

DISSERTATION

SEEING THE FOREST FOR THE SEEDS:
MASTING AND MORTALITY IN DRY FOREST AND WOODLAND ECOSYSTEMS
OF THE ROCKY MOUNTAINS AND COLORADO PLATEAU

Submitted by

Andreas P. Wion

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2022

Doctoral Committee:

Advisor: Miranda D. Redmond

Ian S. Pearse

Camille S. Stevens-Rumann

Monique E. Rocca

Copyright by Andreas P. Wion 2022

All Rights Reserved

ABSTRACT

SEEING THE FOREST FOR THE SEEDS: MASTING AND MORTALITY IN DRY FOREST AND WOODLAND ECOSYSTEMS OF THE ROCKY MOUNTAINS AND COLORADO PLATEAU

For forests to persist on the landscape, tree recruitment must keep pace with tree mortality. Larger, more frequent, and more severe disturbances have raised concerns about the capacity for water-limited forests and woodlands to recover under increasingly hotter climates. For most conifer species, seed availability is the fundamental prerequisite to new tree recruitment. In addition, most conifer species are also masting species, meaning seed production is highly variable among years and synchronous within a population. Masting creates boom and bust patterns of seed availability that shape forest dynamics. In many species, it remains unknown what drives masting or how the mosaic of climate and competition shape patterns of seed production across species ranges. This limits our ability to forecast forest demography across large spatial areas and under uncertain climate futures.

This dissertation is an exploration into two key processes driving forest persistence and loss, mast seeding and tree mortality, in two pine species native to dry forests and woodlands of the Rocky Mountains and Colorado Plateau: piñon pine and ponderosa pine. In chapter one, I examine the spatiotemporal drivers of masting in piñon pine across its latitudinal distribution in Colorado and New Mexico. I demonstrate that masting was driven by favorable weather conditions acting during key phenological periods of cone development: initiation and pollination. Cone production was sensitive to the spatial variability in long-term climate - cooler and wetter sites produced more cones, more frequently than hotter and drier sites. In chapter two, I examined cone

production in ponderosa pine across a large portion of this species' distribution between Arizona and Wyoming. In contrast to piñon pine, I found that individual-level factors like tree size, age, and stand density, were better predictors of cone production than long-term climate or annual weather. In chapter three, I examined patterns of cone production between these two species jointly and related them to large scale modes of climate variability, like the North American monsoon and the El Niño Southern Oscillation. I found similar patterns, where piñon pine cone production was strongly associated with climate while ponderosa pine was not. Range wide synchrony in masting was associated with the North American monsoon, and regional north-south anti-synchrony was associated with the phase of the El Niño Southern Oscillation. Collectively, these chapters highlight contrasting masting patterns among these two, co-occurring pine species of dry forests and woodlands of the Rocky Mountains and Colorado Plateau. I explore the consequences of these contrasting life history strategies for forest management in this region, as well as the potential impacts of a changing climate and disturbance regime on seed production. In the final chapter of this dissertation, I evaluated four drought metrics on their ability to correctly predict piñon pine die-off following a severe drought in 2018. The results highlight how some of these simple climate metrics can be used as an indicator of piñon pine die-off in future, hotter drought events, and I provide a simple framework for evaluating mortality risk at regional scales.

ACKNOWLEDGEMENTS

I want to begin by acknowledging that dissertation was written under somewhat extraordinary circumstances. This research began in May 2017, and continued through four waves of a coronavirus pandemic, two presidential administrations, one insurrection, several record-breaking fires, and as I write this, a ground war in Ukraine. Writing a PhD dissertation is challenging under ordinary circumstances but would be impossible under these circumstances without the help of so many excellent friends, family members, mentors, and colleagues. There are too many people and too little time to properly thank all of them here, but I will try.

I want to begin by acknowledging my advisor, Miranda Redmond. I would have never experienced any of the opportunities afforded to me over the past five years if it wasn't for her. For five years, she has been infinitely patient with me as I pursued various side projects, field trips, and other non-dissertation-distractions. She is a discerning and kind editor, a brilliant scientist, and my most helpful collaborator. I also want to acknowledge Ian Pearse for his friendship and mentorship from the very early days of this research. His enthusiasm for this research was infectious, and never once failed to motivate me when I found myself in dissertation doldrums. These two have played a larger role than anyone in shaping me into the scientist I am now. In addition, I thank my committee members Camille Stevens-Rumann and Monique Rocca for their input on this research and for the lessons they imparted to me- either in class, during committee meetings, or in their spare time. Thank you all so much for your energy, time, and support.

I want to acknowledge my many coauthors on this research - including Peter Weisberg, Kyle Rodman, Tom Veblen, Dave Breshears, Neil Cobb, Sarah Hart, Jeff Carroll, Nashelly Meneses,

and Darin Law. Each one of them has done something important to either make this dissertation more interesting and accessible. It's also important to acknowledge the various funding sources for this research, including the USDA, NSF, and USGS. But I also want to acknowledge two small grants from the Graduate Degree Program in Ecology and The John Marr Ecology Fund that helped fund a portion of this dissertation.

I want to thank my close friends and labmates in the Redmond Lab – including Alison Foster, Noah Amme, Katie Nigro, Ed Hill, Angie Gonzalez, and Ariel Demarest, in addition to the army of undergraduates over the years who helped me collect, process, and analyze this data. Thank you to my close friends at CSU over the years, including Ryan Schroeder, Isaac Dell, Andrew Mann, Katie Jones, Jimmy Matilla, Arian Brazenwood, John Mola, Amy Collins, and several dozen or so people in the Graduate Degree Program in Ecology and the Department of Forest and Rangeland Stewardship. Having smart, kind, and creative science friends are the best part of this job. Thanks to my friends from before graduate school, including Joshua Catalano, Max Broxson, Austin Draving, Leah D, Sarah Winter, Preston So and Sam Wolken. I'm sorry if I've fallen off the face of the earth for the last five years, this was the reason why. Playing music with Max Broxson was my greatest refuge from science and data during graduate school, and I am immensely grateful for his creativity, friendship, for his room and board in southwest Colorado, and his frequent help out in the field. In addition, Sarah Aldea and Austin Draving provided housing in the field when in Santa Fe, NM and Grand Junction, CO. Those were always fun times. As much as I love field work, I love field work more with friends.

Finally, I need to thank my family, who have been my anchor through this entire process. To my mom and dad, Angelene and Kevin, thank you for always supporting me, believing in me, and for trying to understand what I've been doing this whole time. My sisters Bernadette and Emily,

and my niece Olivia, you've all done so much during the last five years too, and I'm so proud of you. To the dogs in my life: Leo, Gila, and Ricky. Last, but certainly never least, thank you to the woman who has been my greatest support through it all. Falling in love during graduate school is a great choice, and marrying Gwen was the best decision I made during my time here. Thank you for always being there for me during this process, I couldn't have done this without you.

PREFACE

For forests to persist into the future, new tree recruitment must exceed mortality (McDowell et al. 2020). Collectively, these two processes (recruitment and mortality) govern demographic rates and population growth in forests and woodlands (Merow et al. 2014). However, recent, accelerating rates of tree mortality have been observed across a range of forest types globally (vanMantgem et al. 2009, Allen et al. 2015). Larger, more frequent, and more severe disturbances like fires and droughts, pathogen-outbreaks, and insect infestations, have raised concerns about the capacity for forests and woodlands to recover under increasingly hotter climates (Milar et al. 2015, Davis et al. 2019, Batllori et al. 2020). Forecasts of tree mortality and recruitment events would be useful tools for managing and conserving forests under uncertain future conditions (Dietze et al. 2018).

In seed-obligate (i.e., non-resprouting) trees, seed availability is a fundamental prerequisite to new tree recruitment (Clark et al. 1999). However, many trees do not produce seeds each year. Rather, many trees are masting species, meaning seed production is highly variable from year to year and often synchronous among individuals. Understanding masting can have benefits that go beyond predicting forest demographic processes. The boom-and-bust pulse of seeds through ecosystems can have cascading impacts on higher trophic levels, including the spillover of zoonotic diseases like *sin Nombre* orthohantavirus in the western US (Mills et al. 1999). Masting is often associated with weather events like temperature or moisture anomalies during the seed development process (Pearse et al. 2016). However, specific weather effects on seed production vary among different species, populations, and even among co-located individuals, suggesting that any potential effects of a changing climate on seed production are unlikely to be uniform across large geographic areas. Range-wide demographic studies are

needed to quantify this spatial variability in demographic rates to identify areas of potential refugia to reproduction and recruitment, or alternatively, areas where extirpation may be likely.

This dissertation is a demographic-based exploration into two key processes driving forest persistence and loss - mast seeding and tree mortality, in two dry pine species of the Rocky Mountains and Colorado Plateau: piñon pine and ponderosa pine. Over the next four chapters, I use a combination of field observations, empirical modeling, and spatial analyses to describe the patterns and drivers of these key demographic rates (i.e., cone production and tree die-off) across a large portion of these species ranges in the western US. The overarching goal of this dissertation was to lay the groundwork for future forecasts of plant demography, which will inform the management and conservation of dry forest and woodland ecosystems into the future.

Research Organization

This dissertation is organized into two parts. The first part contains three chapters, and each explores patterns of seed cone production in widespread, dry conifer species in the western US. I explore these patterns individually in the first two chapters (Chapter 1: piñon pine; Chapter 2: ponderosa pine), and together in the third chapter. Collectively, this section contributes to our understanding of how abiotic (e.g., climate and weather) and biotic factors (e.g., tree size, age, and competition) jointly impact mast seeding at local, regional, and range-wide spatial scales. I describe divergent mast seeding behavior in these two species and explore how this may affect future resilience and recovery under warmer climates and altered disturbance regimes.

The second portion contains one chapter and investigates the spatial patterns of drought-induced mortality (i.e., tree die-off) in piñon pine. Piñon pine is a model species in studies of drought and beetle associated die-off, and multiple climate thresholds have been proposed to

predict the tipping points of piñon pine mortality. I evaluated four of these thresholds based on their ability to correctly predict piñon pine die-off following a severe drought in 2018. The results highlight how some of these simple climate metrics can be used as an indicator of piñon pine die-off in future, hotter drought events. This research is the first, field-based comparison of several climate thresholds hypothesized to predict pinyon pine die-off, and I provide a simple framework for evaluating mortality risk at regional scales.

DEDICATION

For my father, Kevin, and my mother, Angelene.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
PREFACE.....	vii
DEDICATION.....	x
SECTION 1	
Chapter 1. ARIDITY DRIVES SPATIOTEMPORAL PATTERNS OF MASTING ACROSS THE LATITUDINAL RANGE OF A DRYLAND CONIFER SPECIES	
Main Text.....	2
References.....	27
Chapter 2. JOINT IMPACTS OF WEATHER, CLIMATE, AND STAND STRUCTURE ON MAST SEEDING IN PONDEROSA PINE	
Main Text.....	33
References.....	65
Chapter 3. THE EFFECTS OF ENSO AND THE NORTH AMERICAN MONSOON ON MAST SEEDING IN TWO ROCKY MOUNTAIN CONIFER SPECIES	
Main Text.....	73
References.....	94
SECTION 2	
Chapter 4. DEAD AGAIN: PREDICTIONS OF REPEAT TREE DIE-OFF UNDER HOTTER DROUGHTS CONFIRM TIPPING POINTS FOR A DRYLAND CONIFER SPECIES	
Main Text.....	102
References.....	123
CONCLUSION.....	130
APPENDICES.....	132
APPENDIX 1.....	133
APPENDIX 2.....	139
APPENDIX 3.....	141

SECTION 1

CHAPTER 1

¹ARIDITY DRIVES SPATIOTEMPORAL PATTERNS OF MASTING ACROSS THE LATITUDINAL RANGE OF A DRYLAND CONIFER SPECIES

OVERVIEW

Masting, or the synchronous and irregular production of seed crops, is controlled by environmental cues and resource budgets. Increasing temperatures and shifting precipitation regimes may alter the frequency and magnitude of masting, especially in species that experience chronic resource stress. Yet the effects of a changing climate on seed production are unlikely to be uniform across populations, particularly those that span broad abiotic gradients. In this study, we assessed the spatiotemporal patterns of masting across the latitudinal distribution of a widely distributed dryland conifer species, piñon pine (*Pinus edulis*). We quantified seed cone production from 2004-2017 using cone abscission scars in 187 trees from 28 sites along an 1100 km latitudinal gradient to investigate the spatiotemporal drivers of seed cone production and synchrony across populations. Populations from chronically hot and dry areas (greater climatic water deficits and less monsoonal precipitation) tended to have greater interannual variability in seed cone production and smaller crop sizes. Mast years generally followed years with low vapor pressure deficits and high precipitation during key periods of the reproductive process, but the strength of these relationships varied across the region. Populations that received greater monsoonal precipitation were less sensitive to late summer vapor pressure deficits during seed cone initiation yet more sensitive to spring vapor pressure deficits during pollination. Spatially correlated patterns of vapor pressure deficit better predicted synchrony in seed cone production

¹ By Andreas P. Wion, Ian S. Pearse, Peter J. Weisberg, and Miranda D. Redmond. Formatted for and accepted in *Ecography*.

than geographic distance, and these patterns were conserved at distances up to 500 km. These results demonstrate that aridity drives spatiotemporal variability in seed cone production. As a result, projected increases in aridity are likely to decrease the frequency and magnitude of masting in these dry forests and woodlands. Declines in seed production may compound climatic limitations to recruitment and impede tree regeneration, with cascading effects for numerous wildlife species.

INTRODUCTION

The synchronous production of highly variable annual seed crops, also known as masting, is a common reproductive strategy in dry forests and woodlands. Yet plant species that exhibit episodic demographic patterns are likely to be disproportionately affected by a changing climate (Enright et al. 2015). Pulsed demographic processes like seed production (Koenig and Knops 2000, Pearse et al. 2016) and seedling recruitment (Savage et al. 1996, Rother and Veblen 2017) characterize dryland ecosystems, where water availability and evaporative demand strongly drive plant physiology (Loik et al. 2004). Projected increases in the aridity of many drylands throughout the 21st century (Seager et al. 2007, Buotte et al. 2018) portend shifts in species persistence through reductions in the frequency and magnitude of these demographic pulses. Given that successful seed production is the essential prerequisite for plant establishment, disruptions in seed production could act as a bottleneck to tree regeneration (Ruano et al. 2015, Brown et al. 2019). However, we still lack a quantitative understanding of the relationship between seed production and the spatiotemporal heterogeneity in water availability, particularly in comparison to demographic surveys of tree growth (Adams and Kolb 2004, Barger and

Woodhouse 2015, Redmond et al. 2017) and seedling establishment (Savage et al. 1996, Rother and Veblen 2017).

The high interannual variability in seed production may reflect an inability to accumulate enough resources in a single growing season to regularly produce large annual seed crops (i.e. “resource budget hypothesis”, Isagi et al. 1997). A global analysis of masting species suggests that masting is a more common form of reproduction in less productive environments (Kelly and Sork 2002), and water availability has been linked with seed production in some dryland systems (Perez Ramos et al. 2010, Mooney et al. 2011). Indeed, trees in more resource limited environments tend to have more variable seed production and lower long-term averages (Pearse et al. 2017) and seed production has declined in some conifer species in association with increasing temperatures (Mutke et al. 2005, Redmond et al. 2012). If water limitations underlie masting behavior in dryland tree species, it follows that seed production should exhibit greater interannual variability in more water limited environments.

Processes that synchronize ecological phenomena across populations due to correlated environments, also known as Moran effects (*sensu* Moran 1953, Koenig 2002), are well documented in masting species (Koenig and Knops 2000). Weather conditions, particularly during key reproductive processes (such as ovule differentiation, flowering, or pollination), are often strongly associated with seed production (eg. Forcella 1981, Parmenter et al. 2018). The relationship between weather and seed production is hypothesized to synchronize masting among individuals within a population, creating economies of scale that increase pollination efficiency and reduce seed predation (reviewed in Pearse et al. 2016). Disruptions in weather-masting relationships could affect the frequency or synchrony of mast events (Iler and Inouye 2013, Monks et al. 2016), therefore increases in temperature or shifting precipitation regimes could

decrease the future occurrence of large seed crops in masting species. The question remains for many species: Over what extent does synchrony in masting occur, and what role does the spatiotemporal variability in weather play in determining patterns of mast-synchrony across geographically separated populations?

The extent of synchrony and variability in seed production across populations is often difficult to quantify due to the significant investment required in collecting supra-decadal time series across large geographic regions (but see: Koenig and Knops 1998 and 2013). It seems unlikely however that the relationship between seed production and weather should be uniform across areas of diverse climatic or topographic gradients. Tree growth, for example, is well documented to be more sensitive to fluctuations in interannual weather conditions at water limited sites (Fritts 1976, Barger and Woodhouse 2015, Redmond et al. 2017). In addition, recent work from Bogdziewicz et al. (2019) showed sessile oaks (*Quercus petraea*) at colder sites were more responsive to spring temperatures during flowering periods. Following the resource budget hypothesis, dryland ecosystems are strong candidate areas to observe interactions between the spatial patterns of water availability and the temporal fluctuations in weather on seed production.

In this study, we reconstructed 14 years of seed cone production in 28 sites (n = 187 trees) that span climatic gradients across the latitudinal distribution of a widespread conifer in the western United States, piñon pine (*Pinus edulis*, Engelmann). Our objectives were threefold:

Objective 1) Identify the weather conditions that most strongly correlate with piñon pine seed cone production.

Objective 2) Assess how the mean, interannual variability, and synchrony of seed cone production among trees within a population vary across gradients of aridity.

Objective 3) Investigate if trees in more arid environments are more sensitive to the weather conditions associated with masting.

We predict that trees in more arid environments will exhibit lower seed cone production, greater interannual variability of seed cone production, and greater synchrony of reproduction within a site, as reproduction is limited to years to cool and wet years. As such, we expect trees in arid environments to be more sensitive to fluctuations in weather relative to trees that do not experience chronic water limitations. The expected outcome is that patterns of annual seed cone production should be similar among geographically separated populations occupying similar environments.

