severe fire due to the strong persistence of post-fire oak communities (Guiterman et al. 2018). Plots in forest types that are expected to have exceeded their historic fire interval, assuming cessation of frequent fire *ca.* 1900 are noted with an x in Figure 1b. Historic fire interval (HFI) and fire history traits by forest type were selected from fire models developed through the Fire Effect Information System (FEIS) (Fryer and Luensmann 2012).

Using the regeneration cluster to show broad trends, we found the mean elevation by forest type for each regeneration cluster (drought, shade, and low/aspen) (Figure 4). We tested for significance using an ANOVA for the interaction of elevation and forest type, and Tukey's Highly Significant Difference to test for significant difference ($p < 0.05$) in mean elevation of plots sorted into each regeneration cluster by forest type, and across the mixed-conifer groups with and without oak-dominant understory that might lead to vegetation type conversion following fire.

CMTI Difference by Forest Type and Relationship with Elevation

By calculating the tolerance index difference: $\text{CMTI}_{\text{regen}} - \text{CMTI}_{\text{trees}}$ for drought and shade, we found the vector of change in tolerances across demographic groups, and generalized to the mean difference by forest type (Figure 2). The CMTI difference indicates directional trend in the community mean of functional traits across demographic groups: whether towards increasing drought tolerance as in response to increased drought stress, or towards increasing shade tolerance as in response to stand-level disturbance factors.

Comparing mean tolerance for mature trees to regeneration allows for a measure of ecosystem change when a long time series of demography data is not available. However, inference is necessarily limited in that seedling survival to maturity is low and regeneration is highly variable across space (Gray et al. 2005; Bell et al. 2014). As a result, the regeneration index value at any given point may not reflect the future makeup of the forest exactly. Instead, it tracks the potential vector of ecosystem change under current conditions. Integrating relative tolerance at the site level is an attempt to reduce some of this uncertainty, as it is less reliant on the survival of any individual seedling to maturity.

Mean drought and shade CMTI difference values by forest type were classed by historic fire exceedance using FEIS models (Fryer and Luensmann 2012) and tested for significant difference from 0 using one-sample t-tests ($p < 0.05$) and tested for normality using the Shapiro-Wilk test (Figure 3). Mean CMTI difference by regeneration cluster was tested for significance by ANOVA between CMTI difference values and selected elevation and climate variables (Supplementary Figure S-3). A significant difference indicates forest types where regeneration groups had significant increases or decreases in community tolerance, and thus where stressors affecting regeneration success across species are changing.

Climate and Elevation Response

We calculated the correlation between plot drought and shade CMTI difference values and climate variables extracted from PRISM annual values, using mean values for the period 1998-2017, which encompasses recent regeneration establishment (PRISM Climate Group 2016). Variables for analysis were maximum temperature (˚C), total annual precipitation (mm), and maximum vapor pressure deficit (VPD, hPa). These specific drought-related variables were selected to test the degree to which climate is associated with CMTI difference across the sample space.

We used the R package *prism* to get points and values for interpolated data, extracted study area and intersected with publicly-available FIA plot locations (Hart and Bell 2015). The grid cell size of PRISM data is 2.5 arcmin, approximately 4 km on a side, and greater than the 1.6 km maximum uncertainty of the FIA plot locations so our climate means would slightly underestimate fine-scale climate variation due to topographic or other influences.

We used elevation as a classifying variable, as analysis suggests it is relatively accurate even with imprecise "fuzzed" locations (Prisley et al. 2009). To find the elevation at which CMTI difference was greatest, we calculated the inflection point of peak difference in the elevation- CMTI difference relationship for drought and shade with a loess smoothing function (span = 0.75, degree = 2) in R. We found the elevation at which the first derivative of the fitted loess function elevation equaled 0, for the relationship between CMTI difference and plot elevation (i.e., $\delta \frac{i}{\delta} e = 0$ (i = index difference, e = elevation, which was found to be 2500 m)). The elevation where difference was greatest was used as a break point in finding CMTI difference-climate correlations. We tested correlations between PRISM climate variables at plot location, and index difference values grouped below or above 2500 m (Table 3). With this analysis we found the elevation at which community functional tolerance was most different across demographic groups.

Results

By applying the Community Mean Tolerance Index (CMTI) difference, we found strong demographic trends in functional tolerances within and across forest types. We found increases in drought tolerance at lower elevations, and increases in shade tolerance or aspen dominance at higher elevations and more mesic sites across the study area (Figure 1). Depending on species assemblages across tree and regeneration groups, CMTI difference did not precisely track a linear drought-shade tradeoff but moved across the sampling space in ways dependent on species life history traits and past stand history (Figure 2). The greatest difference across demographic groups occurred within mid-elevation forest types, including ponderosa pine and mixed-conifer (Figure 3). The difference findings support our hypotheses relating climate-driven drought tolerance to species composition changes at lower elevations and lower forest ecotones, and disturbance changes driven by altered fire regime contributing to increased shade tolerance at mid-elevation frequent fire forest types. No significant difference in index values by forest type was found based on land ownership, between plots on public and private/tribal lands subject to location manipulation ("swapping"), so all plots were included in the analysis.

CMTI Trends by and across Forest Type

We calculated the CMTI difference for drought and shade tolerance for each major forest type and regeneration cluster grouping of plots. We found significant differences in CMTI trends across multiple forest types, particularly among mid-elevation mixed-conifer and related forest types (Figure 3). The vector of difference (change in the [shade, drought] index values across demographic groups) varied in degree and direction by forest type (Figure 2). The longest vectors (greatest difference) occurred when the regeneration group was substantially different than the tree group in mean tolerance type, generally in groups where species life-history traits influence regeneration patterns. For example, the "Douglas-fir – oak" forest type with a clonal sprouting oak-dominated regeneration group resulted in a more drought tolerant community mean than the mixed-conifer tree group, creating a longer vector of index difference.

In general, low- to mid-elevation mixed-conifer plots had greater drought tolerance in the regeneration group, while higher elevation forest types had increased shade tolerance. For drought CMTI difference, we found significant increases in drought tolerance in the regeneration group for woodland hardwoods ($p = 0.003$), ponderosa pine and mixed-conifer – oak (both $p < 0.001$). We found significant decreases in drought tolerance in Douglas-fir, spruce/fir, and lodgepole pine (all $p < 0.001$).

Shade CMTI difference tended to mirror these findings in accordance with the expected drought-shade tradeoff across mid-elevation ponderosa pine and mixed-conifer forests (Figure 3). Shade tolerance increased in the regeneration group of pinyon/juniper – oak and ponderosa pine (both $p < 0.001$). Shade tolerance decreased in pinyon/juniper, mixed-conifer – oak, and Douglas-fir (all $p < 0.001$). In lower elevation pinyon-juniper forest types, shade tolerance changed significantly, but drought tolerance did not, in part because as species in this forest type already had drought tolerance near the upper margin of the 0-5 index scale (Table 2).

Trends between elevation and regeneration group mean functional tolerance were found across and within forest types. Drought cluster woodland hardwood plots were significantly lower in elevation than shade or low/aspen cluster Douglas-fir ($p < 0.001$), and lower than low/aspen clustered ponderosa pine ($p = 0.010$). Drought cluster mixed-conifer – oak plots were significantly lower than shade cluster Douglas-fir ($p = 0.034$) and low/aspen cluster Douglas-fir ($p < 0.001$). In ponderosa pine and Douglas-fir forest types, drought cluster regeneration groups were found at significantly lower mean elevations than the low/aspen cluster (both $p = 0.010$). In the spruce/fir forest type, the low/aspen cluster had a significantly lower mean elevation than the shade cluster ($p < 0.001$).

Significant directional shifts occurred across demographic groups, between trees and regeneration, in two forest types in the same direction for both tolerance indices. Ponderosa pine plots had higher index values for both drought ($p < 0.001$) and shade ($p < 0.001$) tolerance, reflecting concurrent effects of climate and fire exclusion on the regeneration group species assemblage (Figure 3). Douglas-fir plots had significantly lower drought ($p < 0.001$) and shade ($p < 0.001$) tolerance values, as regeneration index values moved towards the aspen species tolerance value (Figure 2; Figure 3). These cases show directional change, but not in accordance with the expected shade-drought tolerance tradeoff as increasing aspen presence in the regeneration group is driving the mean index response. In this case index trends indicate a mix of species in the regeneration group with a substantially different mean tolerance from the mature trees that make up the affected forest types.

CMTI Elevation and Climate Associations

We found demographic trends in drought and shade CMTI difference by elevation by forest type (Figure 4) and across all plots (Figure 5). Of the grouped plots with similar trends in regeneration tolerance associations (regeneration group cluster), drought cluster plots had the lowest mean elevation, followed by the low/aspen cluster, and the shade cluster had the highest mean elevation ($p < 0.001$) (Table 1). All climate variables were significantly different across regeneration clusters ($p < 0.001$), except between drought and the mean climate and elevation values of plots with no regeneration. Plots with no regeneration had elevation and climate variables statistically identical to drought cluster plots. The index difference for each cluster supported the hypothesis that across forest types, lower and more arid sites tended to move towards drought tolerance while higher and wetter sites had increased shade tolerance (Figure 4, Supplementary Figure S-3).

We found significant differences in mean elevation of plots that fell into different regeneration group tolerance clusters in and across mid-elevation forest types. Across forest types, drought-clustered plots occurred at lower elevations, and shade- and low/aspen-clustered plots tended higher (Figure 4). Lower elevation plots tended to have either no regeneration, or else drought-tolerant regeneration communities. Across forest types, plots with regeneration in the drought tolerance cluster were at a significantly lower elevation than the shade or low/aspen cluster ($p < 0.001$), but not different from plots with no regeneration. Clustering on regeneration CMTI values shows an association between lower elevation, a hotter and drier climate, and a tendency towards functional drought tolerance in the regeneration community.