METHODS

Study species and region

Piñon pine is a masting, dryland conifer that occurs across 100 million acres of the western United States (Romme et al. 2009). Piñon pine is often a model species for a significant amount of dendrochronological and climate change research because of its pronounced sensitivity to climate (Redmond et al. 2017, Breshears et al. 2018). Piñon pine seeds are an important food resource for a diverse array of wildlife species (Chambers et al. 1999) and are also gathered by local communities and commercial harvesters. (Lanner 1981). Previous research has shown that piñon pine seed cone production is strongly negatively associated with late summer temperatures at the time of seed cone initiation (Forcella 1981, Parmenter et al. 2018), and cone production has declined by over 60% in some areas of New Mexico during a 30-year period of climate warming (Redmond et al. 2012).

Seed cone production is initiated when reproductive structures differentiate in the late summer, two years prior to seed maturation (yr₋₂). Seed cones lay dormant overwinter and then undergo wind pollination the following spring (yr₋₁) (Little 1938, Mirov 1967). Pollen grains remain in the unfertilized cones until the proceeding spring (yr₀) when fertilization, followed by rapid growth, occurs. Seeds mature in the fall, about 26 months following seed cone initiation. Discrete phenological periods like seed cone initiation and pollination strongly influence reproductive success in many species yet are often restricted to a matter of weeks or days (eg. Forcella 1981, Parmenter 2018). While damage from insects to seed cones can occur at nearly any point throughout the two-year cycle (Little 1943), severe weather conditions like drought during key phenological periods can exert strong negative controls over seed production (Bogdziewicz et al. 2018).

This species is found across a broad range of environmental conditions, with a distribution spanning 10 degrees of latitude (~1100 km) and commonly occurring in elevations ranging from 1500 – 2500 m above sea level. The North American monsoon drives a bimodal distribution of annual precipitation in this region, decreasing along a south to north gradient across the latitudinal range of this species (Romme et al. 2009). Mean summer temperatures at our sites usually peak in July (ranging from 17.9° - 24.1° C) and are coldest in the month of January (ranging from -5.2° – 4.52° C, PRISM Climate Group 2018).

Field sampling

We sampled 28 sites that spanned gradients of elevation (1000 meters) and latitude (1100 kilometers). Potential sites were identified using existing vegetation classifications (LANDFIRE 2008) in tandem with geographic information systems. The study area was bounded

approximately between 40° and 33° latitude and -109° to -106° longitude. Sites were stratified by latitude and located within 1 kilometer of roads on federal public lands. We used a clustered sampling design wherein sites were paired within latitudinal bands to span the elevational distribution of piñon pine in the region. Doing so allowed us to survey across local (< 20 km) temperature and precipitation gradients in tandem with regional (> 100 km) climatic and physiographic gradients. In the field, we selected study sites that contained a minimum of six reproductively mature, healthy trees within an approximately 40 x 50-meter area. Several sites were excluded from sampling due to inadequate numbers of healthy, cone producing trees, particularly in areas that experienced high levels of drought-related mortality in the past two decades (Breshears et al. 2005). Mean annual precipitation at these sites ranged from 300 mm to 630 mm (1981-2010, PRISM Climate Group 2018). Monsoonal precipitation (July-September) averages 56% of the mean annual precipitation in our southern sites, decreasing to 23% at our higher latitude sites (PRISM Climate Group 2018; Appendix 1 Table A.1.1).

At each site, three 50-meter transects were established perpendicular to the slope and we recorded the physical characteristics of all trees with a diameter at the root collar (DRC) greater than 20 cm within a 5-meter belt upslope from the transect. We measured tree height with a laser range finder and canopy area by taking two perpendicular measurements of the live tree crown. We then sampled 6-8 piñon pine trees per site (randomly selected from our transects) for our cone production analyses. Trees were required to be healthy and reproductively mature, as confirmed by the evidence of at least one cone scar in the previous 15 years. This was determined by observing cones in the canopy of the tree or cutting branches to confirm the presence of cone scars. If six trees that met our sampling criteria were not present within five meters upslope of our transects, we established an additional fourth transect. If this additional

transect did not encompass enough healthy trees to meet our sampling requirements, we sampled the nearest healthy, mature piñon pine of any size within 10 meters of our transects. Damage to the bark can obscure observations of cone scars, particularly further back in time. Thus, trees with conspicuous evidence of severe canopy dieback were excluded from sampling. Low confidence or damaged scars were recorded as null and not included in our analyses. A severe drought in this region in 2002 limited our ability to confidently count cone scars prior to 2004.

We used the cone abscission scar method (Redmond et al. 2016) to quantify historical cone and conelet production from 2004 to 2017. Piñon pine cones leave visible scars at the point of attachment to a branch. Crossdating the presence and absence of scars and any remaining cone or conelets with annual bud scales on the branch allows for the historical reconstruction of cone production in this species (Forcella 1981, Redmond et al. 2016). While this method is highly accurate at distinguishing between years of high and low seed cone production, this method cannot resolve whether seed cones were subsequently aborted prior to seed fall, or the quantity viable seeds were produced (Redmond et al. 2016). We quantified cone production on 6-8 trees at each site by first counting the number of cones and cone scars per year on 6-8 branches per tree and then averaging this value across all branches (following Redmond et al. 2016). This value was then multiplied by the number of cone bearing branches per tree and averaged across all trees sampled for cone production within a site. Branch counts can vary among observers, therefore, estimates of cone bearing branches were performed by a single, consistent observer in the field at all sites.

Statistical Analysis: Masting Metrics

Annual seed cone production was calculated at the site level, as an average of seed cones produced per tree, per year. The long-term mean of seed cone production is this value averaged across all trees and all years. We used the coefficient of variation to describe the population-level interannual variability in cone production (CV_p), which is measured as a ratio of the standard deviation to the mean of site-level cone production (wherein higher values are indicative of greater variability). Synchrony (r) within a site was measured as the pairwise Spearman's correlation (to account for the highly skewed distributions of cone count data) between all trees and across all years at a given site (Table 1.1). Synchrony between sites was calculated as the pairwise Spearman's correlation between sites within a cluster (Appendix 1 Table A.1.1, see below for discussion of clustering methods).

Temporal patterns: Relationship between weather and mast

To identify the weather variables that most strongly influence cone production (Objective 1), we used Spearman's rank correlations to compare mean annual seed cone production at each site ($n=28$) with monthly and bimonthly averages of mean vapor pressure deficit (VPD) and cumulative precipitation (Appendix 1 Table A.1.2 and A.1.3). Conditions like cloud cover, air pressure, and wind speed can influence local weather and plant productivity, but we focused on VPD and precipitation because they strongly influence plant water stress in these dryland ecosystems and are highly correlated with forest growth (Williams et al. 2013; Redmond et al. 2017). VPD is the difference between the amount of moisture in the air (actual vapor pressure) and the amount of moisture the air can hold if it was fully saturated (saturated vapor pressure, Anderson 1936). We assessed running correlations for the three years prior to seed fall (Figure 1.1). We identified the two strongest correlates of seed cone production based on the strongest

Spearman's correlation coefficient. Interpolated weather data were obtained from PRISM at a 4-kilometer resolution (PRISM Climate Group 2018). All analyses were performed in the statistical program R (R Core Team 2016).

Spatial Patterns: Relationship between climate and masting

We examined the effects of the spatial patterns of aridity on piñon pine seed cone production (Objective 2) by focusing on two variables: 30-year normal climatic water deficit (CWD) and monsoonality (percent contribution of July, August, and September precipitation to the mean annual precipitation). Climatic water deficit is the estimated difference between potential and actual evapotranspiration (i.e. the unmet demand for plant-available water), is influenced by changes in solar insolation and topography, and correlates strongly with species distributions (Stephenson 1998). Monsoonality is a spatial measurement of the average seasonal water deficit, which captures the bimodal distribution of precipitation in this region and co-varies strongly with latitude across our sites (Pearson's $r = -0.83$). Monsoonal precipitation provides a significant source of hydrologic relief to plants during the late summer months, when evaporative demand is frequently at its highest and when reproduction is initiated in this species (Little 1938). Moreover, this monsoonal gradient is hypothesized to strongly influence tree sensitivity to annual climate, either due to an increased ability to photosynthesize under greater vapor pressure deficits (Szejner et al. 2016) or genetic adaptation (Mitton and Duran 2004).

Thirty-year averages of climatic water deficit and monsoonality were calculated using field derived measurements of slope, aspect, and latitude with 800-meter resolution PRISM data (PRISM Climate Group 2018) and represent the spatial patterns of water availability at landscape scales. Climatic water deficit was calculated using a Thornthwaite type water balance equation

(Thorntwaite 1948, Dingman 2002) following the equations provided in Lutz et al. (2010), which calculates water loss from a hypothetical standard crop. We used the CWD and AET function in R (Redmond 2018) and assumed a constant soil available water capacity of 200 mm across all sites following Redmond et al. (2017), which is near the upper limit of soil available water capacity in our study region and thus assumes soil available water capacity is not limiting.

We used multiple linear regression to assess the relationship between spatial patterns of water deficits, monsoonality, and masting. We regressed climatic water deficit and monsoonality against mean seed cone production (averaged across all years within a site), interannual variability (CV_p), and synchrony among trees within a site. We hypothesized that tree size would covary with seed cone production and thus included a stand-level covariate to account for differences in tree size among our sites. We used mixed effect models to identify the strongest correlation between three metrics of tree size (live canopy area, basal area measured at root collar, and tree height) and mean seed cone production at the tree-level (see Appendix 1 Table A.1.4 for details). Because canopy area was most strongly related to seed cone production (Appendix 1 Table A.1.4), we averaged mean live canopy area across all trees sampled for seed cone production at each site to include as a covariate in our models. All analyses of spatial patterns were conducted at the site level. We scaled all predictor variables to a mean of zero and a standard deviation of 1 prior to all statistical analyses to facilitate interpretations between coefficients, thus, we report standardized regression coefficients in all models. Variance inflation factors of all models were less than 3 (Zuur et al. 2010) and confirmed using the vif function in the R package “car” (Fox and Weisberg 2019).

Spatiotemporal interactions: Differential sensitivity to the annual drivers of seed cone production

We tested for interactions between spatial patterns of aridity and weather on seed cone production (Objective 3) using generalized linear mixed effect modeling. Specifically, we tested whether climatic water deficit or monsoonalness influenced the sensitivity of annual seed cone production to the two strongest weather correlates identified in Objective 1. Similar to our analyses above, we calculated mean cone production across all trees at a site for each year and thus these analyses were conducted at the site-level rather than the tree-level. We also included mean live canopy area as a covariate in our model. The full model was fit to a negative binomial distribution using the “glmmadmb” package (Fournier et al. 2012). Site was included as a random intercept to account for the repeated measurements (i.e. years) at each site. We tested all possible subsets of model predictors using the dredge function in the “MuMin” package (Barton 2018), ranked these models based on AICc criteria, and averaged all models within four AICc units of the top model (Table 1.2, Appendix 1 Table A.1.6).

Synchrony of seed cone production

Hierarchical cluster analyses were used to identify groups of sites that exhibited synchronous seed cone production. We calculated a Euclidian distance matrix of seed cone production at all sites and across all years using a flexible beta linkage rule of -0.25 to approximate the average linkage between all pairs of sites. Seed cone production was relativized as an annual proportion of the total site production across all years to account for differences in long term productivity or tree size among sites. We plotted the results onto a dendrogram to identify groupings based on shared patterns of mean annual seed cone production and examined

the scale of spatial synchrony across all sites using a Mantel test in the “vegan” package (Oksanen et al. 2018).

Multiple regression on distance matrices (MRM) was used to test the role of weather in structuring the patterns of spatial synchrony. We calculated pairwise geographic distances between all sites and Euclidian distance matrices of the weather correlates identified from Hypothesis 1. These three matrices were then regressed against the Euclidian distance matrix of seed cone production to determine how weather structures spatial synchrony between sites. The model was built in the ecodist package (Goslee and Urban 2007) and significance was determined using a permutation test (n=999, Appendix 1 Table A.1.5).

RESULTS

Temporal patterns: Relationship between weather and masting

We identified two discrete periods with strong associations between seed cone production and weather. These periods correspond to the timing of seed cone initiation and pollination which are two key reproductive processes in pines. The average VPD during the month of August, two years prior to cone maturation (median Spearman’s $\rho = -0.45$, Figure 1.1, Appendix 1 Table A.1.2) and the average VPD during the months of April and May, one year prior to cone maturation (median Spearman’s $\rho = -0.56$, Figure 1.1, Appendix 1 Table A.1.3) were the strongest correlations during each of these respective periods. Annual seed cone production was also positively correlated with precipitation during seed cone initiation (August/September yr-2 median Spearman’s $\rho = 0.44$, Appendix 1 Table A.1.3; Figure 1.1) and pollination (April/May yr-1 median Spearman’s $\rho = 0.50$, Appendix 1 Table A.1.3; Figure 1.1).

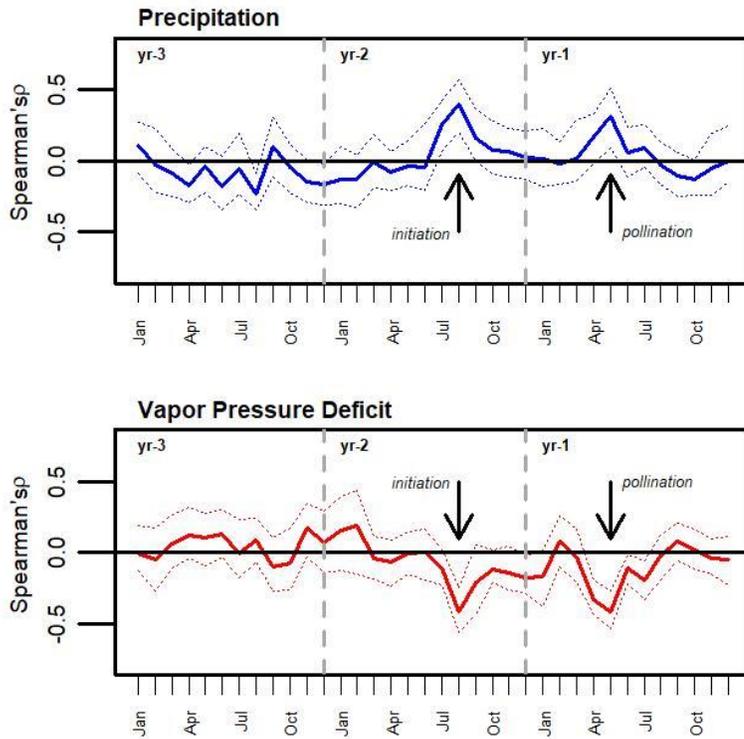


Figure 1.1. Running median Spearman's correlations between annual seed cone production and monthly weather for the three years prior to seed maturation. Solid lines indicate median correlation and dot- ted lines indicate 1st and 3rd quartiles. Top panel shows precipitation (blue line) and bottom panel shows mean vapor pressure deficit (red line). Arrows indicate key phenological periods of seed cone initiation (August, two years prior to seed maturation) and pollination (April/May one year prior to seed maturation).

Spatial Patterns: Relationship between climate and masting

Two components of masting (mean cone production and CV_p) exhibited significant relationships with spatial patterns of aridity (Table 1.1, Figure 1.2). Monsoonalty had a positive association with mean cone production ($\beta = 0.51, P = 0.004$) and a negative association with CV_p

(- 0.30, $P = 0.13$). Inversely, climatic water deficit was associated with higher CV_p ($\beta = 0.52$, $P = 0.009$) and lower mean cone production ($\beta = - 0.44$, $P = 0.008$), indicating that trees at more water limited sites produce smaller and more variable cone crops. Mean live canopy area exhibited a positive association with mean seed cone production ($\beta = 0.32$, $P = 0.043$) but no clear relationship with CV_p ($\beta = - 0.13$, $P = 0.49$). Synchrony between trees at a site showed no relationship with either monsoonality or climatic water deficit, suggesting that the processes that govern local synchrony among trees are relatively uniform across climatic gradients (Table 1.1).

Table 1.1) Model results from multiple linear regression models examining the effects of aridity (climatic water deficit and monsoonality) and mean live canopy area (to account for differences in stand structures) on three masting metrics (mean cone production, CV_p , and within site synchrony). Coefficients are scaled to a mean of zero and a standard deviation of one.

Variable	β	SE	P value
<i>Mean seed cone production model</i>			
Climatic Water Deficit	- 0.44	0.15	0.008
Monsoonality	0.51	0.16	0.004
Mean Live Canopy Area	0.32	0.15	0.043
	$R^2 = 0.54$	$Df = 24$	$P < 0.001$
<i>CV_p model</i>			
Climatic Water Deficit	0.52	0.18	0.009
Monsoonality	- 0.30	0.20	0.13
Mean Live Canopy Area	- 0.13	0.18	0.49
	$R^2 = 0.30$	$Df = 24$	$P = 0.01$
<i>Within site synchrony model</i>			
Climatic Water Deficit	0.17	0.21	0.45
Monsoonality	0.15	0.23	0.99
Mean Live Canopy Area	0.18	0.22	0.42
	$R^2 = 0.06$	$Df = 24$	$P = 0.70$

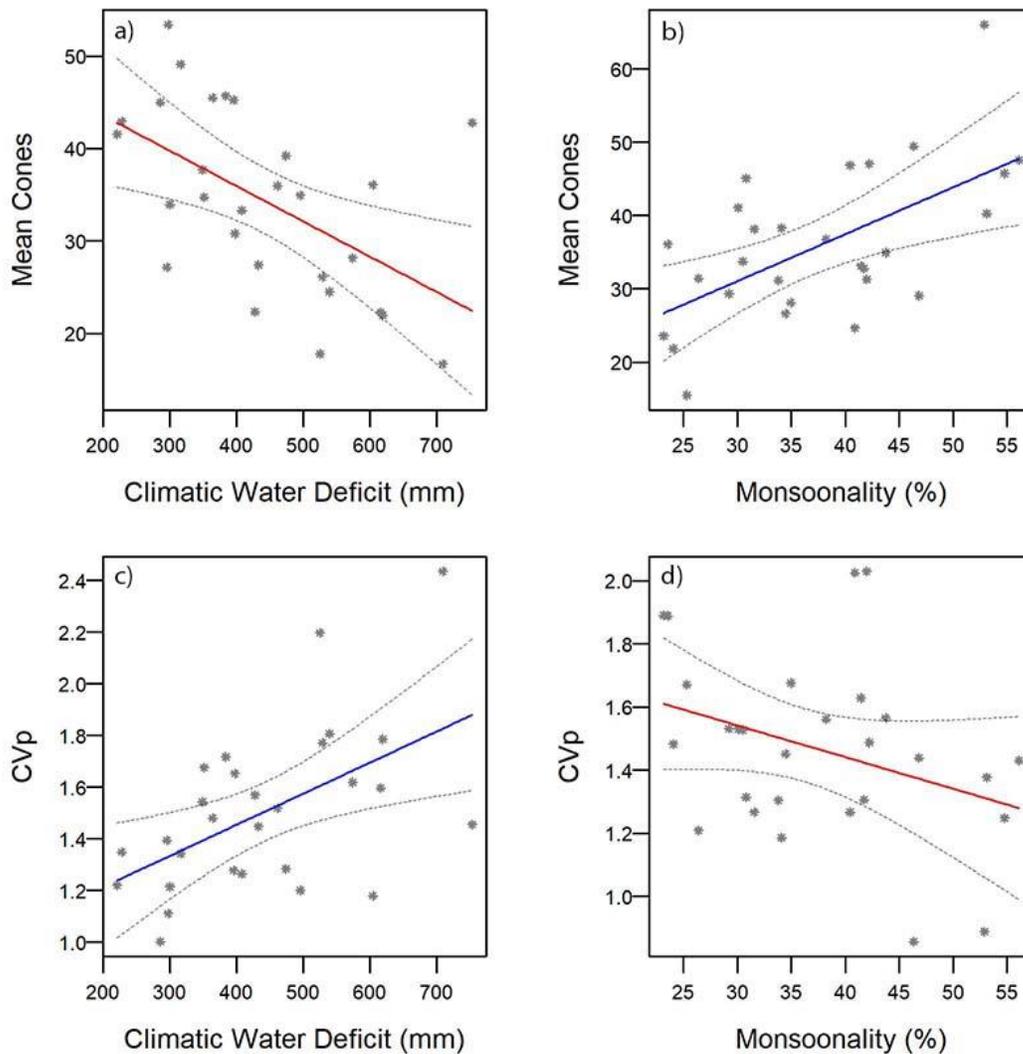


Figure 1.2) Partial residual plots from multiple regression models showing the effects of aridity (30-yr climatic water deficit and monsoonicity) on mean seed cone production (seed cones tree⁻¹yr⁻¹) (panels a and b) and interannual variability of seed cone production (CVp , panels c and d). Solid lines show the predicted mean effect with dashed lines showing the 95% confidence intervals.

Spatiotemporal interactions: Differential sensitivity to the annual drivers of seed cone production

Mean annual seed cone production was strongly associated with weather, aridity, and the interaction between the two (Figure 1.3). We did not detect any significant interactions between climatic water deficit and vapor pressure deficit; however, there were significant interactions between monsoonality and vapor pressure deficit during key periods of the reproductive process, indicating that the seasonal availability of water influenced the sensitivity of trees to evaporative demand (Figure 1.3, Table 1.2). Trees in areas of high monsoonal precipitation were not as strongly negatively associated with vapor pressure deficit during seed cone initiation in the late summer (yr_{-2}) ($P < 0.001$) but were more sensitive to vapor pressure deficit during pollination the following spring (yr_{-1}) ($P = 0.002$). Greater climatic water deficit was associated with decreased annual seed cone production ($\beta = -0.29$, $P < 0.001$) and monsoonality was associated with increased annual seed cone production ($\beta = 0.30$, $P = 0.004$, Table 1.2). Mean live canopy area was also positively associated with seed cone production ($\beta = 0.21$, $P = 0.13$).

Table 1.2) Model averaged coefficients from generalized linear mixed effects models demonstrating the effects of weather, aridity, and the interactions between the two on mean annual seed cone production. Mean live canopy area and the previous year's cone crop were included as covariates in our model. Coefficients are scaled to a mean of zero and a standard deviation of one.

Variable	β	SE	<i>P</i> value
<i>Weather</i>			
April/May VPD yr_{-1}	- 0.54	0.06	< 0.001
August VPD yr_{-2}	- 0.22	0.06	< 0.001
<i>Aridity</i>			
Monsoonality	0.30	0.10	0.004
CWD	- 0.29	0.08	< 0.001
<i>Spatiotemporal Interactions</i>			
April/May VPD yr_{-1} x Monsoonality	- 0.19	0.06	0.002
August VPD yr_{-2} x Monsoonality	0.30	0.07	< 0.001

April/May VPD _{yr-1} x CWD	- 0.02	0.07	0.71
August VPD _{yr-2} x CWD	- 0.08	0.06	0.19
<i>Covariates</i>			
Cones _{yr-1}	- 0.34	0.06	< 0.001
Mean Live Canopy Area	0.21	0.08	0.13

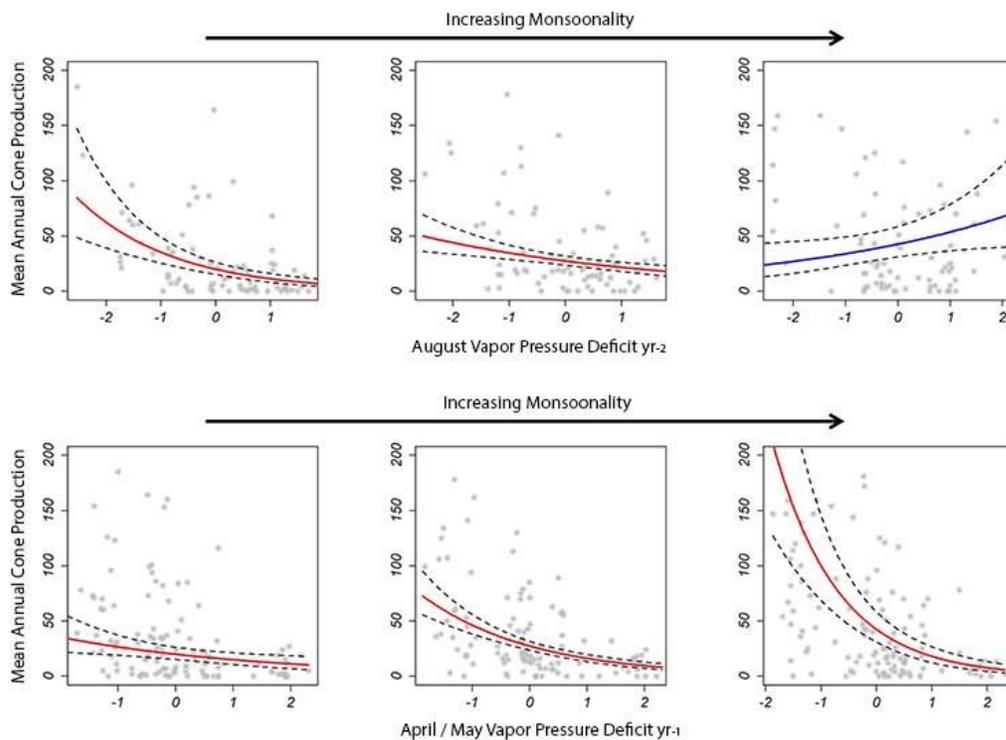


Figure 1.3) Partial residual plots of mean annual seed cone production (seed cones tree⁻¹ yr⁻¹) response to mean vapor pressure deficit at sites of low (10% quartile, left), medium (50% quartile, center) and high (90% quartile, right) levels of monsoonalinity. Top panels show a decreasing sensitivity to vapor pressure deficit during the period of seed cone initiation (August, two years prior to seed maturation) and bottom panels show an increasing sensitivity during seed cone pollination (April/May, one year prior to seed maturation) at higher levels of monsoonalinity. Vapor pressure deficit was scaled to a mean of zero and a standard deviation of 1 at each site. Solid lines show the predicted mean effect with dashed lines showing the 95% confidence intervals.

Synchrony of seed cone production

We identified four clusters of sites that had high synchrony in seed cone production and were for the most part geographically contiguous (Figure 1.4). CV_p within clusters ranged from 1.24 - 1.87. Clusters A and B were located almost entirely within Colorado, and produced on average, approximately 25% fewer seed cones than clusters C and D. Cluster D was located entirely within New Mexico, experienced the highest rates of monsoonal precipitation, and consistently produced the largest cone crops.

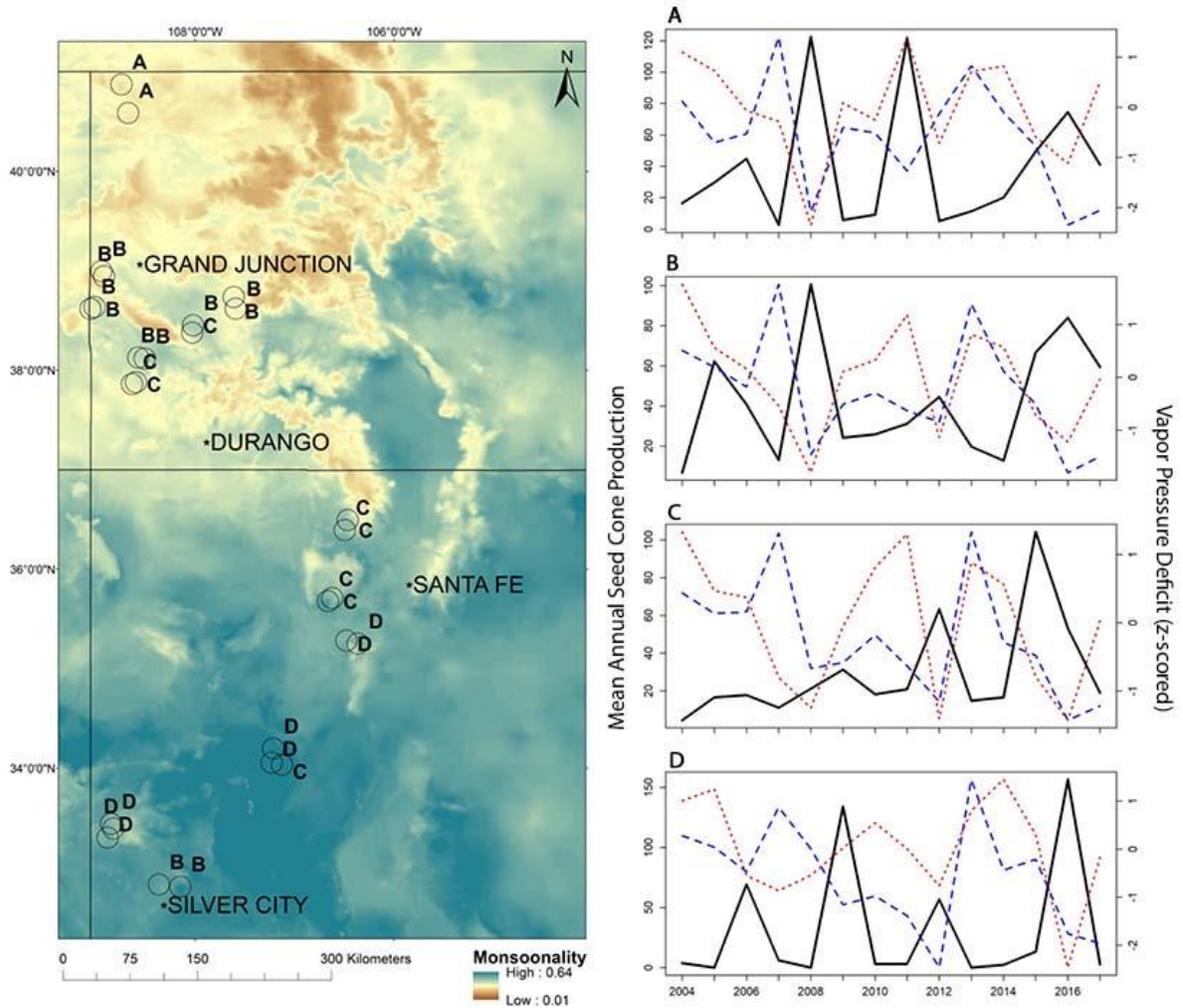


Figure 1.4) Spatial patterns of synchrony (left) and temporal patterns of mean annual seed cone production (seed cones tree⁻¹ yr⁻¹) and associated weather conditions (right) across all study sites. Background coloration of map shows gradient of monsoonality overlaid with distribution of study sites. Letters next to sites indicate cluster association, and selected cities are denoted by a star for reference. Right panels are time series of mean annual seed cone production (left axis, solid black lines) and mean vapor pressure deficits (right axis) during key phenological periods within each cluster from 2004 to 2017. The red dotted line denotes August vapor pressure deficit during seed cone initiation, and the blue dashed line denotes April/May vapor pressure deficits during seed cone pollination. Vapor pressure deficit was scaled to a mean of 0 and a standard deviation of 1 within each cluster.

We detected positive spatial autocorrelation in the synchrony of seed cone production across all sites (Mantel correlation = 0.30, $P = 0.001$) and synchrony remained high at distances up to approximately 500 kilometers (Mantel correlation = 0.20, $P = 0.003$). Vapor pressure deficit during the periods of seed cone initiation (late summer yr₂) and pollination (spring yr₁) were significant predictors of synchrony between sites in our MRM model ($R^2 = 0.29$, $P = 0.001$, Appendix 1 Table A.1.5). Geographic distance was not a significant predictor of between-site synchrony in our model, indicating that the spatial scale of local weather patterns exhibited greater explanatory power than distance alone.

DISCUSSION

Coincident declines in the climatic conditions favorable to seed production and seedling establishment will alter the regeneration niche of many tree species in the future (Enright et al. 2015). In this study, we demonstrate that the spatial patterns of aridity were associated with reductions in mean seed cone crop size and increased interannual variability in seed cone production. Notably, seed cone production was strongly and negatively associated with vapor pressure deficits but the sensitivity of this relationship varied across the latitudinal distribution of

this species in association with spatial patterns of seasonal moisture. As a result, seed availability may be more limiting in arid areas, particularly following years of high vapor pressure deficits or low precipitation. This work demonstrates the potential for a quantitative understanding of conifer seed cone production across large and spatially heterogeneous geographic regions, which is crucial to accurately model changes in forest and woodland demography in response to climate change.

Aridity drives spatial and temporal variation in seed cone production

Our results largely supported our predictions and illustrate the dominant role of water availability in determining variability in seed production across both space and time. Vapor pressure deficit during seed cone initiation and pollination was negatively associated with subsequent annual seed cone production. Similar patterns are seen in Mediterranean oak (*Quercus ilex*), for which greater access to water increased acorn production in both space and time (Perez Ramos et al. 2010). In other systems, however, spatial and temporal correlates of seed production are decoupled. For example, years of high population-level acorn production in valley oak (*Quercus lobata*) are associated with warm spring temperatures, whereas tree-level acorn production is associated with microsites that allow for better access to water (Barringer et al. 2013, Koenig et al. 2015). Our study suggests that evaporative demand during key phenological periods limits reproductive success to irregular intervals and leads to the high variability and episodic nature of mast seeding in this species and likely many others.

The relationship between aridity and the spatiotemporal variability in seed production suggests we can anticipate the impacts of climate change on seed production by understanding changing water dynamics. In other systems where the temporal and spatial correlates of seed

production are decoupled, there can be complex interactions among the drivers of seed production which complicate predictions about the impacts of a changing climate on seed production (Smaill et al. 2011). While our results suggest seed production will be negatively impacted by a warming climate, we demonstrate that these relationships are not uniform across the landscape. The role of summer precipitation, which covaries with latitude in this region, will become increasingly important for maintaining seed cone production in future warmer climates.

We identified clear evidence for Moran effects in the patterns of synchronous seed production across sites. Sites that experienced similar vapor pressure deficits during seed cone initiation and pollination were observed to more frequently mast in concert with one another. The landscape-scale conservation of these relationships points to the potential to develop regional forecasts of mast events, which would prove useful to ecosystem managers and local pine nut gatherers. It is also important to recognize that other weather variables unmeasured in this study may also be useful for future forecasts of masting in this species. Further work is needed to quantify the forecast horizon of masting in this species, although predictions could be made as far as a year or more in advance for piñon pine and further refined in the months preceding seed fall. Challenges to forecasting masting include accounting for the abortion of cones resulting from density dependent impacts of pre-dispersal seed predators and self-pollination.

Broad scale climatic gradients influence sensitivity to annual drivers of seed cone production

Spatial patterning in monsoonal precipitation across the latitudinal distribution of this species affected the sensitivity of seed cone production to vapor pressure deficits. We expected that higher temperatures, which lead to greater vapor pressure deficits, would restrict seed cone

production at the southernmost distribution of our species. Yet the southernmost populations experienced stronger monsoonal climates, which reduced the effects of evaporative demand during seed cone initiation. Annual cone production at sites with stronger monsoonal climates exhibited weaker associations with vapor pressure deficit during reproductive initiation, and these sites exhibited higher mean reproductive output and lower CV_p over the course of this study. Inversely, sites further north were more sensitive to VPD during seed cone initiation but were less sensitive to VPD during pollination. Wetter spring months or greater infiltration of snow melt can act as a buffer against high evaporative demands during pollination in northern portions of piñon pine's range, whereas the lack of spring precipitation further south inversely increases this sensitivity.

This result is intuitive- the onset of the North American monsoon provides significant hydrologic relief to trees during the hottest part of the year (Truettner et al. 2018). Piñon pine also exhibits strong anisohydric tendencies and is efficient at increasing shallow root conductivity following moisture pulses, such as monsoonal storms (Linton et al. 1998, West 2006). Similarly, in southwestern ponderosa pine forests, access to monsoonal precipitation increased the efficiency at which trees were able to maintain photosynthesis under high vapor pressure deficits (Sjenzer et al. 2016). Genetic variation could also explain the differential sensitivity of tree populations to evaporative demand. Alleles associated with longer, narrow stomata in piñon are more frequent in arid microhabitats and in regions with less summer precipitation (Mitton et al. 1998, Mitton and Duran 2004). Stomatal polymorphism likely increases water use efficiency and drought tolerance, and similar relationships may also be present in other tree species that experience seasonal water limitations.