Across all forest types, the drought index difference was greatest at 2500 m in elevation, in the mixed-conifer zone very close to the mean elevation for mixed-conifer – oak plots (mean 2550 m, s.d. 217 m) (Figure 5). Below 2500 m, drought and shade index difference correlations were positive with elevation and precipitation, and negative with maximum temperature and maximum VPD. This means that with increasing elevation and cooler, wetter climate, index difference increased. Low change at lower pinyon/juniper plots and high change at mixed-conifer – oak plots drive the overall trend (Figure 5). Below 2500 m, in predominantly ponderosa pine, woodland hardwoods, and pinyon/juniper forest types, we found strong correlations between climate and index difference across all plots, and especially for drought tolerance, suggesting that climate is driving trends in regeneration group mean tolerance.

The shade CMTI difference across forest types followed a similar trend to the drought difference (Figure 5). Greatest shade tolerance difference among the regeneration group peaked lower, at 2300 m, in the elevation range of the ponderosa pine forest type (mean 2451 m, s.d. 208 m). Peak shade CMTI difference in the ponderosa pine forest type supports our hypothesis linking disruptions to the fire regime to greater shade tolerance across demographic groups, resulting in an increasingly dense and shade-tolerant regeneration community.

Above 2500 m, in predominantly Douglas-fir and spruce-fir forest types, drought CMTI difference was correlated negatively with elevation and precipitation, and positively with maximum temperature and maximum VPD (Table 3). Shade CMTI difference had a slight positive correlation with elevation but correlation with climate variables was low above or below the peak index difference at 2300 m (Table 3). Overall, the CMTI difference correlation with elevation and climate variables above and below the peak index difference for drought and shade tolerance supports a stronger association between drought tolerance and climate variables, especially at higher elevations.

Vegetation Type Conversion to Oak

Examining the potential for mixed-conifer forest transitioning to oak shrubfield following major fire, we found strong associations between greater drought CMTI difference and oak dominated regeneration groups. Drought index difference was greatest for mixed-conifer plots with a substantial oak component to the regeneration group (the "mixed-conifer – oak" forest type) (Figure 1a; Figure 3). Plots with oak-dominated regeneration occurred at low to moderate elevations in frequent-fire adapted forest types including mixed-confer and ponderosa pine (Figure 4). Douglas-fir-dominant mixed-conifer lacking an oak-dominant understory occurred at relatively higher elevations (Table 1). Out of all mixed-conifer or Douglas-fir plots, 48.6% were categorized as plots with oak-dominated regeneration communities.

Discussion

In many areas of the southern Rocky Mountains, forests are undergoing rapid change driven by interactions of disturbance history with episodic drought and climate trends. The specific drivers and trajectories of change vary by forest type and topographic setting. Changes affecting demographic processes including recruitment and mortality contribute to the species and age composition of forest stands and their likelihood of persistence under climate change. The environmental requirements for survival and persistence can be different across age groups for individual species (Law et al. 2019). Conditions supporting recruitment tend to be more limited than that supporting species persistence. Analysis of changes in tolerance at the community level, rather than species, reduces some of the species-level variability inherent in tree regenerative processes and turns the focus onto drivers of change with broader ecosystem effects: drought, climate, and disturbance.

Changes to forest communities are revealed through a functional trait approach that allows us to interpret ecosystem effects on species assemblages broadly (McGill et al. 2006; Weiher et al. 2011; Díaz et al. 2016). We developed the Community Mean Tolerance Index (CMTI) to capture trends in community functional traits contributing to stress tolerance within and among forest types. When community mean tolerance is substantially different among mature trees relative to regeneration, this suggests that recent conditions and stressors have changed since the mature trees became established, favoring the regeneration and recruitment of a community with different stress tolerances.

A larger index difference across demographic groups indicates a greater ecological response to change and more potential for transition to a different forest type following shifting community functional responses. These areas appear to have the greatest potential for type conversion, should current pressures on regeneration and survival continue. It is important to note that the regeneration group indicates tolerances leading to recent establishment success. Recent success may not necessarily apply to future climate and disturbance drivers of forest composition. However, we can reasonably expect drought stress and the legacy of disturbance to continue to drive forest change in the southern Rocky Mountains Rockies (Abatzoglou and Williams 2016; Kitzberger et al. 2017).

We found the greatest differences in community shade and drought tolerance in mid-elevation ponderosa pine and mixed-conifer forest types. The primary factors identified as contributing to the CMTI index findings are summarized in Figure 1: the life history traits of Gambel oak in the southern Rocky Mountains, and fire exclusion. The greatest differences in drought and shade tolerance across demographic groups are found in forest types where the fire regime has been most disrupted from historic conditions by fire exclusion, creating a substantial fire deficit (Falk et al. 2011; Odion et al. 2014; Parks et al. 2015). Plots flagged in both Figure 1a (dense oak understory) and Figure 1b (HFI exceeded), with a significant CMTI difference are especially at risk of type conversion to oak shrubfield following a severe fire. In these areas, the history of climate and disturbance drivers has primed the forest for change.

Similar trends of increasing forest density and community have been found in other areas across the western U.S using species and functional trait approaches. In California forests, stand density was found to increase over the 20th Century, with most new stems being small, and community species dominance shifted from pine to oak as forest density increased, associated with climatic water deficit (McIntyre et al. 2015). We observed similar stand structure changes at dendrochronologically-sampled sites in the southern Rocky Mountains within the study area (Supplementary Figure S-1). In lower elevation, lower-precipitation mixed-conifer stands similarly shifted towards oak-dominated regeneration groups. More mesic areas of mixed-conifer experienced other changes, moving towards a more aspen-dominated system.

Water availability is tied to forest productivity, and O'Connor et al. (2017) associated forest types and site productivity with species assemblage changes across a montane ecosystem under fire exclusion. They found that the greatest divergence from historic forest species composition occurred in intermediate productivity mixed-conifer systems, over the period of fire exclusion. Less difference in species composition was found at very low or very high productivity sites, along an arid-mesic gradient. We found less change in functional tolerance in low elevation pinyon-juniper woodland, hot and dry areas at the low ecotone for trees. The CMTI was better at detecting divergence from a functionally unstable middle elevation mixed-conifer zone, as in O'Connor et al. (2017). The mixed-conifer area is a transition zone between lower elevation drought stress and mid- and upper-forest areas where more mesic conditions and stand-level disturbance history has led to greater stand density with fire exclusion, and the increasing dominance of shade-tolerant species. High CMTI difference at mid-elevations suggests a high velocity of ecological change in species functional tolerance across demographic groups, where climate and disturbance interacts resulting in a regeneration community increasingly different from the surrounding trees.

Coupled effects of drought and fire exclusion can reinforce community structure and composition changes with substantial detriment to forest health and resilience (Enright et al. 2015; Millar and Stephenson 2015). The magnitude and direction of change depends on the capacity of the forest system to resist change or else behave resiliently and reorganize into a new state (Falk 2017). Forest types and areas with low CMTI difference across demographic groups may be relatively resistant to broad-scale drivers of functional trait shifts, though species composition might still change among those with similar stress tolerances. Ecosystem functioning might not be impaired following low-CMTI difference species shifts, but such species-level changes might still be a concern when rare or endemic species are at risk.

Species-Specific Traits with an Outsized Influence on Community Means

Ponderosa pine and mixed-conifer forests that have been subject to fire exclusion are more likely to see fire return in a larger, more severe events likely to kill mature trees (Falk et al. 2011; Margolis et al. 2011; Litschert et al. 2012; Williams 2013; O'Connor et al. 2014). Root sprouting oaks are likely to come back before conifers following severe fire (Pausas and Keely 2014; Hood et al. 2018). Where there is a substantial oak understory (or with oak-dominant regeneration groups as analyzed with the CMTI), forest stands are more likely to recover as oak shrubfield following severe fire, because resprouting oaks would be favored over conifers which would have to recolonize the site through dispersal (Guiterman et al. 2018; Barton and Poulos 2018).

The life-history traits of Gambel oak and FIA sampling strategy had a substantial influence on the CMTI, requiring special attention in interpretation. The effect on the index was driven by the tendency in this area for Gambel oaks with arboreal growth form to root sprout following coppicing or fire in multi-stem forms, often forming a persistent understory shrub layer in these areas (Guiterman et al. 2018). FIA protocols count hardwood stems least 30.48 cm (12 in) tall, and for multi-stem woodland species like Gambel oak count individuals by origin point (genet) (USDA Forest Service 2018 (2)). In Arizona and New Mexico, 2-7 stems per genet are typical for Gambel oak, while further north and northwest 100-10,000 stems per clonal individual are reported (Barton and Poulos 2018). We ran a sensitivity analysis and tested for an overcount of Gambel oak regeneration by dividing the number of seedlings counted by four (based on expected stems per genet) and running the CMTI calculations. We found no difference in significance and results by forest type. Even if Gambel oak seedlings were substantially overcounted, their sum effect on community composition is the same and so the potential for vegetation type conversion to shrubfield following fire.

However, FIA does the seedling count without considering whether Gambel oak is predominantly in a tree or understory shrub form at a sampling plot. As a result, the CMTI for regeneration moves significantly towards drought at plots where Gambel oak is dominant in the understory in any form regardless of its potential to attain tree status, due to the large number of stems.

The influence of oak regeneration on the CMTI highlights the need to understand species autecology and life history adaptations when applying and interpreting community mean indices broadly. Knowing the habits of Gambel oak in these systems also allows for identification of plots with high potential to transition to oak shrubfield following severe fire, assuming that resprouting oak will outcompete conifer dispersal into severe burn areas (Guiterman et al. 2018). The CMTI is useful to find areas primed for vegetation type conversion where demographic data are available.

Species Assemblages Become Less Mixed

Regeneration groups were more homogeneous in species assemblages than mature tree stands. In aggregate, drought tolerant plots became more drought tolerant, shade tolerant plots became more shade tolerant, and low/aspen plots moved towards lower drought and shade tolerance (Figure 2). Regeneration CMTI values tended to be strongly associated with drought, shade, or low/aspen values, moving away from the middle of the drought/shade tolerance space where plots featuring more heterogeneous species assortments are found. Notably, by forest type, lower elevations tended to have a more drought tolerant regeneration group, and higher elevations a more shade tolerant or aspen-dominated regeneration group (Figure 4). The same trends are evident across forest types, when considering all plots sampled (Figure 5). Within the framework of the state factor-interactive control model (Amundson and Jenny 1997), this demonstrates greater climate pressures controlling regeneration processes at lower elevations, while at higher elevations interactive stand effects are of greater importance.

CMTI regeneration clusters of mean tolerance (Supplementary Figure S-3) aligned with the directional movement of index difference along a drought-shade tolerance axis in many but not all cases (Figure 3; Supplementary Figure S-2). Tree CMTI values tend to fill in the tolerance tradeoff sample space more broadly, indicating more mixed species assortments than among regeneration, particularly in mixed-conifer forest plots. This follows the divergence in species composition in mixed-conifer along productivity gradients seen in O'Connor et al. (2017).

Divergence in the regeneration class was most obvious in the mixed-conifer forest type. Mixed-conifer plots with substantial aspen regeneration presence were found at intermediate to higher elevations for the forest type. Plots with more Gambel oak regeneration were found at lower elevations. We hypothesized that increased drought tolerance in the regeneration class is a predictor of potential vegetation type conversion, consistent with the climate change-driven tendency to hotter and drier conditions. Across forest types, plots showing a strong shift and tendency towards drought tolerance in the regeneration class occur at lower elevations and lower forest ecotones, which is consistent with pressures from recent regional drought and likely to continue to affect forest dynamics into the future.

Tree life-history traits, particularly masting (mass reproduction) and shorter dispersal distance of large-seeded conifer species, may contribute to this trend of regeneration CMTI values moving away from the middle (Nathan and Muller-Landau 2000; Mooney et al. 2011). Masting contributes to large classes of seedlings of one species within the dispersal distance of the masting trees, resulting a more uniform species assembly in the regeneration class, and a CMTI value closer to the tolerance value of the masting species, if sampling occurs within a few years of a masting event. High seedling sprouting and mortality rates lead to higher turnover among regeneration, supporting persistence in frequent fire systems and the likelihood that seedlings sprout in suitable microsites for persistence (Pausas and Keely 2014; Kroiss and HilleRisLambers 2015). Life history traits contributing to the regeneration community composition was one factor, along with plot size, skewing the regeneration index values towards the extremes, as fewer species contributed to the regeneration sampled compared to the trees. The CMTI regeneration-tree difference skews the index towards specific species with tolerance traits that have been especially successful at reproduction in recent years. With a sufficiently large sample size of plots by forest type, we are then able to detect broad trends in tolerance across ecosystems.

We found the CMTI most sensitive to change in plant functional types in mid-elevation mixed-conifer forest types. These areas were more likely to show a large degree of change towards one extreme or the other. Lower elevation plots in forest types near the lower extent of habitat suitable for trees tended to have a high drought CMTI value and little space for that value to move in response to influencing factors. A similar effect was noted by Bertrand et al. (2011) in which relatively less change was found in climate-species response in lowland species, and more in upper-elevation species. The regeneration cluster trend in response to elevation and all climate variables was consistent with the hypothesis suggesting that at lower ecotones climate is the dominant driving factor in demographic functional tolerance change. In mid-elevation ponderosa pine and mixed-conifer, changes to the disturbance regime from fire exclusion is the dominant factor driving changing regeneration mean functional tolerance.

Regional ecological effects of climate change are complex and often difficult to disentangle from other drivers (Millar and Stephenson 2015). Projected warming trends with increasing temperature and VPD, and more variable precipitation, superimposed onto landscape scale variation will likely exert continued and increasing climate stress on forests of the region, with increased risk of widespread forest mortality (Allen et al. 2015; Choat et al. 2018). Trends in index correlation with climate variables across elevation indicate stronger climate controls on mean tolerance at lower elevations. Positive correlation between CMTI difference and climate variables at low elevations track the increasing precipitation and productivity with elevation, up to middle elevations where the greatest effects of fire exclusion are found. At higher elevations, a greater influence of stand-level drivers and less influence of top-down controls regenerative processes as shown through mean tolerance.

Currently mesic mixed-conifer could aridify, subjecting a greater area of the forest to drought pressures and leading to greater success of drought -tolerant species at higher elevations and reducing the relative effect of stand-level disturbance. Tracking community demographic shifts through mean functional tolerance lets us interpret the community-scale effects of climate and disturbance stressors. Using the CMTI we can identify areas and forest types actively undergoing change, an important step in encouraging forest resilience and understanding community response to disturbance and climate shifts.

Acknowledgements

Thanks to Steven Leavitt, Valerie Trouet, David Moore, Nathan McDowell for comments and critiques, and Margaret Evans for help with FIA matters.

References Cited

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, *113*(42), 11770-11775.

Adams, H. D. (2005). Tree growth response to drought and temperature along an elevation gradient on a mountain landscape. *Journal of Biogeography*, *32,* 1629-1640.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, *98*(3), 604-613.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 1-55.

Allen, R. B., & Peet, R. K. (1990). Gradient analysis of forests of the Sangre de Cristo Range, Colorado. *Canadian Journal of Botany*, *68*(1), 193-201.

Amundson, R., & Jenny, H. (1997). On a state factor model of ecosystems. *BioScience, 47*(8), 536-543.

Anderegg, L.D., & HilleRisLambers, J. (2016). Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Global Change Biology*, *22*(3), 1029-1045.

Arx, G., Graf Pannatier, E., Thimonier, A., & Rebetez, M. (2013). Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *Journal of Ecology*, *101*(5), 1201-1213.

Bailey, R. G., Avers, P. E., & King, T. (1994). Ecoregions and subregions of the United States (map; scale 1: 7,500,000) (supplementary table of map unit descriptions compiled and edited by McNab WH, Bailey RG). United States Department of Agriculture Forest Service, Washington, DC.

Barton, A. M. (1993). Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. *Ecological Monographs, 63*(4), 367-397.

Barton, A. M., & Poulos, H. M. (2018). Pine vs. oaks revisited: Conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. *Forest Ecology and Management*, *414*(1), 28-40.

Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, *23*(2), 168-180.

Bentz, B. J., Régnière, J., Fettig, C. J., Hansen, E. M., Hayes, J. L., Hicke, J. A., Kelsey, R. G., Negrón, J. F., & Seybold, S. J. (2010). Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience, 60*(8), 602-613.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., Pierrat, J. C., & Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517.

Breshears, D. D., Huxman, T. E., Adams, H. D., Zou, C. B., & Davison, J. E. (2008). Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences*, *105*(33), 11591-11592.

Brusca, R. C., Wiens, J. F., Meyer, W. M., Eble, J., Franklin, K., Overpeck, J. T., & Moore, W. (2013). Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution*, *3*(10), 3307-3319.

Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America, Vol. 2,* p. 119. Washington, DC: United States Department of Agriculture.

Burrill, E. A., Wilson, A. M., Turner, J. A., Pugh, S. A., Menlove, J., Christiansen, G., Conkling, B. L., & David, W. (2017). *The Forest Inventory and Analysis Database: Database description and user guide version 7.2 for Phase 2.* U.S. Department of Agriculture, Forest Service. 946 p. [Online]. [Available at: http://www.fia.fs.fed.us/library/database-documentation/].

Cansler, C. A., & McKenzie, D. (2014). Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. *Ecological Applications*, *24*(5), 1037-1056.

Charrad, M., Ghazzali, N., Boiteau, V., & Niknafs, A. (2014). NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set. *Journal of Statistical Software, 61*(6), 1-36. http://www.jstatsoft.org/v61/i06/.

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531.

Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., D'amato, A. W., Davis, F. W., Hersh, M. H., Ibanez, I., &Jackson, S. T. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, *22*(7), 2329-2352.

Cole, K. L., Fisher, J., Arundel, S. T., Cannella, J., & Swift, S. (2008). Geographical and climatic limits of needle types of one-and two-needled pinyon pines. *Journal of Biogeography*, *35*(2), 257-269.

Crimmins, T. M., Crimmins, M. A., & David Bertelsen, C. (2009). Flowering range changes across an elevation gradient in response to warming summer temperatures. *Global Change Biology*, *15*(5), 1141-1152.

Díaz, S., Purvis, A., Cornelissen, J. H., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, *3*(9), 2958-2975.

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., & Garnier, E., (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167.

Enright, N. J., Fontaine, J. B., Bowman, D. M., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, *13*(5), 265-272.

Evans, M. E., Falk, D. A., Arizpe, A., Swetnam, T. L., Babst, F., & Holsinger, K. E. (2017). Fusing tree-ring and forest inventory data to infer influences on tree growth. *Ecosphere, 8*(7), p.e01889.

Evans, M. E., Merow, C., Record, S., McMahon, S. M., & Enquist, B. J. (2016). Towards process-based range modeling of many species. *Trends in Ecology & Evolution*, *31*(11), 860-871.

Falk, D. A., Heyerdahl, E. K., Brown, P. M., Farris, C., Fulé, P. Z., McKenzie, D., Swetnam, T. W., Taylor, A. H., & Van Horne, M. L. (2011). Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment*, *9*(8), 446-454.

Falk, D. A. (2017). Restoration ecology, resilience, and the axes of change. *Annals of the Missouri Botanical Garden*, *102*(2), 201-216.

Fryer, J. L., & Luensmann, P. S. (2012). Fire regimes of the conterminous United States In: *Fire Effects Information System,* [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us/database/feis/fire_regime_table/fire_regime_table.html#3 [April 17, 2019].