Implications

Our results suggest that predicted increases in water deficits, coupled with increasing evaporative demand, will lead to declines in the frequency and magnitude of mast seed events in climate-sensitive species the future. This trend could depress seedling recruitment, especially following projected increases in overstory mortality events due to wildfire and drought (Williams et al. 2010, Williams et al. 2013, McDowell et al. 2016), and may also negatively impact the various wildlife species that rely on conifer seeds (Christiansen and Whitman 1993, Brown et al. 2001, Fair et al. 2018). Our results, in tandem with previous work from these systems, demonstrate that piñon pine is experiencing significant climate related demographic stress in association with a warming climate. Concurrent declines in seed production (Redmond et al. 2012), seedling establishment (Redmond et al. 2015, Floyd et al. 2015), growth (Redmond et al. 2017), and survival (Breshears et al. 2005) portend a shift in the distribution and persistence of this conifer across the most arid portions of its range. Given piñon pine's role as a keystone species in many ecosystems for providing wildlife habitat (Bombacci and Pejchar 2016), food resources (Ignatov et al. 2017), water retention (Morillas et al. 2017), and carbon storage (Huang et al. 2010), it is vital to understand the potential consequences of this demographic squeeze.

CONCLUSION

Our research demonstrates that seed cone production varies continuously and predictably across climatic gradients and documents the regional synchrony of masting in dry forests and woodlands. The non-linear relationships between weather, climate, and seed cone production highlight the importance of incorporating population-level geographic variability in future studies. Spatiotemporal models of conifer seed cone production and forest demography are key

to anticipating bottlenecks to tree recruitment, predicting range shifts, and identifying spatial refugia for species projected to experience more arid climates.

REFERENCES

- Adams, Henry D., and Thomas E. Kolb. 2005. "Tree Growth Response to Drought and Temperature in a Mountain Landscape in Northern Arizona, USA." *Journal of Biogeography* 32 (9): 1629–40. <https://doi.org/10.1111/j.1365-2699.2005.01292.x>.
- Anderson, Donald B. 1936. "Relative Humidity or Vapor Pressure Deficit." *Ecology* 17 (2): 277–82.
- Barger, Nichole N., and Connie Woodhouse. 2015. "Piñon Pine (*Pinus Edulis* Engelm.) Growth Responses to Climate and Substrate in Southern Utah, U.S.A." *Plant Ecology* 216 (7): 913–23. <https://doi.org/10.1007/s11258-015-0478-4>.
- Barringer, Brian C., Walter D. Koenig, and Johannes M. H. Knops. 2013. "Interrelationships among Life-History Traits in Three California Oaks." *Oecologia* 171 (1): 129–39. <https://doi.org/10.1007/s00442-012-2386-9>.
- Bogdziewicz, Michał, Shealyn Marino, Raul Bonal, Rafał Zwolak, and Michael A Steele. 2018. "Rapid Aggregative and Reproductive Responses of Weevils to Masting of North American Oaks Counteract Predator Satiation." *Ecology*, no. August. <https://doi.org/10.1002/ecy.2510>.
- Bogdziewicz, Michał, Michael A. Steele, Shealyn Marino, and Elizabeth E. Crone. 2018. "Correlated Seed Failure as an Environmental Veto to Synchronize Reproduction of Masting Plants." *New Phytologist* 219 (1): 98–108. <https://doi.org/10.1111/nph.15108>.
- Bogdziewicz, Michał, Jakub Szymkowiak, Marcos Fernández-Martínez, Josep Peñuelas, and Josep M. Espelta. 2019. "The Effects of Local Climate on the Correlation between Weather and Seed Production Differ in Two Species with Contrasting Masting Habit." *Agricultural and Forest Meteorology* 268 (January): 109–15. <https://doi.org/10.1016/j.agrformet.2019.01.016>.
- Bombaci, Sara, and Liba Pejchar. 2016. "Consequences of Pinyon and Juniper Woodland Reduction for Wildlife in North America." *Forest Ecology and Management* 365 (April): 34–50. <https://doi.org/10.1016/J.FORECO.2016.01.018>.
- Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, et al. 2005. "Regional Vegetation Die-off in Response to Global-Change-Type Drought." *Proceedings of the National Academy of Sciences* 102 (42): 15144–48. <https://doi.org/10.1073/pnas.0505734102>.
- Breshears, David D., Charles J. W. Carroll, Miranda D Redmond, Andreas Wion, Craig D. Allen, Neil S. Cobb, Nashelly Meneses, et al. 2018. "A Dirty Dozen Ways to Die: Metrics and Modifiers of Mortality Driven by Drought and Warming for a Tree Species." *Frontiers in Forests and Global Change* 1: 4. <https://doi.org/10.3389/FFGC.2018.00004>.

- Brown, Carissa D., Geneviève Dufour-Tremblay, Ryan G. Jameson, Steven D. Mamet, Andrew J. Trant, Xanthe J. Walker, Stéphane Boudreau, et al. 2018. "Reproduction as a Bottleneck to Treeline Advance across the Circumarctic Forest Tundra Ecotone." *Ecography*, June. <https://doi.org/10.1111/ecog.03733>.
- Brown, J H, T G Whitham, S K Morgan Ernest, and C A Gehring. 2001. "Complex Species Interactions and the Dynamics of Ecological Systems: Long-Term Experiments." *Science* 293 (5530): 643–50. <https://doi.org/10.1126/science.293.5530.643>.
- Buotte, Polly C., Samuel Levis, Beverly E. Law, Tara W. Hudiburg, David E. Rupp, and Jeffery J. Kent. 2018. "Near-Future Forest Vulnerability to Drought and Fire Varies across the Western United States." *Global Change Biology*, no. July: 1–14. <https://doi.org/10.1111/gcb.14490>.
- Chambers, Jeanne C., Stephen B. Vander Wall, and Eugene W. Schupp. 1999. "Seed and Seedling Ecology of Piñon and Juniper Species in the Pygmy Woodlands of Western North America." *Botanical Review* 65 (1): 1–38. <https://doi.org/10.1007/BF02856556>.
- Christensen, Kerry M, and Thomas G Whitham. 1993. "Impact of Insect Herbivores on Competition Between Birds and Mammals for Pinyon Pine." *Ecology*. Vol. 74.
- Enright, Neal J, Joseph B Fontaine, David MJS Bowman, Ross A Bradstock, and Richard J Williams. 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): 265–72. <https://doi.org/10.1890/140231>.
- Fair, Jeanne M., Charles D. Hathcock, and Andrew W. Bartlow. 2018. "Avian Communities Are Decreasing with Piñon Pine Mortality in the Southwest." *Biological Conservation* 226 (December 2017): 186–95. <https://doi.org/10.1016/j.biocon.2018.06.035>.
- Flathers, Kelsey N., Thomas E. Kolb, John B. Bradford, Kristen M. Waring, and W. Keith Moser. 2016. "Long-Term Thinning Alters Ponderosa Pine Reproduction in Northern Arizona." *Forest Ecology and Management* 374: 154–65. <https://doi.org/10.1016/j.foreco.2016.04.053>.
- Forcella, Frank. 1981. "Ovulate Cone Production in Pinyon: Negative Exponential Relationship with Late Summer." *Ecology* 62 (2): 488–91. <http://www.jstor.org/stable/1936722>.
- Huang, Cho ying, Gregory P. Asner, Nichole N. Barger, Jason C. Neff, and M. Lisa Floyd. 2010. "Regional Aboveground Live Carbon Losses Due to Drought-Induced Tree Dieback in Piñon-Juniper Ecosystems." *Remote Sensing of Environment* 114: 1471–79. <https://doi.org/10.1016/j.rse.2010.02.003>.
- Iler, Amy M., and David W. Inouye. 2013. "Effects of Climate Change on Mast-Flowering Cues in a Clonal Montane Herb, *Veratrum tenuipetalum* (Melanthiaceae)." *American Journal of Botany* 100 (3): 519–25. <https://doi.org/10.3732/ajb.1200491>.

- Kelly, Dave, and Victoria L. Sork. 2002. "Mast Seeding in Perennial Plants: Why, How, Where?" *Annual Review of Ecology and Systematics* 33: 427–27. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095433>.
- Koenig, Walter D. 2002. "Global Patterns of Environmental Synchrony and the Moran Effect." *Ecography* 25 (25): 283–88. <http://www.jstor.org/stable/3683734>.
- Koenig, Walter D., and Johannes M. H. Knops. 1998. "Scale of Mast-Seeding and Tree-Ring Growth." *Nature* 396 (6708): 225–26. <https://doi.org/10.1038/24293>.
- Koenig, Walter D., and Johannes M.H. Knops. 2013. "Large-Scale Spatial Synchrony and Cross-Synchrony in Acorn Production by Two California Oaks." *Ecology* 94 (1): 83–93. <https://doi.org/10.1890/12-0940.1>.
- Koenig, Walter D., Johannes M.H. Knops, William J. Carmen, and Ian S. Pearse. 2015. "What Drives Masting? The Phenological Synchrony Hypothesis." *Ecology* 96 (1): 184–92. <https://doi.org/10.1890/14-0819.1>.
- Koenig, Walter D, and Johannes M H Knops. 2000. "Patterns of Annual Seed Production by Northern Hemisphere Trees: A Global Perspective." *Am. Nat* 155 (155): 59–69. <https://www.journals.uchicago.edu/doi/pdfplus/10.1086/303302>.
- Lanner, Ronald M. 1981. *The Pinon Pine: A Natural and Cultural History*. 1st ed. Reno, Nevada: University of Nevada Press. <https://books.google.com/books?hl=en&lr=&id=gvNrFdk5VsgC&oi=fnd&pg=PR9&dq=ronald+lanner+pinon+pine&ots=uWPsAGiBAe&sig=gez8RBKXU1A77RlaXuICMrmH0AA#v=onepage&q=ronald+lanner+pinon+pine&f=false>.
- Linton, M J, J S Sperry, and D G Williams. 1998. "Limits to Water Transport in *Juniperus Osteosperma* and *Pinus Edulis*: Implications for Drought Tolerance and Regulation of Transpiration." *Functional Ecology* 12 (6): 906–11. <https://doi.org/10.1046/j.1365-2435.1998.00275.x>.
- Little, Elbert L. 1943. "Common Insects on Pinyon (*Pinus Edulis*)." *Journal of the New York Entomological Society* 51 (4): 239–52.
- Loik David D Breshears William K Lauenroth Jayne Belnap, Michael E. 2004. "A Multi-Scale Perspective of Water Pulses in Dryland Ecosystems: Climatology and Ecohydrology of the Western USA." *Oecologia* 141: 269–81. <https://doi.org/10.1007/s00442-004-1570-y>.
- Lutz, James A., Jan W. van Wagendonk, and Jerry F. Franklin. 2010. "Climatic Water Deficit, Tree Species Ranges, and Climate Change in Yosemite National Park." *Journal of Biogeography* 37 (5): 936–50. <https://doi.org/10.1111/j.1365-2699.2009.02268.x>.

- McDowell, N G, A P Williams, C Xu, W T Pockman, L T Dickman, S Sevanto, R Pangle, et al. 2016. "Multi-Scale Predictions of Massive Conifer Mortality Due to Chronic Temperature Rise." *Nature Climate Change*. <https://doi.org/10.1038/NCLIMATE2873>.
- McDowell, N. G., A. P. Williams, C. Xu, W. T. Pockman, L. T. Dickman, S. Sevanto, R. Pangle, et al. 2016. "Multi-Scale Predictions of Massive Conifer Mortality Due to Chronic Temperature Rise." *Nature Climate Change* 6 (3): 295–300. <https://doi.org/10.1038/nclimate2873>.
- Mitton, J. B., M. C. Grant, and A. M. Yoshino. 1998. "Variation in Allozymes and Stomatal Size in Pinyon (*Pinus Edulis*, Pinaceae), Associated with Soil Moisture." *American Journal of Botany* 85 (9): 1262–65. <https://doi.org/10.2307/2446636>.
- Mitton, Jeffrey B., and Kristy L. Duran. 2004. "Genetic Variation in Piñon Pine, *Pinus Edulis*, Associated with Summer Precipitation." *Molecular Ecology* 13 (5): 1259–64. <https://doi.org/10.1111/j.1365-294X.2004.02122.x>.
- Monks, Adrian, Joanne M. Monks, and Andrew J. Tanentzap. 2016. "Resource Limitation Underlying Multiple Masting Models Makes Mast Seeding Sensitive to Future Climate Change." *New Phytologist* 210: 419–30. <https://doi.org/10.1111/nph.13817>.
- Mooney, Kailen A., Yan B. Linhart, and Marc A. Snyder. 2011. "Masting in Ponderosa Pine: Comparisons of Pollen and Seed over Space and Time." *Oecologia* 165: 651–61. <https://doi.org/10.1007/s00442-010-1742-x>.
- Moran, PAP. 1953. "The Statistical Analysis of the Canadian Lynx Cycle. 1. Structure and Prediction." *Australian Journal of Zoology* 1 (2): 163. <https://doi.org/10.1071/ZO9530163>.
- Morillas, L., R. E. Pangle, G. E. Maurer, W. T. Pockman, N. McDowell, C. W. Huang, D. J. Krofcheck, et al. 2017. "Tree Mortality Decreases Water Availability and Ecosystem Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S." *Journal of Geophysical Research: Biogeosciences* 122 (12): 3343–61. <https://doi.org/10.1002/2017JG004095>.
- Mutke, Sven, Javier Gordo, and Luis Gil. 2005. "Variability of Mediterranean Stone Pine Cone Production: Yield Loss as Response to Climate Change." *Agricultural and Forest Meteorology*. <https://doi.org/10.1016/j.agrformet.2005.08.002>.
- Park Williams, A., Craig D. Allen, Alison K. Macalady, Daniel Griffin, Connie A. Woodhouse, David M. Meko, Thomas W. Swetnam, et al. 2013. "Temperature as a Potent Driver of Regional Forest Drought Stress and Tree Mortality." *Nature Climate Change* 3: 292–97. <https://doi.org/10.1038/nclimate1693>.
- Pearse, Ian S., Walter D. Koenig, Kyle A. Funk, and Mario B. Pesendorfer. 2015. "Pollen Limitation and Flower Abortion in a Wind-Pollinated, Masting Tree." *Ecology* 96 (2): 587–93. <https://doi.org/10.1890/14-0297.1>.

- Pearse, Ian S., Walter D. Koenig, and Dave Kelly. 2016. "Mechanisms of Mast Seeding: Resources, Weather, Cues, and Selection." *New Phytologist* 212: 546–62. <https://doi.org/10.1111/nph.14114>.
- Pearse, Ian S, Jalene M LaMontagne, and Walter D Koenig. 2017. "Inter-Annual Variation in Seed Production Has Increased over Time (1900-2014)." *Proceedings. Biological Sciences* 284 (1868): 20171666. <https://doi.org/10.1098/rspb.2017.1666>.
- Romme, William H., Craig D. Allen, John D. Bailey, William L. Baker, Brandon T. Bestelmeyer, Peter M. Brown, Karen S. Eisenhart, et al. 2009. "Historical and Modern Disturbance Regimes, Stand Structures, and Landscape Dynamics in Piñon–Juniper Vegetation of the Western United States." *Rangeland Ecology & Management* 62 (3): 203–22. <https://doi.org/10.2111/08-188R1.1>.
- Rother, Monica T., and Thomas T. Veblen. 2017. "Climate Drives Episodic Conifer Establishment after Fire in Dry Ponderosa Pine Forests of the Colorado Front Range, USA." *Forests* 8 (159): 1–14. <https://doi.org/10.3390/f8050159>.
- Ruano, Irene, Rubén Manso, Mathieu Fortin, and Felipe Bravo. 2015. "Extreme Climate Conditions Limit Seed Availability to Successfully Attain Natural Regeneration of Pinus Pinaster in Sandy Areas of Central Spain." *Canadian Journal of Forest Research* 45: 1795–1802. <https://doi.org/10.1139/cjfr-2015-0257>.
- Savage, Melissa, Peter M. Brown, and Johannes Feddema. 1996. "The Role of Climate in a Pine Forest Regeneration Pulse in the Southwestern United States." *Ecoscience* 3 (3): 310–18. <https://www.jstor.org/stable/pdf/42900650.pdf>.
- Seager, Richard, Mingfang Ting, Isaac Held, Yochanan Kushnir, Jian Lu, Gabriel Vecchi, Huei-Ping Huang, et al. 2007. "Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America." *Science* 316: 1181–84.
- Shelef, Oren, Peter J Weisberg, and Frederick D Provenza. 2017. "The Value of Native Plants and Local Production in an Era of Global Agriculture." *Frontiers in Plant Science Front. Plant Sci* 8 (8). <https://doi.org/10.3389/fpls.2017.02069>.
- Shepperd, Wayne D, Carleton B Edminster, and Stephen A Mata. 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. https://www.fs.fed.us/rm/pubs_exp_forests/manitou/rmrs_2006_shepperd_w001.pdf.
- Smaill, Simeon J., Peter W. Clinton, Robert B. Allen, and Murray R. Davis. 2011. "Climate Cues and Resources Interact to Determine Seed Production by a Masting Species." *Journal of Ecology* 99 (3): 870–77. <https://doi.org/10.1111/j.1365-2745.2011.01803.x>.

- Stephenson, Nathan. 1998. "Actual Evapotranspiration and Deficit: Biologically Meaningful Correlates of Vegetation Distribution across Spatial Scales." *Journal of Biogeography* 25 (5): 855–70. <https://doi.org/10.1046/j.1365-2699.1998.00233.x>.
- Szejner, Paul, William E Wright, Flurin Babst, Soumaya Belmecheri, Valerie Trouet, Steven W Leavitt, James R Ehleringer, and Russell K Monson. 2016. "Latitudinal Gradients in Tree Ring Stable Carbon and Oxygen Isotopes Reveal Differential Climate Influences of the North American Monsoon System." *Journal of Geophysical Research: Biogeosciences* 121: 1978–91. <https://doi.org/10.1002/2016JG003460>.Received.
- Thornthwaite, C. W. 1948. "An Approach toward a Rational Classification of Climate." *Geographical Review* 38 (1): 55. <https://doi.org/10.2307/210739>.
- Truettner, Charles, William R.L. Anderegg, Franco Biondi, George W. Koch, Kiona Ogle, Christopher Schwalm, Marcy E. Litvak, John D. Shaw, and Emanuele Ziaco. 2018. "Conifer Radial Growth Response to Recent Seasonal Warming and Drought from the Southwestern USA." *Forest Ecology and Management*, no. January: 1–8. <https://doi.org/10.1016/j.foreco.2018.01.044>.
- West, Adam Gerard. 2006. "The Influence of Seasonality of Precipitation on Transpiration in Piñon-Juniper Woodlands."
- Whipple, Amy V., Neil S. Cobb, Catherine A. Gehring, Susan Mopper, Lluvia Flores-Rentería, and Thomas G. Whitham. 2019. "Long-Term Studies Reveal Differential Responses to Climate Change for Trees Under Soil- or Herbivore-Related Stress." *Frontiers in Plant Science* 10 (February): 1–14. <https://doi.org/10.3389/fpls.2019.00132>.
- Williams, A Park, Craig D Allen, Constance I Millar, Thomas W Swetnam, Joel Michaelson, Christopher J Still, and Steven W Leavitt. 2010. "Forest Responses to Increasing Aridity and Warmth in the Southwestern United States." *Proceedings of the National Academy of Sciences of the United States of America* 107 (50): 21289–94. <https://doi.org/10.1073/pnas.0914211107>.
- Zlotin, R. I., and R. R. Parmenter. 2008. "Patterns of Mast Production in Pinyon and Juniper Woodlands along a Precipitation Gradient in Central New Mexico (Sevilleta National Wildlife Refuge)." *Journal of Arid Environments*. <https://doi.org/10.1016/j.jaridenv.2008.02.021>.
- Zuur, Alain F., Elena N. Ieno, and Chris S. Elphick. 2010. "A Protocol for Data Exploration to Avoid Common Statistical Problems." *Methods in Ecology and Evolution* 1 (1): 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.