Fulé, P. Z., Covington, W. W., Moore, M. M., Heinlein, T. A., & Waltz, A. E. (2002). Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography*, *29*(1), 31-47.

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., & Neill, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*(9), 2630-2637.

Garnier, E., & Navas, M. L. (2012). A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development*, *32*(2), 365-399.

Gitlin, A. R., Sthultz, C. M., Bowker, M. A., Stumpf, S., Paxton, K. L., Kennedy, K., Muñoz, A., Bailey, J. K., & Whitham, T. G. (2006). Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology*, *20*(5), 1477-1486.

Gleason, K. E., Bradford, J. B., Bottero, A., D'Amato, A. W., Fraver, S., Palik, B. J., Battaglia, M. A., Iverson, L., Kenefic, L., & Kern, C. C. (2017). Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere*, *8*(7), e01849.

Gray, A. N., Zald, H. S., Kern, R. A., & North, M. (2005). Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. *Forest Science*, *51*(3), 198-210.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, *52,* 107–145.

Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, *9*(1), 1315.

Guiterman, C. H., Margolis, E. Q., Allen, C. D., Falk, D. A., & Swetnam, T. W. (2018). Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. *Ecosystems*, *21*(5), 943-959.

Hallik, L., Niinemets, Ü., & Wright, I. J. (2009). Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *New Phytologist*, *184(*1), 257-274.

Hart, E. M., & Kendon Bell, K. (2015). prism: Download data from the Oregon prism project. R package version 0.0.6 http://github.com/ropensci/prism DOI:10.5281/zenodo.33663

Hessburg, P. F., Spies, T. A., Perry, D. A., Skinner, C., Taylor, A.H., Brown, P. M., Stephens, S. L., Larson, A. J., Churchill, D.J ., Povak, N. A., & Singleton, P. H. (2016). Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *Forest Ecology and Management, 366*, 221-250.

Heyerdahl, E. K., Brubaker, L. B., & Agee, J. K. (2001). Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. *Ecology*, *82*(3), 660-678.

Heyerdahl, E. K., Loehman R. A., & Falk, D. A. (2019). A multi-century history of fire regimes along a transect of mixed-conifer forests in central Oregon, USA. *Canadian Journal of Forest Research, 49,* 76–86.

Hood, S. M., Varner, J. M., van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*, *13*(11), 113004.

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, *106*(Supplement 2), 19685-19692.

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153-160.

Kassambara, A., & Mundt, F. (2017). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.5. https://CRAN.R-project.org/package=factoextra

Kitzberger, T., Falk, D. A., Westerling, A. L., & Swetnam, T. W. (2017). Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. *PLoS One, 12*(12), e0188486.

Koenig, W. D., & Knops, J. M. (2000). Patterns of annual seed production by northern hemisphere trees: a global perspective. *The American Naturalist*, *155*(1), 59-69.

Kolb, T. E., Grady, K. C., McEttrick, M. P., & Herrero, A. (2016). Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. *Forest Science*, *62*(6), 641-651.

Kroiss, S. J., & HilleRisLambers, J. (2015). Recruitment limitation of long-lived conifers: implications for climate change responses. *Ecology*, *96*(5), 1286-1297.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J., & Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, *15*(8), 831-840.

Law, D. J., Adams, H. D., Breshears, D. D., Cobb, N. S., Bradford, J. B., Zou, C. B., Field, J. P., Gardea, A. A., Williams, A. P., & Huxman, T. E. (2019). Bioclimatic envelopes for individual demographic events driven by extremes: Plant mortality from drought and warming. *International Journal of Plant Sciences*, *180*(1), 53-62.

Liang, L., Hawbaker, T. J., Zhu, Z., Li, X., & Gong, P. (2016). Forest disturbance interactions and successional pathways in the Southern Rocky Mountains. *Forest Ecology and Management, 375,* 35-45.

Litschert, S. E., Brown, T. C., & Theobald, D. M. (2012). Historic and future extent of wildfires in the Southern Rockies Ecoregion, USA. *Forest Ecology and Management, 269*, 124-133.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2018). cluster: Cluster Analysis Basics and Extensions. R package version 2.0.7-1.

Margolis, E. Q., Swetnam, T. W., & Allen, C. D. (2007). A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research*, *37*(11), 2227-2241.

Margolis, E. Q., Swetnam, T. W., & Allen, C. D. (2011). Historical stand-replacing fire in upper montane forests of the Madrean Sky Islands and Mogollon Plateau, southwestern USA. *Fire Ecology*, *7*(3), 88-107.

Martínez-Vilalta, J., & Lloret, F. (2016). Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. *Global and Planetary Change*, *144*, 94-108.

Mast, J. N., Veblen, T. T., & Linhart, Y. B. (1998). Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *Journal of Biogeography*, *25*(4), 743-755.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178-185.

McIntyre, P. J., Thorne, J. H., Dolanc, C. R., Flint, A. L., Flint, L. E., Kelly, M., & Ackerly, D. D. (2015). Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences*, *112*(5), 1458-1463.

Millar, C. I., & Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, *349*(6250), 823-826.

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, *96*(5), 884-893.

Mooney, K. A., Linhart, Y. B., & Snyder, M. A. (2011). Masting in ponderosa pine: comparisons of pollen and seed over space and time. *Oecologia*, *165*(3), 651-661.

Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography*, *32*(2), 299-309.

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278-285.

Nigh, G. D., & Everett, R. (2007). Years-to-stump-height and years-to-breast-height models for interior Douglas-fir, western larch, and ponderosa pine. *Northwest Science*, *81*(4), 293-305.

Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs*, *76*(4), 521-547.

Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, *260*(10), 1623-1639.

Normand, S., Zimmermann, N. E., Schurr, F. M., & Lischke, H. (2014). Demography as the basis for understanding and predicting range dynamics. *Ecography*, *37*(12), 1149-1154.

O'Connor, C. D., Falk, D. A., Lynch, A. M., & Swetnam, T. W. (2014). Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleño Mountains, Arizona, USA. *Forest Ecology and Management*, *329,* 264–78.

O'Connor, C. D., Falk, D. A., Lynch, A. M., Swetnam, T. W., & Wilcox, C. P. (2017). Disturbance and productivity interactions mediate stability of forest composition and structure. *Ecological Applications*, *27*(3), 900-915.

Odion, D. C., Hanson, C. T., Arsenault, A., Baker, W. L., DellaSala, D. A., Hutto, R. L., Klenner, W., Moritz, M. A., Sherriff, R. L., Veblen, T. T., & Williams, M. A. (2014). Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PloS One*, *9*(2), p.e87852.

Parks, S. A., Miller, C., Parisien, M. A., Holsinger, L. M., Dobrowski, S. Z., & Abatzoglou, J. (2015). Wildland fire deficit and surplus in the western United States, 1984–2012. *Ecosphere*, *6*(12), 1-13.

Pausas, J. G., & Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, *204*(1), 55-65.

Prisley, S. P., Wang, H. J., Radtke, P. J., & Coulston, J. (2009). Combining FIA plot data with topographic variables: Are precise locations needed?. In: McWilliams, Will; Moisen, Gretchen; Czaplewski, Ray, comps. Forest Inventory and Analysis (FIA) Symposium 2008; October 21-23, 2008; Park City, UT. Proc. RMRS-P-56CD. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10 p. (Vol. 56).

PRISM Climate Group (2016). Oregon State University, http://prism.oregonstate.edu, created 3-24-2016. [Accessed July 3, 2018]

QGIS Development Team (2016). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Radeloff, V. C., Hammer, R. B., Stewart, S. I., Fried, J. S., Holcomb, S. S., & McKeefry, J. F. (2005). The wildland–urban interface in the United States. *Ecological Applications*, *15*(3), 799-805.

Reichstein, M., Bahn, M., Mahecha, M. D., Kattge, J., & Baldocchi, D. D. (2014). Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences*, *111*(38), 13697-13702.

Reyer, C. P., Brouwers, N., Rammig, A., Brook, B. W., Epila, J., Grant, R. F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., & Medlyn, B. (2015). Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology, 103*(1), 5-15.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ricotta, C. (2005). Through the jungle of biological diversity. *Acta biotheoretica*, *53*(1), 29-38.

Savage, M., & Mast, J. N. (2005). How resilient are southwestern ponderosa pine forests after crown fires?. *Canadian Journal of Forest Research*, *35*(4), 967-977.

Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *AIBS Bulletin*, *54*(7), 661-676.

SEINet Portal Network (2019). http//:swbiodiversity.org/seinet/index.php. Accessed on January 09, 2019.

Slowikowski, K. (2018). ggrepel: Automatically Position Non-Overlapping Text Labels with 'ggplot2'. R package version 0.8.0. https://CRAN.R-project.org/package=ggrepel

Smith, T., & Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, *83* (1989), 49-69

Thuiller, W., Slingsby, J. A., Privett, S. D., & Cowling, R. M. (2007). Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *PLoS One*, *2*(9), e938.

USDA Forest Service (2018) (1). *Forest Inventory and Analysis Database 1.7.2.00,* St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station. [Available at: http://apps.fs.fed.us/fiadb-downloads/datamart.html]

USDA Forest Service (2018) (2). *FOREST INVENTORY AND ANALYSIS NATIONAL CORE FIELD GUIDE VOLUME I: FIELD DATA COLLECTION PROCEDURES FOR PHASE 2 PLOTS Version 8.0.* U.S. Department of

Agriculture, Forest Service. 451 p. [Online]. [Available at: https://www.fia.fs.fed.us/library/field-guides-methods-proc/index.php].

USDA, NRCS, (2019). The PLANTS Database (http://plants.usda.gov, 9 January 2019). National Plant Data Team, Greensboro, NC 27401-4901 USA.

Vandewalle, M., De Bello, F., Berg, M. P., Bolger, T., Doledec, S., Dubs, F., Feld, C. K., Harrington, R., Harrison, P. A., Lavorel, S., & Da Silva, P. M. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, *19*(10), 2921-2947.

Veblen, T. (2000). Disturbance patterns in southern Rocky Mountain forests. In: R. L. Knight et al. (Eds) *Forest Fragmentation in the Southern Rocky Mountains*, (pp. 31-54) Colorado University Press, Boulder.

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, 111(38), 13690-13696.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2403-2413.

Westerling, A. L., Hidalgo, H. G., Cayan, D. R., & Swetnam, T. W. (2006). Warming and earlier spring increase western US forest wildfire activity. *Science*, *313*(5789), 940-943.

White, M. A., & Vankat, J. L. (1993). Middle and high elevation coniferous forest communities of the North Rim region of Grand Canyon National Park, Arizona, USA. *Vegetatio*, 109(2), 161-174.

Wickham, H. (2017). tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse

Wickham, H. (2007). Reshaping data with the reshape Package. Journal of Statistical Software, 21(12), 1-20. URL http://www.jstatsoft.org/v21/i12/.

Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., Kerkhoff, A. J., McCarthy, M. C., Michaletz, S. T., Swenson, N. G., & Asner, G. P. (2018). Climate shapes and shifts functional biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences*, p.201813723.

Williams, J. (2013). Exploring the onset of high-impact mega-fires through a forest land management prism. *Forest Ecology and Management*, *294,* 4-10.

Table and Figure Captions

Table 1. Forest Type Mean Variables.

Means of fire history characteristics from FEIS fire models, elevation, and climate variables, by FIA forest type, with the percentage of plot-condition sampling units reported as a given forest type. HFI is historic fire interval exceedance, with average interval years and yes/maybe/no if that interval has been exceeded assuming cessation of fire *ca.* 1900. Standard deviation for all variables available is in parentheses. Climate variables are a mean of extracted PRISM annual values at plot-condition locations for the period 1998-2017.

Table 2. Tolerance Values by Species.

Tree species present in the study, with tolerance values as derived from Niinemets and Vallarades (2006). Tolerance values are on a scale of 0-5 for each characteristic, 0 being least and 5 being most tolerant, and with a confidence interval (CI) given when multiple studies were used to derive the value. Code (species) is used in Figure 2 to identify species values in the drought-shade tolerance tradeoff space. # Trees and % Regen. (FIA estimated seedling count) is the number of each species present across the 864 plot-conditions (unique sampling sites) included in the study area.

Table 3. CMTI-Climate Correlations

Spearman-rank correlations (significant at $p < 0.05$, NS where not significant) between PRISM climate variables (means, 1998-2017) and drought and shade index difference (regeneration – tree) for plot-condition sampling units with regeneration below or above the elevation of peak difference for drought (2500 m) and shade (2300 m) tolerance. The elevation break points are where drought index difference peaked, as determined by the inflection point of the first derivative of the loess smoothed relationship between elevation and the drought tolerance index difference, the point at which it switches from a positive to negative relationship. Positive relationships between the index difference and variable indicate increased change to the regeneration mean tolerance value.

Figure 1. Landscape-Scale Ecosystem Tolerance Trajectories

(a) Interpolated drought tolerance CMTI difference (regeneration – tree). Oak-dominated regeneration plots are indicated by yellow triangles (>30% oak regeneration and <10% oak trees) as they tend to strongly influence mean drought tolerance. Drought tolerance is interpolated from plot-condition points using inverse distance weighting and classified into five equal intervals covering the mean ± 2 standard deviations of the difference, with red shades indicating a trend towards drought tolerance and blue shades indicating a trend away from drought tolerance.

(b) Interpolated shade tolerance CMTI difference (regeneration – tree). The black x indicates plots where the forest type indicates the historic fire interval (HFI) has been exceeded with the absence of fire since the late 1800s. Shade tolerance is interpolated from plot-condition points using inverse distance weighting and classified into five equal intervals covering the mean ± 2 standard deviations of the difference, with purple shades indicating a trend towards shade tolerance and orange shades indicating a trend away from shade tolerance.

The base map for (a) and (b) is a hillshaded 30m-DEM with counties (black lines) and major rivers (blue lines) defining study region. River across north border is Arkansas River in

Colorado, River along west border is Rio Grande in Colorado and New Mexico. The small river near south end of study area feeding into the Rio Grande is the Santa Fe River, which is important to local forest and water resource management.

Figure 2. Mean CMTI Difference Vector by Forest Type

Solid lines indicate mean plot tolerance value changes across demographic groups, between tree group (solid dot) and regeneration group (open triangle), by forest type, with standard deviation. Where oak dominated the regeneration groups (Supplementary Figure S-2), regeneration index value skewed towards drought tolerant and so these plots were analyzed separately as "[forest type] – oak" plots, with dotted lines indicating demographic changes. Species point tolerance values for drought and shade tolerance are included within the tolerance tradeoff space as gray codes, for all species recorded (see Table 2 for scientific and common names).

Figure 3. CMTI Differences by Forest Type

(a) Boxplot of drought and shade tolerance index differences (regeneration – tree), by forest type. Forest types with significant difference from 0 are starred, indicating significant directional changes in the mean tolerance of the regeneration group ($p < 0.05$, one-sample *t*-test). The cottonwood/ash group was excluded due to low sample size. Boxes are filled with the historic fire exceedance (HFI) condition assuming cessation of fire *ca.* 1900: Y (yes, red), M (maybe, blue), N (no, green).

Figure 4. Regeneration Cluster by Elevation

Here we see elevation trends in tolerance within forest types. Plot-condition elevations grouped by regeneration index *k* means clusters, with significant differences using ANOVA plus Tukey's HSD, among forest types (star above solid line indicates significantly different clusters), and between similar mid-elevation forest types and clusters (star with dashed line is significantly different from crossed diamonds, but diamonds are not significantly different from other diamonds on the line). Plots are grouped by dominant regeneration tolerance as determined by *k* means clustering: drought (white), shade (black), low/aspen (medium gray), and NA (plots with no regeneration, light gray).The cottonwood/ash group was excluded for low sample size.

Figure 5. Stress Difference-Elevation Relationship across Forest Types

Plot-condition drought (black circles) and shade (open circles) index difference by elevation across all forest types. Loess smoothing (span = 0.75) for drought (solid line) and shade (dashed line) with standard error (gray areas). The vertical lines indicate the elevations at which we find the greatest change in drought or shade functional tolerance across tree and regeneration demographic groups, The solid vertical line at 2500 m indicates point where the first derivative of the smoothed drought response equals 0 (see text). The dashed vertical line at 2300 m indicates similarly the maximum difference in shade tolerance among demographic groups.

Tables

Table 1. Forest Type Mean Variables.

		Fire Characteristics			Plot Mean (SD)			
Forest Type	**% Plot-conds.**	**Avg. HFI**	**HFI ex.**	**Fire Severity Class**	**Elev. (m)**	**PPT (mm)**	**Tmax (˚C)**	**VPD max**
Pinyon / juniper	32.1%	526	N	stand-replacing	2141 (284)	394 (59)	17.8 (2.2)	18.0 (2.7)
Pinyon / juniper - oak	4.9%	526	N	stand-replacing	2242 (238)	427 (51)	17.1 (1.6)	16.9 (1.9)
Woodland hardwoods	6.0%	50	M	stand-replacing	2423 (295)	502 (88)	15.4 (2.0)	14.9 (2.3)
Ponderosa pine	19.0%	10	Y	non-lethal	2451 (208)	491 (59)	15.6 (1.8)	14.9 (1.9)
Mixed Conifer - oak	5.6%	25	Y	non-lethal	2550 (217)	520 (81)	14.9 (1.9)	14.2 (2.2)
Douglas-fir	9.8%	165	Y	mixed severity	2825 (240)	598 (104)	12.8 (2.0)	12.0 (2.1)
Spruce / fir	15.5%	210	N	stand-replacing	3189 (279)	726 (143)	10.2 (2.0)	9.7 (1.7)
Lodgepole pine	0.9%	300	N	stand-replacing	2894 (150)	524 (82)	11.8 (1.8)	11.6 (1.7)
Limber / bristlecone	1.3%	500	N	stand-replacing	3037 (343)	580 (87)	11.0 (2.0)	10.5 (1.5)
Cottonwood / ash	0.8%	110	M	mixed severity	2227 (401)	428 (61)	16.7 (2.9)	16.6 (3.2)
Aspen	4.2%	165	M	mixed severity	3046 (182)	664 (120)	10.8 (1.6)	10.3 (1.4)

Table 2. Tolerance Values by Species.

Species	Common name	Code	# Trees	# Regen.	Drought tolerance (CI)	Shade tolerance (CI)
Abies concolor	white fir	ABCO	1,725	742	1.91 (0.12)	4.33 (0.28)
Abies lasiocarpa	subalpine fir	ABLA	88	182	2.02 (0.02)	4.83 (0.15)
Abies lasiocarpa var. arizonica	corkbark fir	ABLAA	1,691	1,104	2.02 (NA)	4.83 (NA)
Acer negundo	boxelder	ACNE2	12	12	3.03 (0.82)	3.47 (0.1)
Juniperus deppeana	alligator juniper	JUDE2	1	0	5 (NA)	2 (NA)
Juniperus monosperma	oneseed juniper	JUMO	2261	104	5 (NA)	2 (NA)
Juniperus scopulorum	Rocky Mountain juniper	JUSC2	1,229	207	4.97 (0.03)	1.48 (0.27)
Picea engelmannii	Engelmann spruce	PIEN	3,836	851	2.58 (0.3)	4.53 (0.07)
Picea pungens	blue spruce	PIPU	181	38	2.88 (0.12)	3.54 (0.32)
Pinus aristata	Rocky Mountain bristlecone pine	PIAR	236	12	4.97 (0.03)	1.25 (0.25)
Pinus contorta ssp. latifolia	lodgepole pine	PICO	482	1	4.21 (0.38)	1.48 (NA)
Pinus edulis	common or two-needle pinyon	PIED	4,839	855	4.97 (0.03)	1.44 (0.05)
Pinus flexilis	limber pine	PIFL2	570	70	4.72 (0.22)	1.56 (0.15)
Pinus ponderosa	ponderosa pine	PIPO	3,621	303	4.32 (0.32)	1.64 (0.15)
Populus deltoides	plains cottonwood	PODEM	3	0	1.57 (0.23)	1.76 (0.38)
Populus tremuloides	quaking aspen	POTR5	3,025	1,869	1.77 (0.23)	1.21 (0.18)
Populus angustifolia	narrowleaf cottonwood	POAN3	24	12	1.77 (0.23)	1.35 (NA)
Pseudotsuga menziesii	Douglas-fir	PSME	3,599	465	2.62 (0.41)	2.78 (0.18)
Quercus gambelii	Gambel oak	QUGA	2,936	13,988	4.97 (0.03)	2.09 (0.09)
Total Individuals			**30,359**	**20,815**		

Table 3. CMTI-Climate Correlations.