CHAPTER 2

²JOINT IMPACTS OF WEATHER, CLIMATE, AND STAND STRUCTURE ON MAST SEEDING IN PONDEROSA PINE

OVERVIEW

Tree recruitment is shaped by climate, disturbance, and seed availability. Many trees are masting species, meaning seed production is highly variable from year to year and often synchronous within a stand. Masting remains poorly understood, and it is uncertain how a changing climate, altered disturbance regimes, and shifting management priorities may impact the timing and magnitude of future seed production across species ranges. We aimed to better understand what drives masting in a widely distributed conifer species in western North America, Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*) dominated ecosystems. We surveyed ca. 15 years of cone production in 275 individuals from 49 locations varying in both climate and stand structure and which encompassed a 1300 km latitudinal gradient between Arizona and South Dakota, USA. We used mixed models to test competing hypotheses behind the drivers of annual cone production, and modeled the mean, interannual variability, and synchrony of cone production as a function of tree size, age, neighborhood competition, and climate (30-year average of climatic water deficit [CWD] and actual evapotranspiration [AET]). Weather and climate only weakly described annual cone production in ponderosa pine (R^2_m of top model = 1.6%, $R^2_c = 30.1\%$), indicating substantial individual-level variability among years and among sites. Importantly, we found that tree size and neighborhood competition were strong drivers of the mean, interannual variability, and synchrony of cone production at the individual-

² By Andreas P. Wion, Ian S. Pearse, Kyle C. Rodman, Thomas T. Veblen, and Miranda D. Redmond.

level. Larger and open grown trees produced more cones with greater synchrony than smaller, densely grown trees, and larger trees also had lower interannual variability in cone production. Our study suggests that masting in ponderosa pine is driven by individual-level variability and strongly influenced by local, demographic factors like competition and tree size. Thus, management interventions that target these factors could also be powerful tools to alter tree recruitment in the future.

INTRODUCTION

The composition and distribution of future forests depends on recruitment (Sharma et al. 2021, McDowell et al. 2020). For many seed-obligate (non-resprouting) species, seed availability is a primary filter on new tree recruitment (Gratzer et al. 2021, Crofts and Brown 2020, Brown et al. 2019, Clark et al. 1999). But seed production is still a relatively poorly understood component of tree demography, and it is uncertain how seed production may be affected by warming temperatures, altered disturbance regimes, or shifting management strategies (Hackett-Pain and Bogdziewicz 2021, Vacchiano et al. 2021, Bogdziewicz 2021). This is in part because many trees are masting species, meaning individual-level seed production varies from year to year, often synchronously within a population (Pearse et al. 2016). Mast years (or infrequent years of synchronous, large seed crops) are often driven by interannual variability in weather (Pearse et al. 2016), but the magnitude and frequency of seed crops vary among individuals of different sizes (Bogdziewicz et al. 2020, Minor and Kobe 2017, 2019), ages (Pesendorfer et al. 2020), stand densities (Andrus et al. 2020, Flathers et al. 2016), and climate regimes (Bogdziewicz et al. 2019, Koenig et al. 2020, Wion et al. 2019). For many species, it remains unknown how the complex mosaic of climate and competition jointly shapes mast seeding across species ranges. Yet this information is necessary to anticipate disturbance and climate change impacts on future

seed production and recruitment potential (Clark et al. 2021, Sharma et al. 2021), and to inform how management decisions (thinning, burning, and logging) might affect future seed availability (e.g., Pearse et al. 2021).

Masting imparts a cost on trees by foregoing opportunities for recruitment in years when seed production is either low or absent (Pearse et al. 2016). Masting also, however, provides advantages by creating economies of scale, or fitness benefits accrued at the individual-level through synchrony at the population-level, like predator satiation (Janzen 1971, Linhart et al. 2014) and pollination efficiency (Moreira et al. 2014). As a result, changes in the synchrony or interannual variability of seed production can have greater effects on seed availability than changes in the overall mean of individual-level seed production (Bogdziewicz et al. 2021). For example, decreases in the variability and synchrony of seed production in European beech (*Fagus crenata*) led to a greater proportion of seeds being predated by insects, despite an overall increase in seed production by individual trees (Bogdziewicz et al. 2021). Understanding what shapes the variability and synchrony of seed production is crucial for managing masting species into the future.

The resource budget hypothesis of masting (Isagi et al. 1997, Crone and Rapp, 2014) posits that plants are unable to acquire the resources sufficient to produce large, annual seed crops. Instead, plants store resources across multiple years to expend in infrequent, synchronous mast events. Weather acts as a proximate driver of masting by either triggering or vetoing the mechanisms that lead to successful seed initiation, pollination, or seed maturation (Pearse et al. 2014, 2016). Under this hypothesis, climate change may affect future seed production by altering the frequency and magnitude of vetoes and triggers of mast years (Bogdziewicz 2021). Alternatively, seed production may be driven and synchronized by a “cue” (i.e., a signal without

a direct, physical effect on seed maturation) that allows individual plants to reap the benefits of synchronized, population-level reproduction (Kelly et al. 2013). For example, the difference in temperature between the year of seed initiation and the year prior (“ ΔT ”) has been identified as a predictor of mast years in many species (Kelly et al. 2013, LaMontagne et al. 2021). Under this alternative hypothesis of masting, increasing mean temperatures are not expected to have significant impacts on seed production, because the difference in temperatures between any two years are not expected to change substantially (LaMontagne et al. 2021) Identifying which weather variables, and precisely how these variables affect seed production (i.e., as ‘proximate drivers’ or as ‘cues’) is necessary to anticipate climate change impacts on future seed production.

Range-wide demographic studies are key tools for assessing how plant populations may respond to a changing climate (Doak and Morris 2010). Recent research has challenged the assumption that all populations of a species respond identically to weather (Bogdziewicz et al. 2019, Wion et al. 2019, Koenig et al. 2020, Nussbaumer et al. 2016, Roland et al. 2014), suggesting any potential effects of a changing climate on masting may not unfold uniformly across the landscape. For example, in widely distributed species, populations may be limited by different climatic factors, or limited to different degrees across gradients of environmental stress (Ronald et al. 2014, Pearse et al. 2017, Bogdziewicz et al. 2019, Wion et al. 2019). Under a warming climate, plants in more stressful environments or at the margins of their distributions may be most sensitive to changes in climate-driven resource availability (e.g., environmental stress hypothesis; Pearse et al. 2017). The sensitivity of individual-level seed production to weather shapes the synchrony and variability of masting at the population-level, which in turn has important implications for forecasting mast years and assessing potential climate change impacts on plant and animal populations.

Disturbances like fire and drought, and human actions like thinning and logging, contribute to a complex mosaic of seed availability across the landscape by altering the spatial patterns and size and age distribution of trees within a stand. Local-scale variation in competition and tree sizes (i.e., stand structure) alter levels of competition for light, water, and nutrients, which impacts reproduction in many species (Andrus et al. 2020, Minor and Kobe 2019). Generally, larger trees and trees with greater access to abundant light, water, and nutrients produce more seeds than smaller trees growing in more competitive or less productive environments (Greene et al. 2002, Minor and Kobe 2017, 2019). Larger trees also tend to have fewer years without seed production, which lowers their variability and synchrony compared to smaller trees (Bogdziewicz et al. 2020). But other studies have found age, which is imperfectly related to size, to be a stronger predictor of changes in reproductive variation and synchrony over time, suggesting ontogenetic changes in resource dynamics may also play an important role in shaping masting behavior (Pesendorfer et al. 2020). If demographic attributes and stand structure strongly regulate seed production, then it stands to reason that management interventions that target these factors could also be powerful tools to alter tree recruitment.

To fill these gaps in our knowledge, we set out to quantify the role of weather, climate (i.e., the long-term energy and water balance of a site), and stand structures (i.e., demographic factors like size, age, and neighborhood competition) on mast seeding in a widespread conifer species native to western North America, Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*). Ponderosa pine is an ecologically and economically important conifer species found in montane forests, parks, and woodlands throughout western North America (Burns and Honkala, 1990). The production of a single crop of cones takes a little more than two full years. Initiation of cones occurs in the summer, two years before maturation (T-2), and pollination

occurs the following spring, one year before maturation (T-1). Seeds and cones rapidly mature in the final year (T) and are dispersed by wind and gravity (Krannitz and Duralia 2004). Cone abscission scars were used to reconstruct ca. 15 years of cone production of 275 trees from 49 sites, which spanned a 1300 km latitudinal gradient across a large portion of this species distribution in the western United States.

Previous work in a population of this species near Boulder, Colorado, USA, related mast years to several possible proximate drivers: below average summer temperatures and above average summer precipitation during the year of cone initiation (T-2), and spring temperatures during the year of cone pollination (T-1). However, relationships to temperature and precipitation were inconsistent in a separate population 100 km south and 1000 meters higher in elevation (Mooney et al. 2011). Further studies in this region have yet to resolve these differences in masting drivers across different sites. Only one study has assessed absolute temperature vs ΔT as drivers of cone production in ponderosa pine and found greater support for the absolute temperature model over the ΔT model (Morieria et al. 2015). Yet that study was limited in scope to a single population, and a recent assessment of North American conifers found broad support for ΔT across many taxa (which included ponderosa pine among multiple other “hot climate” pine species; LaMontagne et al., 2021). Another recent study found that ponderosa pine reproduction was largely asynchronous across much of its distribution and was not strongly related to large scale modes of climate variability like the El Niño Southern Oscillation or the North American monsoon (Wion et al. 2021). Therefore, the annual drivers of ponderosa pine seed production remain uncertain and warrant more detailed study.

Our research was driven by the following questions:

- 1) Which weather variables best explain patterns of annual cone production in ponderosa pine?
- 2) How does the relationship between weather and masting change across sites of varying climate conditions (i.e., the long-term water and energy balance at an individual site)?
- 3) How does spatial variability in climate and stand structures (tree size, age, and neighborhood competition) jointly affect the mean, synchrony, and interannual variability of cone production of individual trees?

We assessed evidence in the context of the resource budget (i.e., “proximate drivers) and “differential cue” hypotheses of masting. We hypothesized that cone production would be positively associated with cool and wet summer weather, consistent with previous studies in this species and other species in this region (Mooney et al. 2011, Wion et al. 2019, Parmenter et al. 2018). Under the resource budget hypothesis, we would expect the relationship between weather and cone production to be stronger in drier and less productive environments, because reproduction is more strongly and frequently limited by climate. Consequently, we expect drier and less productive sites to exhibit greater interannual variability in cone production, greater synchrony among trees in a site, and lower mean cone production. We also expected smaller and younger trees, and trees with a high density of neighbors, to exhibit greater interannual variability, lower synchrony, and a lower mean of cone production. Under the differential cue hypothesis of masting, we would expect trees to be strongly synchronous with one another, both within sites and among closely located sites that share similar annual summer weather. We would not expect the strength of the relationship between weather and cone production to vary substantially among sites of differing climatic conditions, because this would negate the synchronizing effect and fitness benefits of a hypothetical cue.



Figure 2.1) Top: Ponderosa pine dominated woodland, with *Pinus edulis* and *Juniperus osteosperma*, near Douglas Mountain, Moffat County, Colorado, USA. Mean 30-year actual evapotranspiration is relatively low, indicating low availability of energy and moisture, and climatic water deficit is high indicating chronic drought stress. Notice exposed bedrock, sparse understory, and relatively few, large, open grown trees. Bottom: Ponderosa pine dominated forest in Black Hills, Pennington County, South Dakota, USA, Co-occurring species include *Picea glauca* and *Betula papyrifera*. Mean 30-year actual evapotranspiration is relatively high

and climatic water deficit is low, indicating simultaneous availability of energy and moisture (warm and wet climate) and little drought stress. Notice continuous grass cover with abundant seedlings, and dense regeneration in background.

METHODS

Data Collection

The study area included ponderosa pine dominated forests and woodlands in the US states of Arizona, New Mexico, Colorado, Wyoming, and South Dakota. This area was bounded by 35° – 45° north latitude and -112° and -103° west longitude, or approximately a 1300 km latitudinal gradient. Site selection occurred by first locating potential field sites – locations within our study area that contained ponderosa pine and were within 1 km of an accessible road or trail. Sites were compiled from multiple research projects (see Rodman et al. 2020), so multiple sites (n = 31) were intentionally sampled within refugia of burn perimeters or located in unburned forests near these perimeters. After navigating to these points, we confirmed that each site contained at least five reproductively mature trees within 50 meters of a randomly placed plot center. Field sampling in Colorado and New Mexico (n = 34) occurred primarily in 2018. Sites in Wyoming (n = 4), South Dakota (n = 7), Arizona (n = 2), and northwestern Colorado (n = 2) were sampled in 2020.

We collected seed cone production data from 275 trees at 49 sites using the cone abscission scar method (Forcella 1978, Redmond et al. 2016). This method involves sampling multiple branches from focal trees and counting the abundance or absence of cone scars (evidence of past reproduction) in relation to bud scale scars. We counted the number of cone bearing branches on each tree, which allows us to scale the estimates of cones per branch to the tree-level. This method has been used in several species (Bouchard and Pernot 2020, Wion et al. 2019), including ponderosa pine (Rodman et al. 2020), and is highly effective at distinguishing

years of high from low seed production at the individual-level, and at distinguishing between high and low cone producing trees (Redmond et al., 2016).

Emerging, unfertilized conelets that were observed in the year of sampling were not counted, because the timing of field sampling often spanned the emergence of these conelets (early to mid-summer) and could not consistently be recorded across sites. Some sites (n=10) that were established in 2018 were opportunistically resampled in 2019 for an additional year of data during a mast year. This was performed with binocular counts of cones across at least five random branches, and averaging observations across branches to the tree level (identical to the approach for counting evidence of reproduction in cone scar method).

At each site, we randomly sampled between 5-7 mature trees for cone production data. We counted cone scars on at least five, reproductively mature trees at each site using at least 5 branches from each tree – a sample size shown to adequately capture interannual variation in cone production at the individual and population level (Redmond et al. 2016). Because sampling occurred over multiple years, and branches on some trees were only able to be sampled over a shorter timespan, the length of the time series varied among trees and across sites. Damage from herbivory or accrued over time by weathering obscures older cone scars, and thus trees were not sampled beyond the year 2001 (mean number of sampling years per tree = 14.5 years). The majority of series (95.5%, n=260) were longer than 10 years (max = 19 years), and the shortest time series was 6 years (n = 1).

We collected information on focal tree size (measured as diameter at breast height [DBH] or approximately 140 cm above the ground) and neighborhood competition using a basal area prism (adjustment factor = 5). We took increment cores from all trees sampled in 2018 to estimate individual tree ages. Trees were cored using either a 5mm or 12mm increment borer at

20-40 cm above the root collar, and cores were sanded and dated using standard dendrochronological techniques. Tree age was estimated by correcting for the offset from pith and the time to reach coring height (See Rodman et al. 2021 for details). We excluded trees that could not be dated due to a high occurrence of missing rings, rotted centers, or completely missed piths. We obtained estimates of tree age for roughly half of all trees in the final analysis ($n = 139$, 50.5% of trees). Because of the reduced sample size, analyses including age were performed separately (see below).

Masting Metrics

We calculated three metrics commonly used to describe masting behavior among individual trees: mean annual cone production, interannual variability, and synchrony. Annual cone production was sampled at the tree-level and all analyses were kept at the scale of the individual tree. Mean annual cone production was calculated as the average cone production per tree, across all years sampled. Interannual variability at the individual-level was calculated as the coefficient of variation (CV_i) or the ratio of the standard deviation to the mean. Higher values of CV_i indicate larger, between year differences in cone production at the tree-level. Synchrony was calculated as Pearson's pairwise cross correlation of cone production between a focal tree and all other trees sampled for cone production at the site (values range from -1 to 1, with 1 being perfectly synchronous).

Weather and Climate Variables

We used monthly PRISM climate data at a 4km^2 resolution to describe weather across our study area (PRISM Climate Group 2021). We focused on two meteorological variables -

precipitation and vapor pressure deficit (VPD) - which is tightly and exponentially related to maximum temperature (Grossiord et al. 2020). VPD is the difference between potential vapor pressure when the air is saturated with water and the actual vapor pressure of the atmosphere (Anderson 1936) and describes the atmospheric demand for water from plants and soils. Larger VPD values indicate warmer and drier conditions.

Monthly mean VPD and cumulative precipitation data were extracted at each site for the 3-year period preceding each observation of annual cone production. This length of time includes the events of cone pollination (year T-1 before cone maturation) and cone initiation (T-2 before cone maturation), as well as the “differential cue” period (the difference between years T-2 and T-3, Kelly et al. 2013). We aggregated monthly data into running three-month means (or sums, in the case of precipitation) to account for latitudinal variation in seasonal timing in our data and to smooth the high variability among individual months. Monthly precipitation and VPD were z-score standardized to a mean of zero and a standard deviation of one within each site, to account for climatic differences across sites and isolate deviations from the long-term mean. Vapor pressure deficit was calculated using PRISM derived mean temperature and dew point, using the equations in Williams et al. (2013).