	Shade (2300 m)		Drought (2500 m)	
	Below	**Above**	**Below**	**Above**
Elevation (m)	0.29	-0.09	0.42	-0.36
Precipitation (mm)	0.51	-0.13	0.48	-0.24
Max Temp (˚C)	-0.30	0.08	-0.39	0.32
Max VPD (hPa)	-0.34	0.09	-0.44	0.32

Figures

Figure 1. Landscape-Scale Ecosystem Tolerance Trajectories

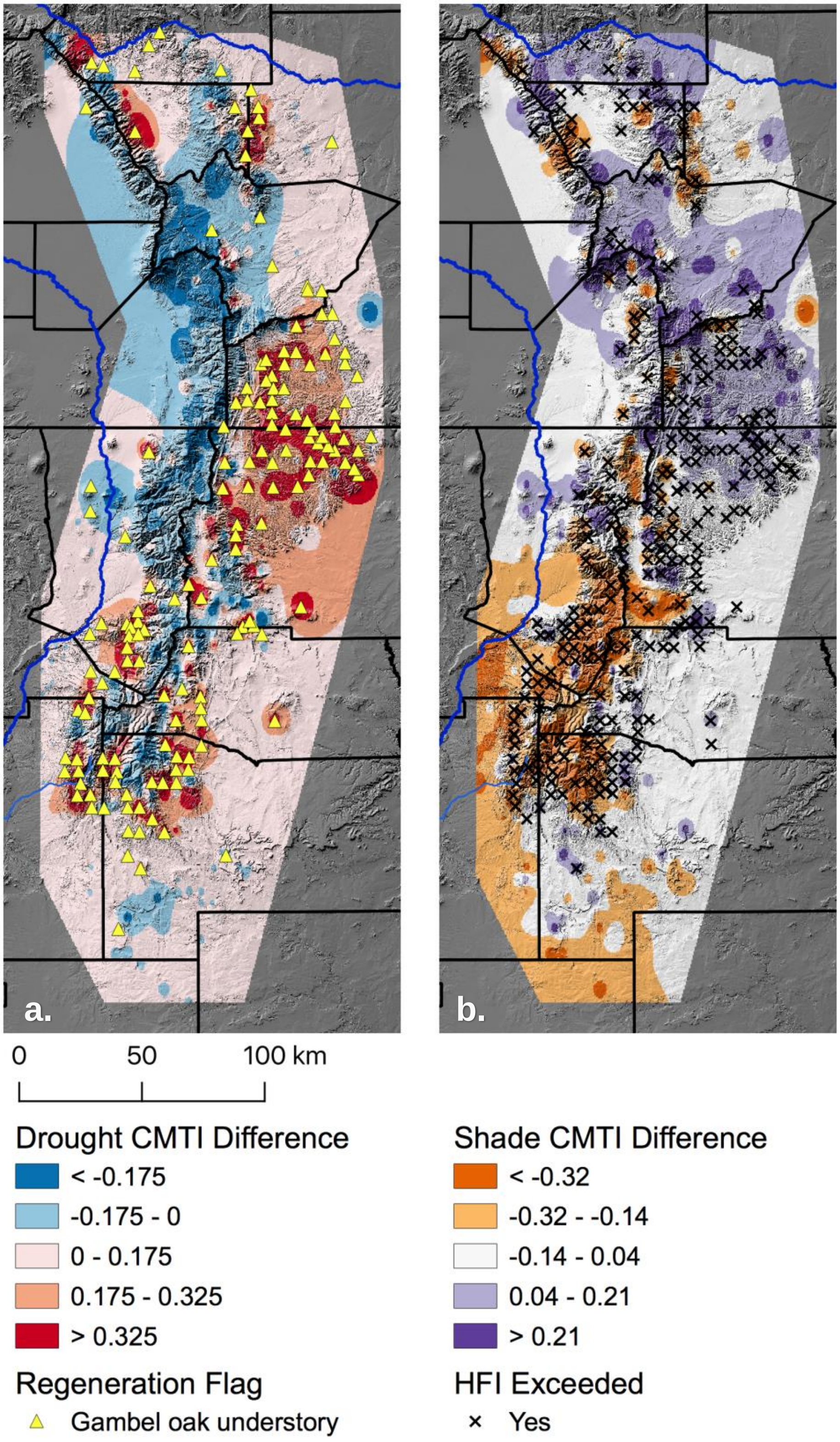


Figure 2. Mean CMTI Difference Vector by Forest Type

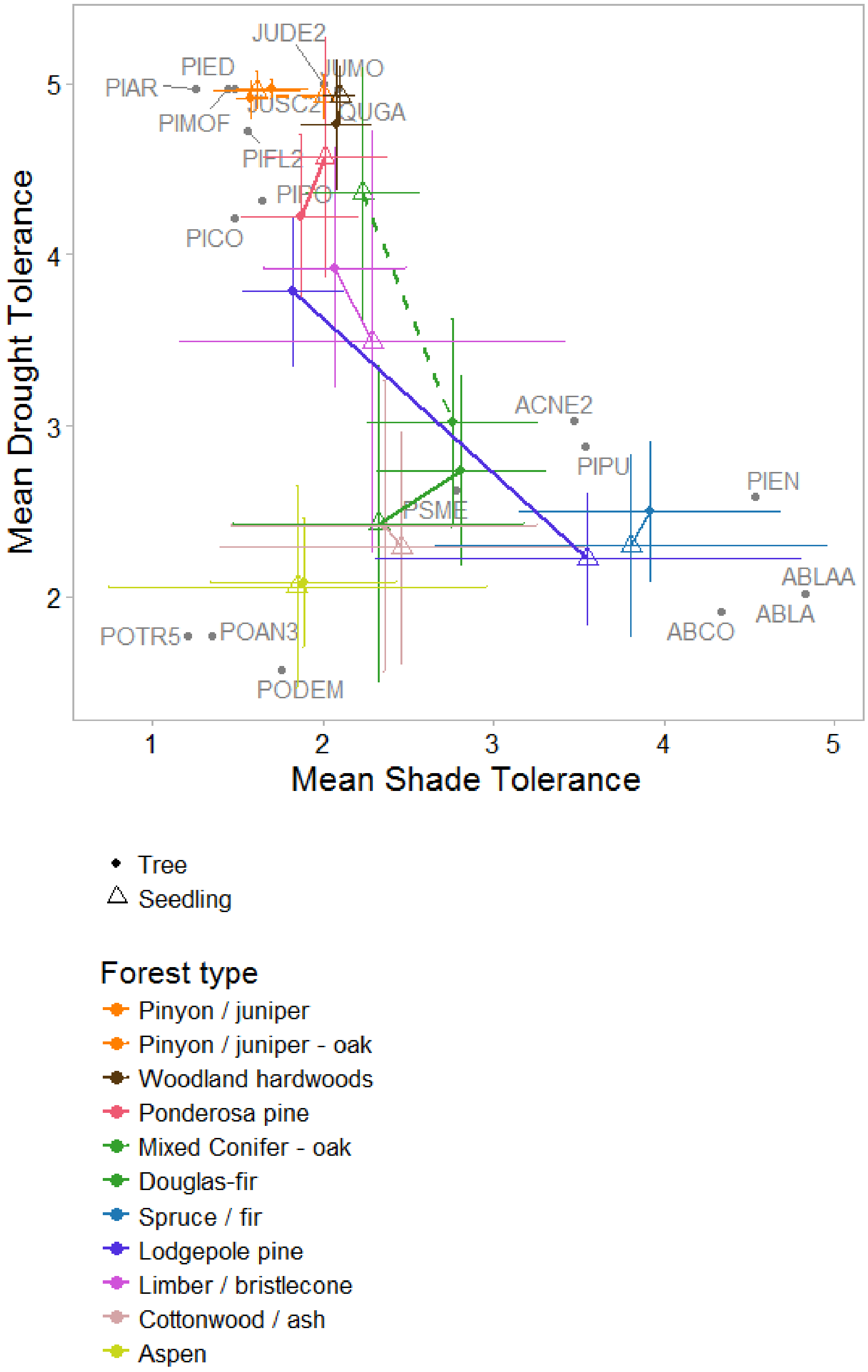


Figure 3. CMTI Differences by Forest Type

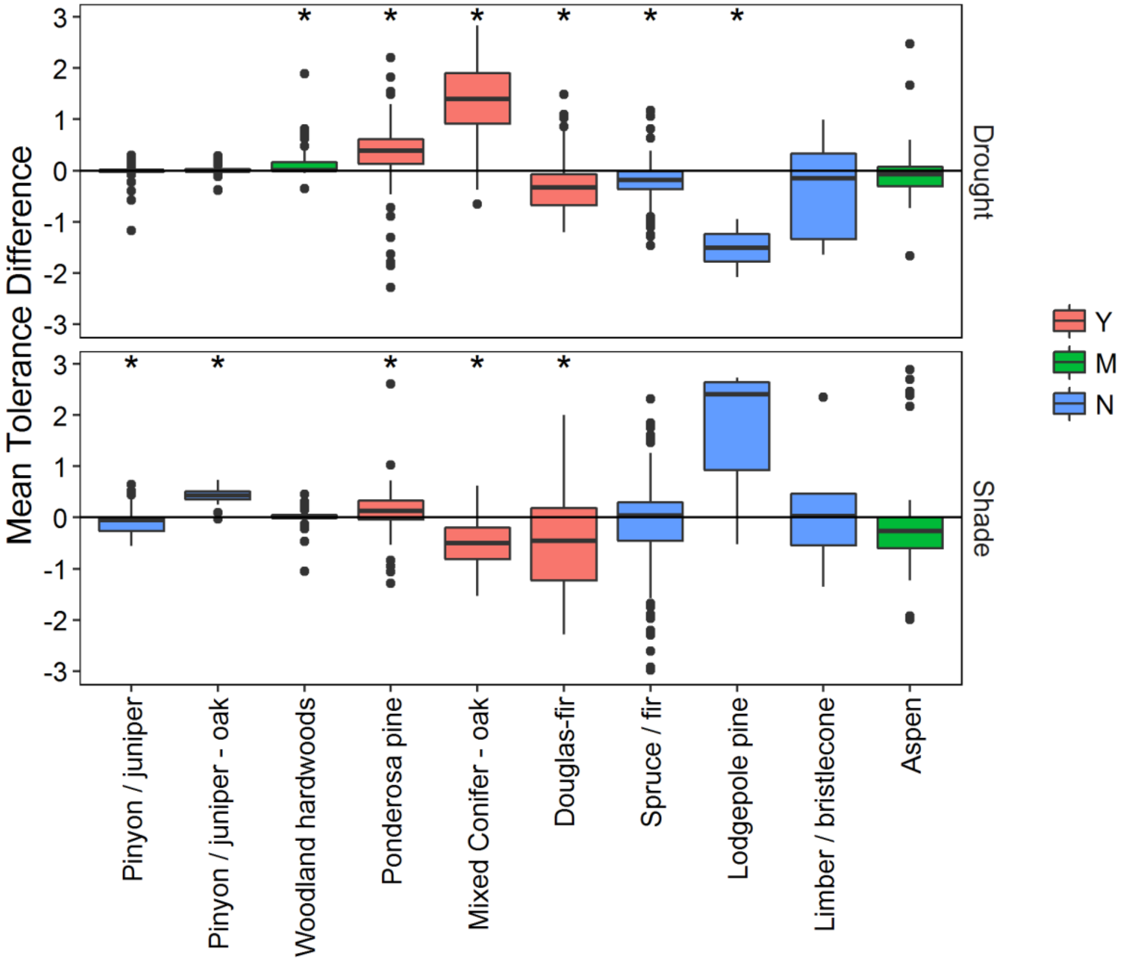


Figure 4. Regeneration Cluster by Elevation

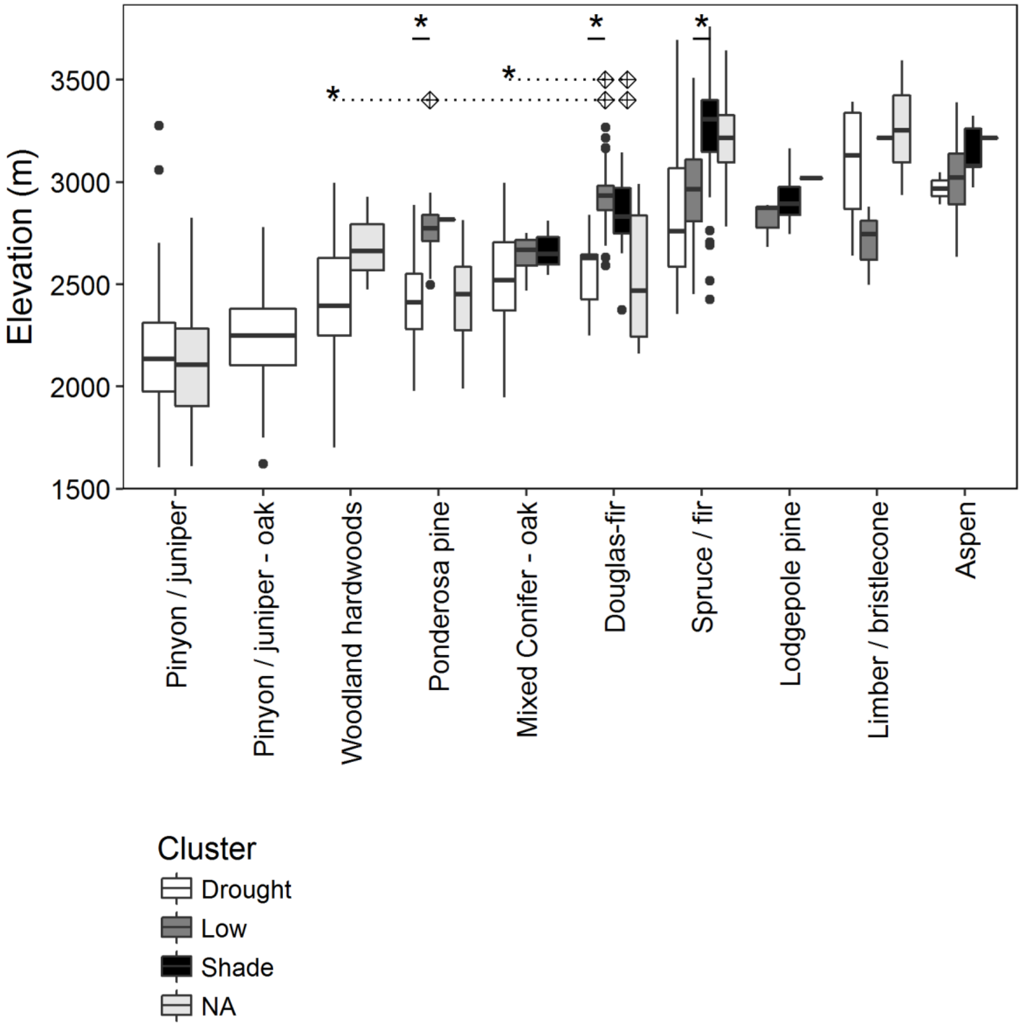
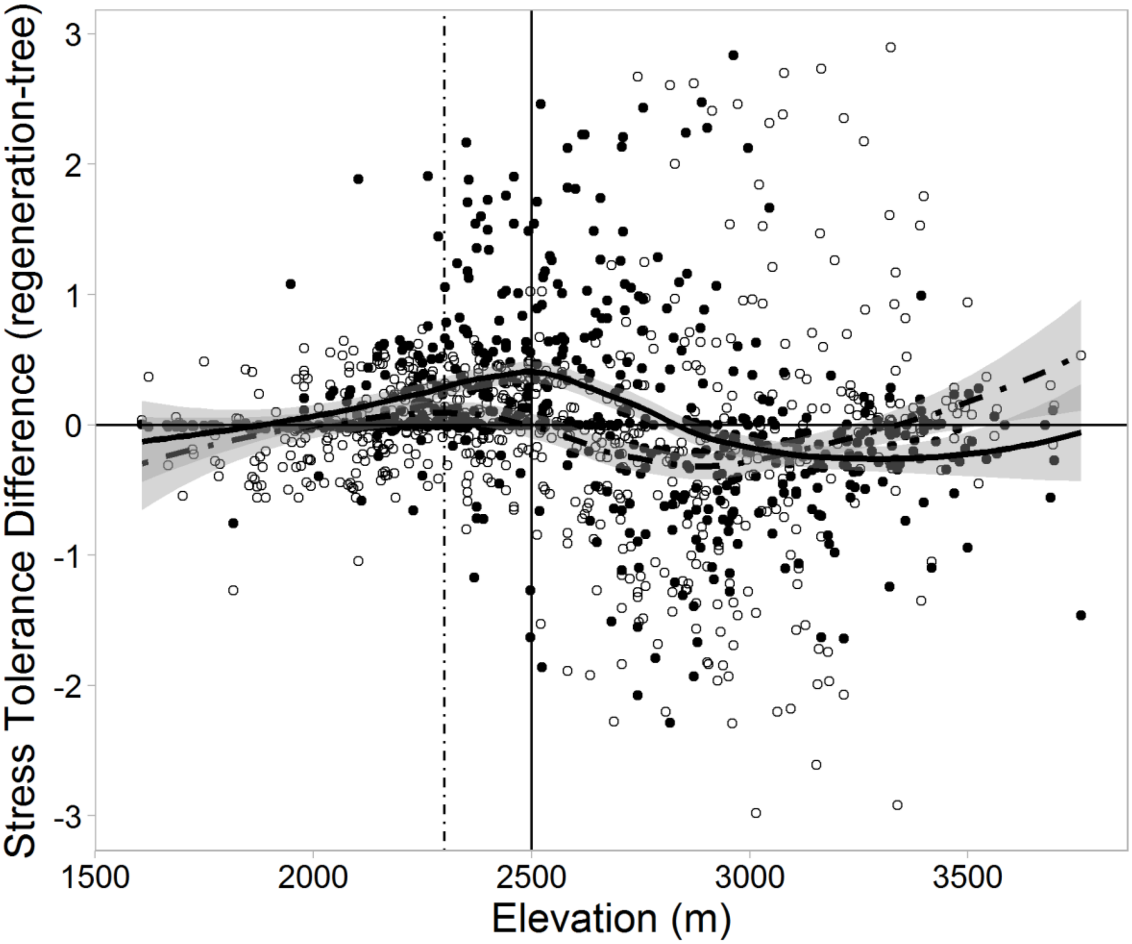
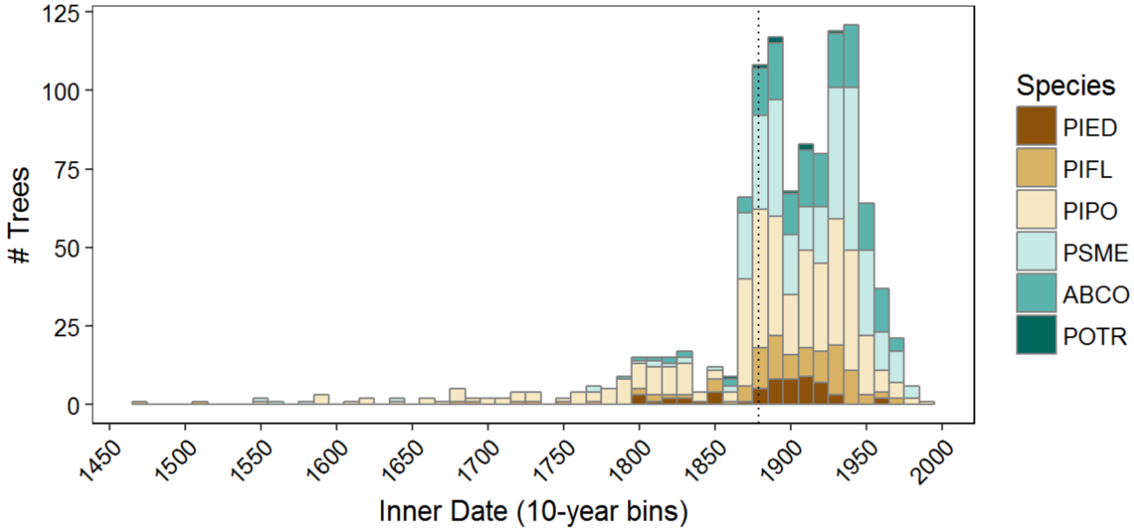