We calculated ΔT as the difference in mean temperature of the peak boreal summer months (June, July, and August) between the year of cone initiation (T-2) and the year prior (T-3). Negative values of ΔT indicate years where T-3 was warmer than T-2, and positive values indicate years where year T-3 was cooler than T-2. We also calculated the difference between summer VPD during the same time period (i.e., ΔVPD , analogous to the ΔT model) to match our analyses containing VPD. Similarly, negative values of ΔVPD indicate a high evaporative demand in year T-3 that was followed by lower evaporative demand in year T-2, and positive

values indicate the opposite pattern (low evaporative demand in T-3 followed by high evaporative demand in T-2).

To describe climatic differences across the study area, we utilized two variables that describe the spatial variability in energy and water balance among sites. The first was the 30-year average of actual evapotranspiration (AET), or the water lost through evaporation and transpiration that is constrained by moisture availability (i.e., precipitation). High values of AET are associated with warmer and wetter climates and high amounts of primary productivity, low values of AET are associated with cooler and drier climates and low amounts of primary productivity. The second was the 30-year average of climatic water deficit (CWD), the difference between potential and actual evapotranspiration. This describes the evaporative demand of a site that is unmet by moisture availability and is used as a proxy for aridity or dryness (Stephenson 1990, 1998). Higher values of CWD are associated with hotter and drier climates. Values were extracted at the center point locations for each site from gridded 4km² Terra Climate products (Abatzoglou et al. 2018).

Table 2.1) Description and ranges of the constituent parts of models predicting masting behavior (mean, interannual variability, and synchrony among trees at a site) at the tree-level.

Abv.	Description	Type	Range
CV _i	Interannual variability of cone production at tree-level	Response	0.41 – 4.24
r	Synchrony of cone production between trees at site	Response	- 0.33 – 0.90
μ	Mean of cone production at tree-level	Response	1 - 512
CWD	30-year average of Climatic Water Deficit	Predictor	353 – 781 (mm)
AET	30-year average of Actual Evapotranspiration	Predictor	275 – 548 (mm)
DBH	Diameter of tree at breast height	Predictor	11.8 – 98 (cm)
BA5	Basal area of neighborhood surrounding focal tree	Predictor	0 – 22.96 (m/ha)
AGE	Age of tree in 2018 (<i>n</i> = 136)	Predictor	40 – 238 (yrs)

Statistical Analyses: Which weather variables best explain patterns of annual cone production in ponderosa pine?

We performed analyses was to identify the most parsimonious combination of “proximate drivers,” and compare this against a “differential cue” model to test hypotheses about the drivers of masting in ponderosa pine. We began by identifying potential combinations of precipitation and VPD during the three-years prior to seed maturation (i.e., the cone development phase) that we hypothesized would be associated with subsequent ponderosa pine cone production. We calculated the Spearman’s correlation coefficient between site-level annual cone production (averaged across all trees per year to avoid pseudo-replication) and each weather variable. We then reduced this matrix by ranking all variables based on their median correlation coefficient (measured across all sites) as an indicator of which variables and time periods were most strongly associated with cone production across the greatest number of sites (Table 2.2, similar to Wion et al. 2019). Notably, these univariate correlations were lower than weather-masting relationships reported for other populations of dry pine species in this region (Mooney et al. 2011, Wion et al. 2019). Nevertheless, these analyses indicated two key points: 1) the differential cue Δ VPD was the strongest univariate correlation with cone production across the greatest number of sites, outperforming Δ T, and 2) mid-summer VPD and precipitation during the year of cone initiation (June – September, year T-2) were the strongest absolute predictors of cone production (Table 2.2). We used these preliminary results to guide the inclusion of weather variables in the model building process.

Table 2.2) Median and one standard deviation (σ) values calculated from 49 Spearman’s correlations (ρ) between site-level cone production (averaged across all trees per year) and the seven strongest weather variables analyzed. The number of sites (and respective proportions) with statistically significant Spearman’s correlations ($P < 0.05$) is also reported. Fewer than a quarter of all sites sampled had statistically significant relationships with any weather variables. The notation T denotes the year of cone maturation, and the number indicates the years prior to cone maturation. Cone initiation occurs in year T-2. Abbreviations are JJA = June, July, and

August, and JAS = July, August, September. Δ VPD and Δ T are calculated as the difference between summer mean temperature or VPD (June, July, August) between year T-2 and T-3.

Weather variable	Median Spearman's ρ	σ Spearman's ρ	n sites (% total) $P < 0.05$
Δ VPD	- 0.30	0.24	8 (16.3%)
T-2 PPT JJA	0.27	0.24	11 (22.4%)
T-2 VPD JAS	- 0.25	0.20	3 (6.1%)
T-2 PPT JAS	0.24	0.21	4 (8.1%)
Δ T	- 0.20	0.24	7 (14.2%)
T-3 VPD JJA	0.20	0.23	3 (6.1%)
T-2 VPD JJA	- 0.19	0.20	6 (12.2%)

The differential cue hypothesis rests on two key premises – the *difference* in temperatures (or in this case, VPD) between years better explains cone production compared to *absolute* temperature or VPD in either year, and the improbability of multiple, consecutive years of large temperature differentials explains the patterns of negative autocorrelation of seed production in trees (or the tendency for “bust” years to follow “boom” years). To explicitly test these assumptions, and following previous research on this topic (Monks et al. 2016, Moriera et al. 2015, Pearse et al. 2014) we included two additional variables in our model selection process. We tested models containing absolute summer VPD in year T-3 (June, July, and August; the strongest univariate correlation in year T-3 [Table 2.2]), and we also included cone production in the year prior to maturation (i.e., negative autocorrelation in T-1) as a covariate in all models.

We tested all possible two-way combinations of plausible VPD and precipitation variables. We used generalized linear mixed models (GLMMs) and an information theoretic approach to assess the effects of weather on ponderosa pine cone production. Annual cone

production data arose from an overdispersed count process at the scale of the individual tree, which were grouped within sites. Therefore, we specified a GLMM with a negative binomial error distribution (quadratic parametrization, i.e., “nbinom2”) and an observational-level random effect (Harrison et al. 2014), as well as a random intercept of tree nested within site to account for the hierarchical structure of the data. All model terms were scaled to a standard deviation of one and centered on zero to facilitate comparisons of effect sizes. Collinearity of predictor variables in all models was confirmed to be low (variable inflation score < 2). We ranked models based on AIC, which balances model parsimony with explanatory power, and retained the model with the lowest AIC score as the top model (Appendix 2, Table A.2.1). Models within 4 AIC units of each other were considered equally parsimonious, and we retained or reported the simpler of the two models.

Statistical Analyses: How does the relationship between weather and mastling change across sites of varying climate conditions?

After identifying a top model of annual cone production, we tested whether the relationship between weather and cone production was conditioned on the long-term climate of a site. We built models with interaction terms between each weather variable (identified from the top model above) and 30-year averages of AET and CWD. If either model reduced AIC from a top identified model without the interaction effect, we selected the model with the lowest AIC as the final (i.e., “full”) model.

We report the difference in AIC values from a null (random intercept only) model, and we also report standardized coefficients and errors from this full model. We report the goodness of fit top models using the marginal pseudo R^2 for mixed models (Nakagawa and Schielzeth,

2013), describing the fixed effects components of the top model. Pseudo R^2 values describe the relationship between model predictions and observations after accounting for a distribution specific variance component and a latent residual variance and are constrained to values between 0-100% (Nakagawa and Schielzeth, 2013).

Statistical Analyses: How do long term climate and forest structure shape masting behavior?

We used multi-model inference to determine the influence of forest structure and long-term climate on masting behavior at the scale of the individual-tree. We built linear mixed models that predicted the mean, synchrony, and interannual variability as a function of tree size (diameter at breast height), tree age (when cored in 2018), neighborhood competition (basal area surrounding focal tree), and 30-year climate averages (CWD and AET; measured at the site-level). Structural attributes (tree size, age, and neighborhood competition) were measured or collected in the field, at the scale of the individual focal tree. Tree age estimates were available for only about half of trees (n=136) and were not consistently available across all trees at each site. Therefore, we performed identical but separate analyses to determine the effects of age on masting behavior. We tested linear and non-linear (quadratic) effects of tree size and neighborhood competition and log-transformed mean cone production to conform to the assumptions of linear modeling. Site was included as a random intercept in all models.

For each model describing masting behavior, we tested all subsets of the full model (i.e., containing all predictors) and compared model fits based on AICc scores using the dredge function in the MuMIn package (Barton 2020). We calculated the model averaged coefficients and standard errors for all top models (within 4 AIC units of the top model). As a measure of

goodness of fit, we calculated the marginal and conditional pseudo R^2 for mixed models (Nakagawa and Schielzeth, 2013).

All models were built using the package `glmmTMB` (Brooks et al. 2020) using the statistical software R (R Core Group, 2022). Data carpentry was performed using the `data.table` package (Dowle and Srinivasan, 2021), and data visualizations were made using the `ggplot2` package (Wickham 2016), `patchwork` (Pedersen 2020), `scico` (Pedersen and Cramer 2020), and `PNW colors` (Lawlor 2020) packages.

RESULTS

Across a 1300 km latitudinal gradient in the southern Rocky Mountains, we observed high variability in ponderosa pine cone production, both across years and among trees. Mean CV_i across all sites was 1.71, and the average pairwise synchrony value among trees within a site was 0.46, which is slightly more variable and less synchronous than prior studies, but still within the range of what has been reported for other populations of ponderosa pine (e.g., Mooney et al. 2011).

Model comparisons based on AIC indicated that a model containing summer VPD in the year prior to cone initiation (June, July, August T-3) and precipitation during year of cone initiation (June, July, August, T-2) best explained annual cone production in ponderosa pine. Both relationships were positive, indicating that years of high cone production followed years of high evaporative demand in T-3 and wetter than average years in T-2. Using this model, we tested for an interaction effect between each of the weather predictors (summer VPD T-3 and precipitation in T-2) and the two long-term climate predictors (30-year CWD and AET; Figure 2.2). We found strong evidence ($P < 0.001$) to support the hypothesis that trees respond to

weather differently based on the climate of a site. Interaction models reduced AIC from the weather-only model by at least 10 AIC points, and the top model reduced AIC by 36.5 AIC points. This model contained an interaction between 30-year AET and VPD in T-3, and 30-year CWD and precipitation in T-2, as well as the stand-alone effects of these variables, and cone production in the year prior to maturation as a covariate. The goodness of fit from this full model was low (R^2_m or the variance explained by only fixed effects = 1.6%, and R^2_c or the variance explained by both fixed and random effects = 30.1%, Table 2.3); however, the relatively larger proportion of R^2_c indicated there was strong variability among trees and among sites that was captured by these nested random effects.

Table 2.3) Standardized model coefficients, standard errors, and associated *P* values from full model of annual cone production at the individual tree-level. Higher values of 30-year climatic water deficit (CWD) are associated with hotter, drier climates. Δ VPD is calculated as the difference in vapor pressure deficit between year T-2 and T-3 prior to cone maturation. Cone production in the year prior to maturation (Cones^{T-1}) was included as a covariate.

<i>Cone Abundance Model</i>				<i>Mast Failure Model</i>			
	β (se)	T value	P value		β (se)	T value	P value
T-2 PPT JJA	0.09 (0.02)	4.19	<0.001		-0.30 (0.06)	-5.15	<0.001
T-3 VPD JJA	0.07 (0.02)	3.3	<0.001		-0.37 (0.03)	-9.8	<0.001
CWD x T-2 PPT JJA	0.02	0.02	0.42		-0.27 (0.04)	2.2	<0.001
AET x T-3 VPD JJA	0.02 (0.02)	-1.03	0.30		0.08 (0.04)	-6.5	0.03
AET	-0.15 (0.09)	0.3	0.08		0.04 (0.13)	0.335	0.73
CWD	-0.09 (0.09)	-0.97	0.33		0.13 (0.13)	1.01	0.31
Cones ^{yr⁻¹}	- 0.05 (0.02)	-2.0	0.04		0.15 (0.04)	3.5	<0.001
$R^2_m = 1.6\%$				$R^2_c = 30.1\%$			
				ΔAIC (null) = 283.36		$N = 4004$ tree/yrs	

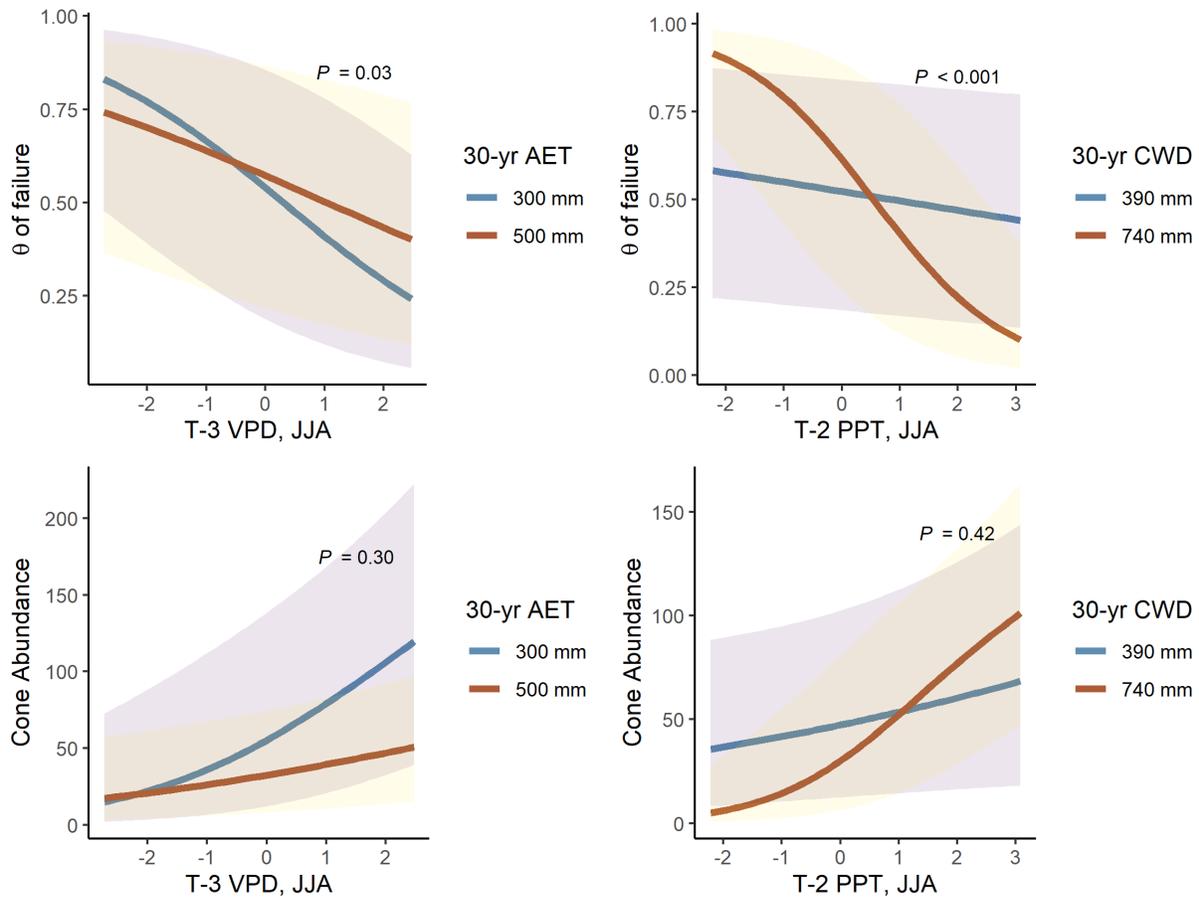


Figure 2.2) Marginal predictions from model of annual cone production model highlight the significant interaction between climate (30-year average of climatic water deficit [CWD] and actual evapotranspiration [AET]) and summer weather (mean vapor pressure deficit [VPD] and precipitation [PPT] in June, July, and August [JJA]) on the probability of a mast failure (top row) and annual cone abundance (bottom row) at the individual tree-level. Values chosen to represent high and low CWD and AET values correspond to approximately the 10th and 90th percentiles of the observed data. Shading represents the predicted 95% confidence intervals. High CWD (hotter and drier sites) were and low AET (cooler and drier) sites more sensitive to interannual variation in weather. The R^2_m was 1.6%, and R^2_c was 32.9%.

Effects of stand structures and climate on masting

Tree size and neighborhood competition were consistently the most important variables predicting masting behavior of individual trees (i.e., mean, synchrony, and interannual variability). Larger trees were less variable ($\beta = -0.4$, $P = 0.03$; Figures 2.3 and 2.4) and produced more cones overall ($\beta = 0.72$, $P = 0.001$; Figures 2.3 and 2.4). Greater basal area, a

proxy for competition, was non-linearly associated with synchrony ($\beta = -0.06$, $P = 0.03$; Figures 2.3 and 2.4). Synchrony was highest and remained relatively steady at low and intermediate levels of competition, before steeply declining at the highest levels of neighborhood competition. In models of masting behavior that contained age, the only significant effect of age was found in the synchrony model. Older trees were on average less synchronous among trees within a site ($\beta = -0.06$, $P = 0.02$; Appendix 2 Figure A.2.1), indicating that old trees were more often producing cones out of step with nearby trees.

We also highlight several potentially relevant non-linear trends (i.e., quadratic effects), that were marginally significant ($P < 0.1$) in the model averaged coefficients of the top models, specifically in models of mean cone production and interannual variability. We noted greater decreases in CV_i at larger tree sizes (i.e., quadratic effect of DBH; $\beta = 0.31$, $P = 0.054$; Figures 2.3 and 2.4), and non-linear declines in cone production at higher levels of competition ($\beta = -0.25$, $P = 0.084$; Figures 2.3 and 2.4). Goodness of fit explained by fixed effects of these models (R^2_m) ranged from 10.2 – 36.2%, and goodness of fit from both random and fixed effects (R^2_m) ranged from 35.9 - 57.4%.