Figure 5. Stress Difference-Elevation Relationship Across Forest Types



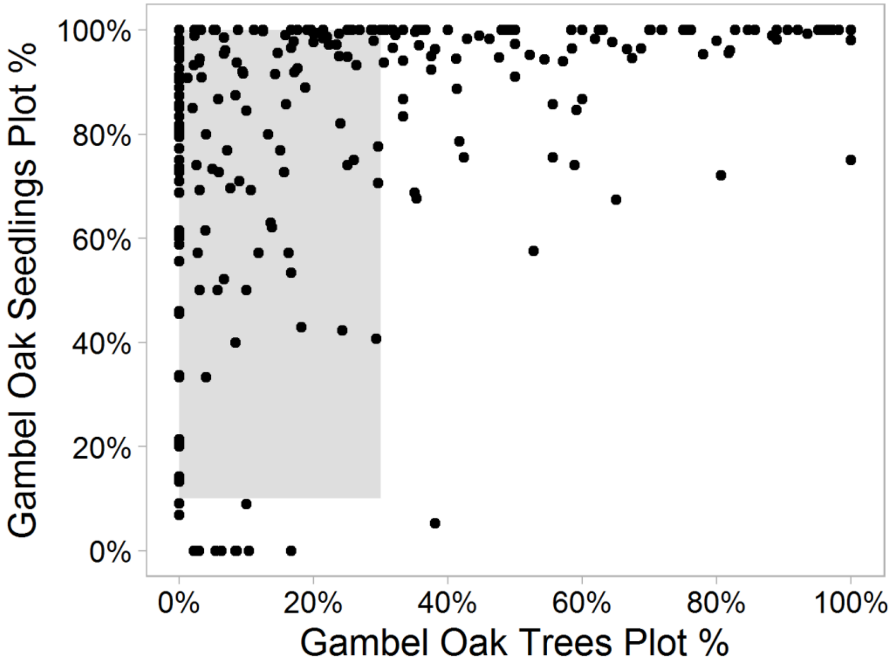
Supplemental Information

S-1. Southwest Mixed-Conifer Stand Age Structure



Stand-age structure for live and dead trees from the six dominant species at 58 randomly sampled plots stratified by elevation in the Little Tesuque Watershed, Santa Fe National Forest, New Mexico, USA. Fire-scar samples and remnant wood from non-plot locations, collected to extend the chronology, are also included, resulting in the long tail of the histogram. This figure demonstrates the substantial increase in tree establishment found at randomly-sampled plots following the exclusion of fire in late 1800s. Vertical dotted line is at 1879, the year of the last widespread fire in the watershed (Margolis et al. 2007). Age histogram bars are in 10-year bins; tree inner date is pith date when available or within 5-10 rings, at approximately 10 cm above ground level, so inner years are not the exact date of tree establishment, but generally within a decade.

S-2. Oak Understory Cutoff



FIA plots with Gambel Oak (*Quercus gambelii* Nutt.) presence, plotted by relative oak percentage of trees and regeneration. Gray box indicates plots with less than 30% oak trees and more than 10% oak seedlings. These plots had less than median % Gambel oak presence yet substantial regeneration presence, and were separated in the analysis as forest types with oak-dominated regeneration.

S-3. Regeneration Tolerance Index Cluster

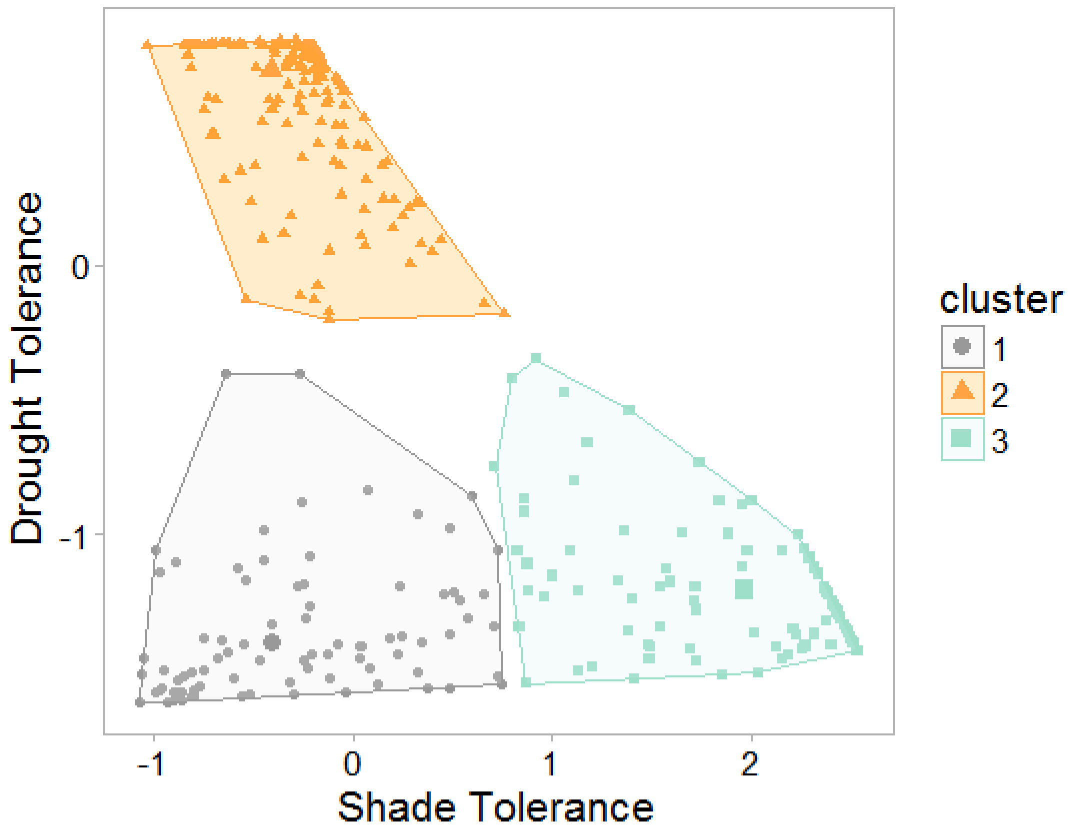


Figure S-3

(a) Cluster assignments for plots based on mean regeneration shade and drought tolerance values, where drought = 2, shade = 3, and low/aspen = 1. Generally we saw movement away from the central area where species community was more mixed and towards higher drought, shade, or neither/increasing aspen dominance. Regeneration (seedlings) was counted at microsites that contributed towards the predominance of one species or another, depending on the nearby seed trees and tendency for conifers to reproduce in large numbers. Trends in tolerance across demographic groups were made clearer as a result of FIA sampling strategy. We found similar trends across sites sampled for Appendix B, where plot sampling size did not vary across trees and regeneration.

		Mean by Cluster				CMTI Mean Difference	
Regeneration Cluster	**% Plot-conds.**	**Elevation (m)**	**PPT (mm)**	**Tmax (˚C)**	**VPD max**	**Drought**	**Shade**
No Regen	18.5%	2331 (453)	448 (127)	16.3 (3.4)	16.3 (3.9)	NA	NA
Drought	52.4%	2327 (300)	455 (85)	16.5 (2.3)	16.2 (2.7)	0.33 (0.58)	-0.03 (0.37)
Low/Aspen	14.1%	3153 (317)	630 (116)	11.9 (1.9)	11.2 (1.8)	-0.46 (0.47)	-0.77 (0.86)
Shade	14.9%	2912 (237)	699 (150)	10.5 (2.3)	10.0 (2.2)	-0.23 (0.56)	0.53 (0.86)

(b) Means (standard deviation in parentheses when applicable) for plot climate (water year precipitation (mm), annual maximum temperature (ºC), and annual maximum vapor pressure deficit) and elevation, and CMTI values, for plots grouped by *k* means clustering on regeneration index values, with the % of plots grouped in each cluster (% Plot-cond.). “No Regen” cluster is made up of plots with no regeneration present.