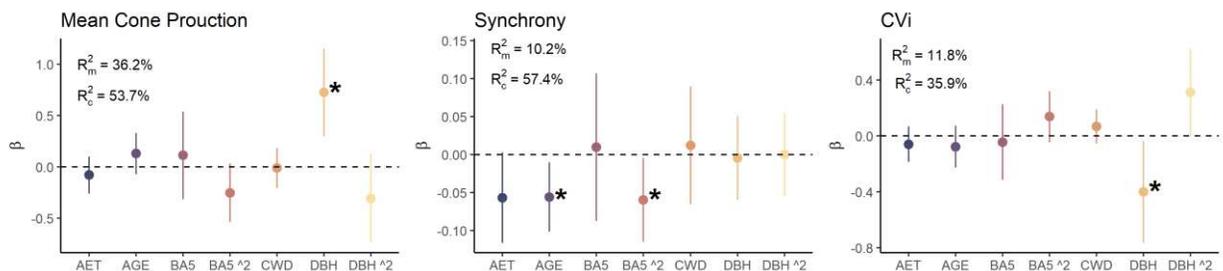


Figure 2.3) Model averaged coefficients and standard errors from the subset of top mixed models predicting the mean of cone production, synchrony, and interannual variability (CV_i). Site was fit as a random effect. Model coefficients are standardized and scaled to facilitate interpretation

across models and among terms. Statistical significance ($P = 0.05$) denoted by asterisks. Abbreviations are as follows: AET = 30-year average of actual evapotranspiration, BA5 = neighborhood basal area, a proxy for neighborhood competition, CWD = 30-year average of climatic water deficit, DBH = diameter of tree at breast height, $\wedge 2$ = quadratic terms.

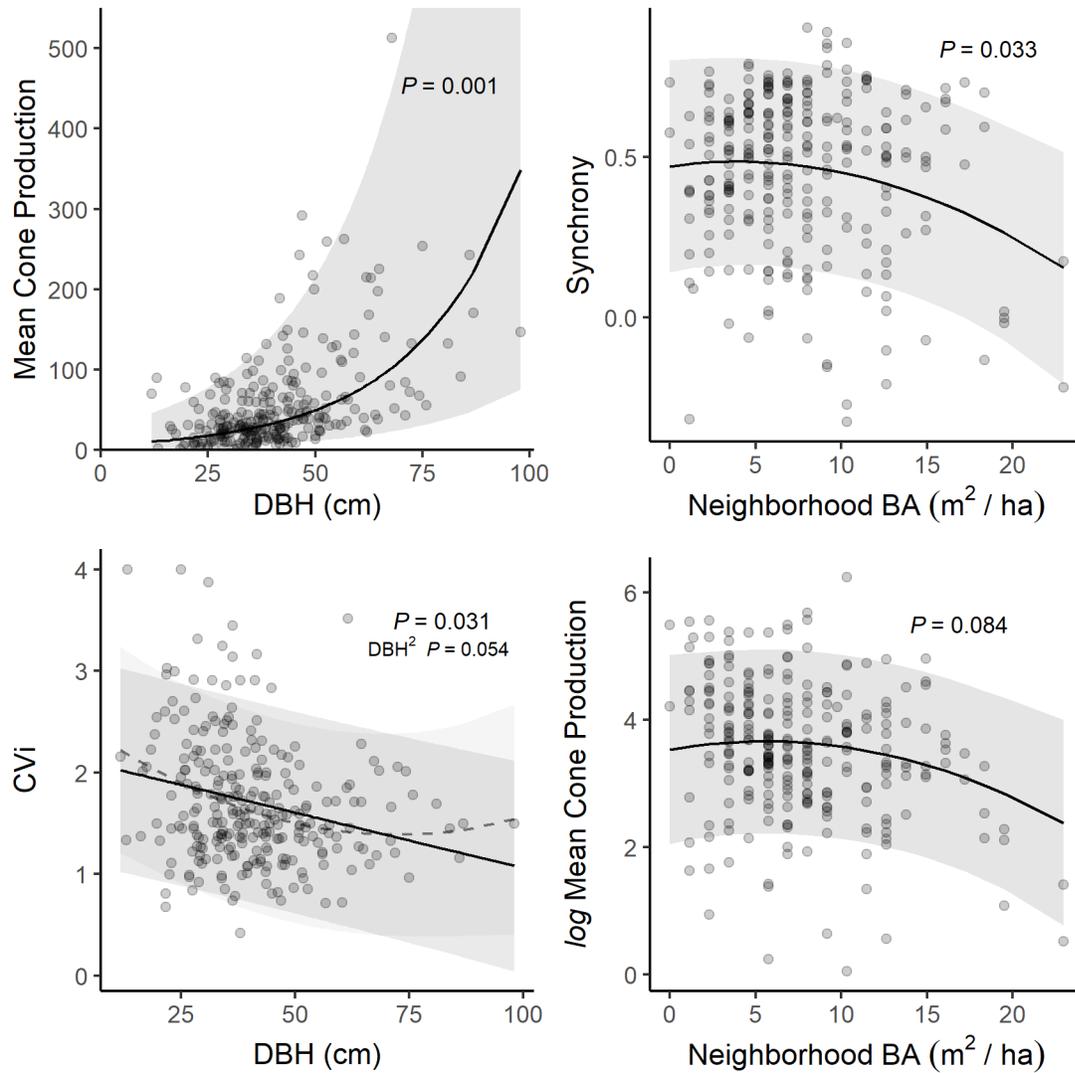


Figure 2.4) Selected marginal predictions from models describing the effects of tree size (measured as diameter at breast height [DBH]) and neighborhood competition [BA]) on masting behavior (mean, synchrony, and interannual variability [CV_i]) at the individual tree-level. Dashed line in lower left panel denotes marginally significant quadratic effect of tree size on CV_i. Shading represents the predicted 95% confidence intervals.

DISCUSSION

Recruitment of many forests is governed by seed availability, but our knowledge of the basic factors that drive and shape seed production remain limited. We surveyed ponderosa pine cone production across the southern Rocky Mountains to assess how mast seeding and its relationship to weather, climate, and stand structure varied across a large portion of this species' range. We note three key findings related to our hypotheses: First, absolute VPD and precipitation explained the observed patterns of cone production better than Δ VPD, but on average, weather only weakly described patterns of annual cone production. Second, the effects of VPD were stronger at sites with a low 30-year AET, and the effects of precipitation were stronger at sites with a high 30-year CWD (hotter and drier sites), suggesting differential sensitivity to the drivers of masting across the range of ponderosa pine. Lastly, the effects of tree size and neighborhood competition were consistently more important than long-term climate in shaping masting behavior (the mean, variability, and synchrony) of individual trees. Our study provides evidence that masting in ponderosa pine is dominated by individual-level variability and strongly influenced by local, neighborhood-level factors. Current efforts to reduce stand density and conserve large trees in ponderosa pine forests may have important, secondary impacts on seed availability.

What drives masting in ponderosa pine?

Our current understanding of masting provides us with two competing hypotheses to explain the mechanisms behind weather and seed production relationships. Weather either acts as

a “cue” to synchronize reproduction among individuals (Kelly et al. 2013) or as a proximate effect on masting vetoes and triggers (Pearse et al. 2014). Model comparisons indicated greater support for the hypothesis that masting in ponderosa pine is driven by “proximate drivers”, in this case summer VPD and precipitation, rather than a “cue” like ΔT or ΔVPD . This result is inconsistent with a recent study that found broad support for the ΔT model across many North American conifers (LaMontagne et al. 2021), but in line with a similar finding from Moreira et al. (2015). If masting in ponderosa pine were driven by a “cue”, we would expect the relationship to this cue to be a strong and consistent driver of reproduction among individuals across widely separated sites, in order for individual plants to reap the benefits of synchronized seed production (Kelly et al. 2013). Our findings do not support this interpretation, because weather was neither a strong driver nor a widely consistent driver of reproduction across the studied populations (e.g., relatively low correlation coefficients and goodness of fit of models).

Notably, the relationship between precipitation and cone production was strongest at hotter and drier sites, which were characterized by higher 30-year averages of climatic water deficit, and the relationship between VPD and cone production was strongest at cooler and drier sites, which were characterized by low 30-year averages of actual evapotranspiration. This pattern suggests populations may be limited by different climatic factors (i.e., energy or moisture), which leads to differential sensitivity to these weather drivers across the range of ponderosa pine. In this study, sites in cooler, drier environments are likely more limited by energy, and are more sensitive to the interannual fluctuations in VPD, whereas sites in hotter, drier environments are likely limited by moisture, and thus are more sensitive to interannual fluctuations in precipitation. Nevertheless, most sites had no clear relationship to the studied

weather variables, suggesting that reproduction in many populations of ponderosa pine may be relatively insensitive to warming temperatures from climate change.

The observed pattern corroborates previous findings that the relationship between ponderosa pine seed production varies at highly local scales. Mooney et al. (2011) described a breakdown in the relationship between weather and masting across a distance as short as 100 km, and we observe similar trends here. Seed production was occasionally synchronous between nearby sites but was just as often asynchronous at local scales (see Wion et al. 2021 for discussion of synchrony among these sites). This could be because of fine-scale genetic variation among populations, or because of steep environmental gradients in topographically complex areas (like the Rocky Mountains) that are not captured by coarse resolution models of climate and weather. This could lead to variation in the triggers of masting among genetically or climatically separated populations, or differences in the primary factors limiting reproduction across species ranges. As suggested here, the relative influence of precipitation and temperature may shift along a gradient of climatic stress (Redmond et al., 2018), leading to divergent climatic associations between leading and trailing edges of species ranges (Roland et al. 2014). How this affects recruitment and population growth remains a key question.

Strong masting behavior (high synchrony and variability) may also be selected for in populations experiencing higher rates of predation, like selection for serotiny in lodgepole pine (Talluto and Benkman 2014, Benkman and Slepiewski 2004). Previous studies have documented evidence for multiple, co-occurring fitness benefits from masting in a single population of ponderosa pine, including predator satiation (Linhart et al. 2014) and pollen-coupling (Moreira et al. 2014). The relative importance of these fitness trade-offs may vary based on their ecological context, for example, predator satiation may exert stronger influences on masting behavior in

stands with high amounts of seed predation, whereas pollen coupling may be more important in isolated trees or groups of trees in woodland or park settings. Thus, the mosaic of factors that ultimately select for masting in different populations could drive highly variable masting dynamics at highly local scales.

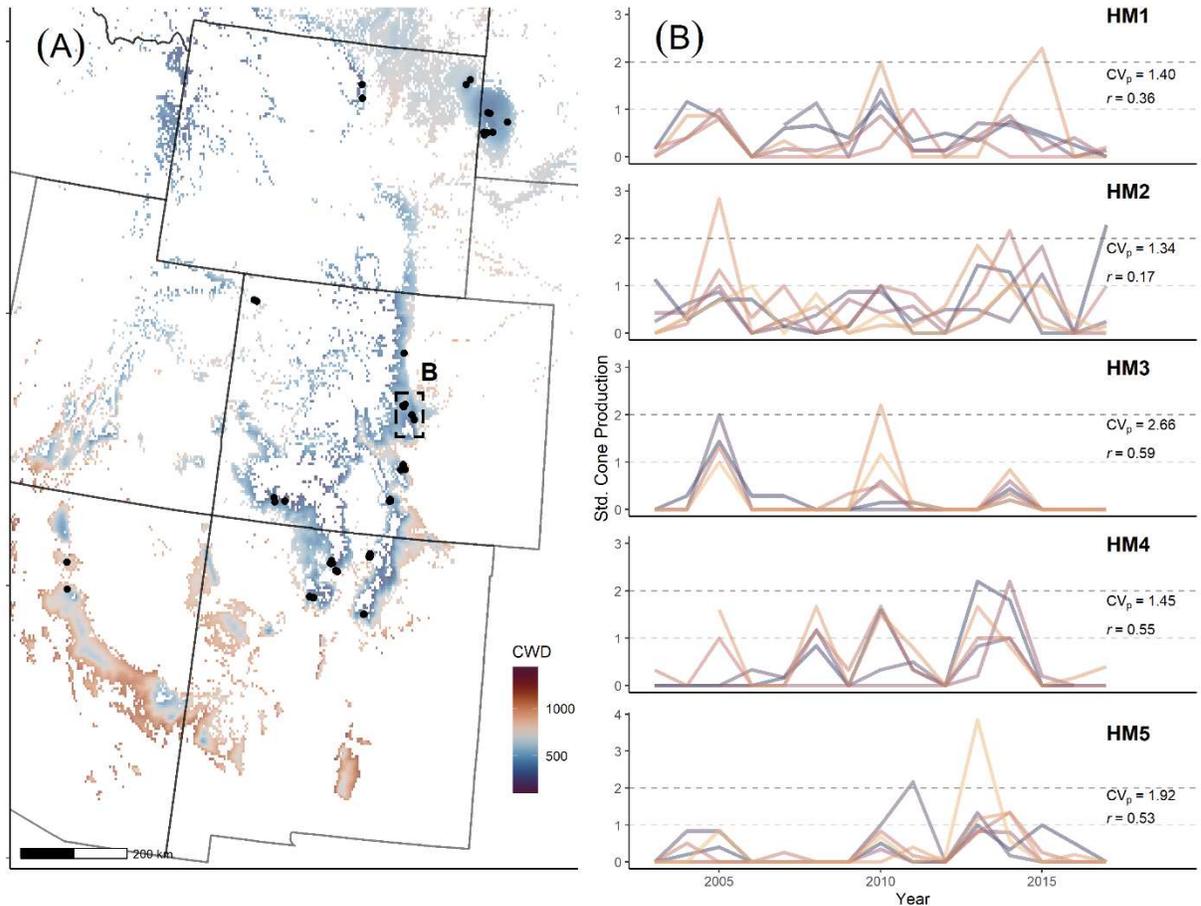


Figure 5) Patterns of masting in ponderosa pine in selected populations across the southern Rocky Mountains. Panel A (left) shows the distribution of study sites (black dots) overlaid against the distribution of ponderosa pine across the study region. Background colors show range of 30-year mean climatic water deficit (CWD, mm/year), with blue colors denoting on average cooler and wetter climates (low CWD) and red colors denoting hotter and drier areas (high CWD). The right panel highlights how annual cone production varies across five co-located sites along the southern Front Range of central Colorado between 2004-2018. Sites presented here are between 1-30 km apart from one another, and the 30-year CWD at these sites ranged from ~ 380 – 660 mm/year, which is close to the overall mean of our sites (533 mm/year). Each line represents an individual tree sampled for cone production, which was standardized at the tree

level (number of cones produced per branch sampled) to visualize individual-level investment in reproduction overtime. Annual cone production, variability (CV_p ; coefficient of variation at the population-level), and synchrony (r ; mean, pairwise correlation among all trees at the site) were highly variable among sites - even between closely located sites.

Managing ponderosa pine ecosystems for masting

Models of masting behavior pointed to both tree size and competition as the most important predictors of the mean, variability, and synchrony at the individual tree level. This result is not particularly surprising, as it aligns closely with a century of forest science in these ecosystems. Large and open grown trees produce more seeds than smaller and more densely grown trees (Pearson 1923, Schubert 1974, Krannitz and Durallia 2004), in part due to greater crown area to support more cones and greater access to resources (light, water, and nutrients) required for large seed crops. This is also corroborated by long-term evidence from thinning experiments, which also show higher levels of cone production in lower to intermediate density stands, as well as greater levels of seedling establishment and survival (i.e., recruitment) following high seed years (Flathers et al. 2016, Kolb et al. 2020). Importantly, it suggests that management efforts targeted to conserve large trees and reduce stand density may be an important, overlooked tool to regulate future recruitment.

A study from the Front Range of Colorado estimated that after accounting for losses to seed predators and viability, only 14% of seed crops remained available for germination, and only following relatively large seed years (Shepperd et al. 2006). This suggests that although larger trees may produce more cones, more often, seed availability for recruitment may still only be present in mast years. An important limitation of this study is that we assessed cone production, which describes individual-level investment into reproduction, and not total seed availability or viability. Therefore, the question remains - how do factors like variability and

synchrony in individual-level cone production translate to overall seed availability on the landscape?

Generally, it is presumed that high synchrony in seed and cone production translates to higher overall seed availability, because it builds the economies of scale necessary to offset the costs of masting (Pearse et al. 2016). This interpretation is generally supported in our data by the observation of identical, hump shaped relationships between neighborhood competition and mean cone production and synchrony, and corroborates observations from long term thinning experiments (Flathers et al 2016). Both mean cone production and synchrony peaked at low- to intermediate values of competition before steeply declining at high levels of competition. It remains unknown whether trees with a low CV_i (more frequent cone producers) produce significant quantities of viable seeds in years of low to moderate cone production. Despite the likelihood of poor seed viability in off-years, these trees are still likely to be the biggest producers during mast years and thus may have outsized impacts on recruitment and building economies of scale in masting populations.

For managers concerned with maintaining or increasing seed availability on the landscape, the results of this study support current efforts to conserve and protect large ponderosa pine trees on the landscape, and to restore more open, parklike stand structures across low elevation, montane forests from which fire has been historically excluded (Allen et al. 2002, Battaglia et al. 2018). In addition, managers should aim to proactively conserve these trees on the landscape by thinning smaller diameter trees and reintroducing low severity fire to reduce neighborhood competition and crown-fire risk. Such treatments are likely to have concurrent, synergetic impacts on forest resilience by reducing drought stress of mature trees, opening new

niches for seedling recruitment in the understory, and increasing the mean and synchrony of seed production in the overstory (Bradford et al. 2021, McCauley et al. 2022).

How will a changing climate and shifting disturbance regimes affect masting?

It remains highly uncertain whether and how a changing climate will affect future seed production (Hackett-Pain and Bogdziewicz 2021). The results of this study suggest that ponderosa pine cone production in many populations may not be strongly impacted by continued climate warming and associated increases in water deficit, relative to other dry conifers in this region (e.g., Redmond et al. 2012). Ponderosa pine cone production was only weakly associated with absolute temperature and precipitation. In contrast, cone production of other dry pine species (Redmond et al. 2012, Wion et al. 2019, Mutke et al. 2005), such as piñon pine, conforms to the environmental stress hypothesis (Pearse et al 2017) because they produce smaller and more variable crops at hotter, drier sites. Those species have already experienced crop declines associated with a warming climate (Redmond et al., 2012; Mutke et al., 2005). If seed production in ponderosa pine is driven by proximate effects of vetoes and triggers, then warming temperatures may lead to an increased frequency of veto years, although these effects will likely be limited, given the relatively weak associations with climate and weather. Future consequences of climate change on seed availability and consumers are also highly uncertain. Continued, long-term studies across broad extents are needed to assess current and ongoing changes in reproduction dynamics.

Changing disturbance regimes are likely to have an impact on the patterns of masting behavior in ponderosa pine forests, through reductions in tree density and the loss of large and old trees across the landscape. Ponderosa pine is considered an archetypal fire-adapted species in

the western US (Stevens et al. 2020) and is widely distributed species across a range of forest types and climatic conditions (Burns and Honkala 1991). Many ponderosa pine forests have experienced increases in tree density over the past century – both the result from the legacies of fire exclusion policies and recovery from historical land use (e.g., grazing, logging, and mining, Naficy et al. 2010, Rodman et al. 2019). Areas adapted to historic, low-severity fire regimes (commonly low elevation and lower latitude forests with a grass dominated understory) are likely most affected by human-caused deviations from fire regimes, and where the goals of reducing fire risk and ecosystem restoration likely converge (Rodman et al. 2019). In ponderosa pine forests strongly affected by legacies of fire exclusion, increases in tree density have likely contributed to an overall decrease in the total amount of seed production of individual-trees, and possibly reduced benefits associated with variability and synchrony of mast seeding, such as predator satiation.

The loss of large trees as a consequence of disturbance may have an outsized impact on seed availability across the landscape. Large trees are preferential hosts of bark beetles (Stephenson et al. 2015) and face heightened threats from increasing drought stress from hotter temperatures (Bennet et al. 2015, McDowell et al. 2015). Increased frequency of high severity, stand replacing fires also threaten the persistence of large and old trees on the landscape (Millar et al. 2015). Because large trees were also less variable (lower CV_i , indicating smaller between-year differences in cone production), they may have important impacts on post-fire recruitment, especially in species that are limited to narrow windows of recruitment. Notably, it remains understudied how the *timing* of seed production, relative to fire and climate, may influence post-fire ponderosa pine regeneration, which is a crucial piece of missing information in our understanding of post-fire landscape management (Stevens et al. 2021). While the loss of large

trees from drought and fire have clear negative impacts on seed availability, our research suggests that reductions in tree density from controlled, low severity disturbances may also positively impact the synchrony and variability of reproduction, which could potentially affect future patterns of ecosystem recovery.

CONCLUSION

We conducted a broad survey of ponderosa pine cone production to better understand what drives and shapes masting behavior, and how it varies across a large portion of this species' distribution in the southern Rocky Mountains. We show that absolute VPD and precipitation were weak associates of ponderosa pine masting in some populations, but these effects were not uniform across the landscape, and further work should be done to resolve the drivers of masting in climate insensitive populations. Importantly, we demonstrate that large and open grown trees were the most productive individuals, and conserving these individuals is likely the shortest path to maintaining reproductive potential in the era of accelerating disturbances. Current efforts to restore fire-excluded ponderosa pine forests to open, parklike stand structures are also likely to have positive impacts on seed availability, through increases in the mean and synchrony of individual-tree cone production. Long-term monitoring of both seed production and recruitment will continue to be the most useful tool for determining climate change impacts on tree demographic processes, and how they influence population growth rates across species ranges.

REFERENCES

- Abatzoglou, John T., Solomon Z. Dobrowski, Sean A. Parks, and Katherine C. Hegewisch. 2018. "TerraClimate, a High-Resolution Global Dataset of Monthly Climate and Climatic Water Balance from 1958-2015." *Scientific Data* 5: 1–13. <https://doi.org/10.1038/sdata.2017.191>.
- Allen, Craig D., Melissa Savage, Donald A. Falk, Kieran F. Suckling, Thomas W. Swetnam, Todd Schulke, Peter B. Stacey, Penelope Morgan, Martos Hoffman, and Jon T. Klingel. 2002. "Ecological Restoration of Southwestern Ponderosa Pine Ecosystems: A Broad Perspective." *Ecological Applications* 12 (5): 1418–33. [https://doi.org/10.1890/1051-0761\(2002\)012\[1418:EROSPP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2).
- Anderson, Donald B. 1936. "Relative Humidity or Vapor Pressure Deficit." *Ecology* 17 (2): 277–82.
- Andrus, Robert A., Brian J. Harvey, Ashley Hoffman, and Thomas T. Veblen. 2020. "Reproductive Maturity and Cone Abundance Varies with Tree Size and Stand Basal Area for Two Widely Distributed Conifers." *Ecosphere* 11 (5): e03092. <https://doi.org/10.1002/ecs2.3092>.
- Battaglia, Mike A., Benjamin Gannon, Peter M. Brown, Paula J. Fornwalt, Antony S. Cheng, and Laurie S. Huckaby. 2018. "Changes in Forest Structure since 1860 in Ponderosa Pine Dominated Forests in the Colorado and Wyoming Front Range, USA." *Forest Ecology and Management* 422 (April): 147–60. <https://doi.org/10.1016/j.foreco.2018.04.010>.
- Benkman, Craig W., and Adam M. Siepielski. 2004. "A Keystone Selective Agent? Pine Squirrels and the Frequency of Serotiny in Lodgepole Pine." *Ecology*. <https://doi.org/10.1890/04-0177>.
- Bennett, Amy C, Nathan G Mcdowell, Craig D Allen, and Kristina J Anderson-Teixeira. 2015. "Larger Trees Suffer Most during Drought in Forests Worldwide." *Nature Plants*. <https://doi.org/10.1038/NPLANTS.2015.139>.
- Bogdziewicz, Michał. 2021. "How Will Global Change Affect Plant Reproduction? A Framework for Mast Seeding Trends." *New Phytologist*, 1–7. <https://doi.org/10.1111/nph.17682>.
- Bogdziewicz, Michał, Andrew Hacket-Pain, Dave Kelly, Peter A. Thomas, Jonathan Lageard, and Andrew J. Tanentzap. 2021. "Climate Warming Causes Mast Seeding to Break down by Reducing Sensitivity to Weather Cues." *Global Change Biology* 27 (9): 1952–61. <https://doi.org/10.1111/gcb.15560>.
- Bogdziewicz, Michał, Michael A. Steele, Shealyn Marino, and Elizabeth E. Crone. 2018. "Correlated Seed Failure as an Environmental Veto to Synchronize Reproduction of Masting Plants." *New Phytologist* 219 (1): 98–108. <https://doi.org/10.1111/nph.15108>.

- Bogdziewicz, Michał, Jakub Szymkowiak, Rafael Calama, Elizabeth E. Crone, Josep M. Espelta, Peter Lesica, Shealyn Marino, et al. 2020. “Does Masting Scale with Plant Size? High Reproductive Variability and Low Synchrony in Small and Unproductive Individuals.” *Annals of Botany* 126 (5): 971–79. <https://doi.org/10.1093/aob/mcaa118>.
- Bogdziewicz, Michał, Jakub Szymkowiak, Marcos Fernandez-Martinez, Josep Peñuelas, and Josep M. Espelta. 2019. “The Effects of Local Climate on the Correlation between Weather and Seed Production Differ in Two Species with Contrasting Masting Habit.” *Agricultural and Forest Meteorology*, no. January: 1–21. <https://doi.org/10.1016/j.agrformet.2019.01.016>.
- Bouchard, Mathieu, and Clementine Pernot. 2020. “Climate and Size of Previous Cone Crops Contribute to Large-Scale Synchronous Cone Production in Balsam Fir.” *Canadian Journal of Forest Research*, 1–33.
- Brown, Carissa D., Geneviève Dufour-Tremblay, Ryan G. Jameson, Steven D. Mamet, Andrew J. Trant, Xanthe J. Walker, Stéphane Boudreau, et al. 2019. “Reproduction as a Bottleneck to Treeline Advance across the Circumarctic Forest Tundra Ecotone.” *Ecography* 42 (1): 137–47. <https://doi.org/10.1111/ecog.03733>.
- Burns, Russell M, and Barbara H Honkala. 1990. “Silvics of North America: Volume 1. Conifers.” *Silvics of North America*, 877. <https://doi.org/10.1094/PHYTO-95-0284>.
- Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. “Interpreting Recruitment Limitation in Forests.” *American Journal of Botany* 86 (1): 1–16. <https://doi.org/10.2307/2656950>.
- Clark, James S, Robert Andrus, Melaine Aubry-kientz, Yves Bergeron, Michal Bogdziewicz, Don C Bragg, Dale Brockway, et al. 2021. “Continent-Wide Tree Fecundity Driven by Indirect Climate Effects.” *Nature Communications*, 1–11. <https://doi.org/10.1038/s41467-020-20836-3>.
- Crofts, Anna L., and Carissa D. Brown. 2020. “The Importance of Biotic Filtering on Boreal Conifer Recruitment at Alpine Treeline.” *Ecography*, 1–16. <https://doi.org/10.1111/ecog.04899>.
- Crone, Elizabeth E., and Joshua M. Rapp. 2014. “Resource Depletion, Pollen Coupling, and the Ecology of Mast Seeding.” *Annals of the New York Academy of Sciences* 1322: 21–34. <https://doi.org/10.1111/nyas.12465>.
- Doak, Daniel F., and William F. Morris. 2010. “Demographic Compensation and Tipping Points in Climate-Induced Range Shifts.” *Nature* 467 (7318): 959–62. <https://doi.org/10.1038/nature09439>.
- Flathers, Kelsey N., Thomas E. Kolb, John B. Bradford, Kristen M. Waring, and W. Keith Moser. 2016. “Long-Term Thinning Alters Ponderosa Pine Reproduction in Northern

- Arizona.” *Forest Ecology and Management* 374: 154–65.
<https://doi.org/10.1016/j.foreco.2016.04.053>.
- Forcella, Frank. 1978. “Irregularity of Pinyon Cone Production and Its Relation to Pinyon Cone Moth Predation.” *Madroño*. California Botanical Society. <https://doi.org/10.2307/41424164>.
- Gratzer, Georg, Mario B Pesendorfer, Frederik Sachser, Laura Wachtveitl, Ursula Nopp-mayr, Jerzy Szwagrzyk, and Charles D Canham. 2021. “Does Fine Scale Spatiotemporal Variation in Seed Rain Translate into Plant Population Structure?,” 1–12.
<https://doi.org/10.1111/oik.08826>.
- Greene, David F, Christian Messier, Hugo Asselin, and Marie-Josée Fortin. 2002. “The Effect of Light Availability and Basal Area on Cone Production in *Abies Balsamea* and *Picea Glauca*.” *Canadian Journal of Botany* 80: 370–77. <https://doi.org/10.1139/B02-020>.
- Grossiord, Charlotte, Thomas N Buckley, Lucas A Cernusak, Kimberly A Novick, Benjamin Poulter, Rolf T W Siegwolf, John S Sperry, and Nate G McDowell. 2020. “Plant Responses to Rising Vapor Pressure Deficit.” *The New Phytologist* 226 (9): 1550–66.
<https://doi.org/10.1111/nph.16485>.
- Hackett-pain, Andrew, and Michał Bogdziewicz. 2021. “Climate Change and Plant Reproduction : Trends and Drivers of Mast Seeding Change.” *Phil Trans Roy Soc B*, no. March.
- Isagi, Y., K. Sugimura, A. Sumida, and H. Ito. 1997. “How Does Masting Happen and Synchronize?” *Journal of Theoretical Biology* 187 (2): 231–39.
<https://doi.org/10.1006/jtbi.1997.0442>.
- Janzen, D H. 1971. “Seed Predation by Animals.” *Annual Review of Ecology and Systematics* 2 (1): 465–92. <https://doi.org/10.1146/annurev.es.02.110171.002341>.
- Kelly, Dave, Andre Geldenhuis, Alex James, E. Penelope Holland, Michael J. Plank, Robert E. Brockie, Philip E. Cowan, et al. 2013. “Of Mast and Mean: Differential-Temperature Cue Makes Mast Seeding Insensitive to Climate Change.” *Ecology Letters*.
<https://doi.org/10.1111/ele.12020>.
- Koenig, Walter D., Reyes Alejano, Maria Dolores Carbonero, Pilar Fernández-Rebollo, Johannes M.H. Knops, Teodoro Marañón, Carmen M. Padilla-Díaz, et al. 2016. “Is the Relationship between Mast-Seeding and Weather in Oaks Related to Their Life-History or Phylogeny?” *Ecology* 97 (10): 2603–15. <https://doi.org/10.1002/ecy.1490>.
- Koenig, Walter D., Johannes M.H. Knops, and William J. Carmen. 2020. “Intraspecific Variation in the Relationship between Weather and Masting Behavior in Valley Oak, *Quercus Lobata*.” *Canadian Journal of Forest Research* 50 (12): 1299–1306.
<https://doi.org/10.1139/cjfr-2020-0098>.

- Kolb, Thomas E., Kelsey Flathers, John B. Bradford, Caitlin Andrews, Lance A. Asherin, and W. Keith Moser. 2020. "Stand Density, Drought, and Herbivory Constrain Ponderosa Pine Regeneration Pulse." *Canadian Journal of Forest Research*, January, 1–10. <https://doi.org/10.1139/cjfr-2019-0248>.
- Krannitz, Pamela G, Thomas E Duralia, Pamela G Krannitz1, and Thomas E Duralia1. 2004. "Cone and Seed Production in Pinus Ponderosa: A Review." *Source: Western North American Naturalist Western North American Naturalist* 64 (642): 208–18. <http://www.jstor.org/stable/41717364>.
- LaMontagne JM, Redmond MD, Wion AP, Greene DF. 2021. "An Assessment of Temporal Variability in Mast Seeding of North American Pinaceae." *Philosophical Transactions of the Royal Society B-Biological Sciences* 376: 20200373.
- Linhart, Yan B., Xoaquín Moreira, Marc A. Snyder, and Kailen A. Mooney. 2014. "Variability in Seed Cone Production and Functional Response of Seed Predators to Seed Cone Availability: Support for the Predator Satiation Hypothesis." *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.12231>.
- Mccauley, Lisa A, John B Bradford, Marcos D Robles, Robert K Shriver, Travis J Woolley, and Caitlin A Andrews. 2022. "Landscape-Scale Forest Restoration Decreases Vulnerability to Drought Mortality under Climate Change in Southwest USA Ponderosa Forest." *Forest Ecology and Management* 509 (September 2021): 120088. <https://doi.org/10.1016/j.foreco.2022.120088>.
- McDowell, Nate G., Craig D. Allen, Kristina Anderson-Teixeira, Brian H. Aukema, Ben Bond-Lamberty, Louise Chini, James S. Clark, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science (New York, N.Y.)* 368 (6494). <https://doi.org/10.1126/science.aaz9463>.
- Mcdowell, Nathan G, and Craig D Allen. 2015. "Darcy's Law Predicts Widespread Forest Mortality under Climate Warming." *Nature Climate Change* 5: 669–72. <https://doi.org/10.1038/NCLIMATE2641>.
- Millar, Constance I., and Nathan L. Stephenson. 2015. "Temperate Forest Health in an Era of Emerging Megadisturbance." *Science* 349 (6250): 823–26. <https://doi.org/10.1126/science.aaa9933>.
- Minor, David M., and Richard K. Kobe. 2019. "Fruit Production Is Influenced by Tree Size and Size-Asymmetric Crowding in a Wet Tropical Forest." *Ecology and Evolution*, no. September 2018: 1–15. <https://doi.org/10.1002/ece3.4867>.
- Minor, David M., and Richard K. Kobe. 2017. "Masting Synchrony in Northern Hardwood Forests: Super-Producers Govern Population Fruit Production." *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.12729>.

- Mooney, Kailen A., Yan B. Linhart, and Marc A. Snyder. 2011. "Masting in Ponderosa Pine: Comparisons of Pollen and Seed over Space and Time." *Oecologia* 165: 651–61. <https://doi.org/10.1007/s00442-010-1742-x>.
- Moreira, Xoaquin, Luis Abdala-Roberts, Yan B. Linhart, and Kailen A. Mooney. 2014. "Masting Promotes Individual- and Population-Level Reproduction by Increasing Pollination Efficiency." *Ecology* 95 (4): 801–7.
- Moreira, Xoaquín, Luis Abdala-Roberts, Yan B. Linhart, and Kailen A. Mooney. 2015. "Effects of Climate on Reproductive Investment in a Masting Species: Assessment of Climatic Predictors and Underlying Mechanisms." *Journal of Ecology* 103: 1317–24. <https://doi.org/10.1111/1365-2745.12434>.
- Moreira, Xoaquín, Luis Abdala-Roberts, Ignacio M. Pérez-Ramos, Johannes M. H. Knops, Mario B. Pesendorfer, Walter D. Koenig, and Kailen A. Mooney. 2019. "Weather Cues Associated with Masting Behavior Dampen the Negative Autocorrelation between Past and Current Reproduction in Oaks." *American Journal of Botany* 106 (1): 51–60. <https://doi.org/10.1002/ajb2.1210>.
- Mutke, Sven, Javier Gordo, and Luis Gil. 2005. "Variability of Mediterranean Stone Pine Cone Production: Yield Loss as Response to Climate Change." *Agricultural and Forest Meteorology*. <https://doi.org/10.1016/j.agrformet.2005.08.002>.
- Naficy, Cameron, Anna Sala, Eric G. Keeling, Jon Graham, and Thomas H. DeLuca. 2010. "Interactive Effects of Historical Logging and Fire Exclusion on Ponderosa Pine Forest Structure in the Northern Rockies." *Ecological Applications* 20 (7): 1851–64. <https://doi.org/10.1890/09-0217.1>.
- Nakagawa, Shinichi, and Holger Schielzeth. 2013. "A General and Simple Method for Obtaining R² from Generalized Linear Mixed-Effects Models." *Methods in Ecology and Evolution* 4 (2): 133–42. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- Nussbaumer, Anita, Peter Waldner, Sophia Etzold, Arthur Gessler, Sue Benham, Iben Margrete Thomsen, Bruno Bilde Jørgensen, et al. 2016. "Patterns of Mast Fruiting of Common Beech, Sessile and Common Oak, Norway Spruce and Scots Pine in Central and Northern Europe." *Forest Ecology and Management* 363: 237–51. <https://doi.org/10.1016/j.foreco.2015.12.033>.
- Park Williams, A., Craig D. Allen, Alison K. Macalady, Daniel Griffin, Connie A. Woodhouse, David M. Meko, Thomas W. Swetnam, et al. 2013. "Temperature as a Potent Driver of Regional Forest Drought Stress and Tree Mortality." *Nature Climate Change* 3: 292–97. <https://doi.org/10.1038/nclimate1693>.
- Parmenter, Robert R, Roman I Zlotin, Douglas I Moore, and Orrin B Myers. 2018. "Environmental and Endogenous Drivers of Tree Mast Production and Synchrony in Piñon-Juniper-Oak Woodlands of New Mexico." *Ecosphere*. <https://doi.org/10.1002/ecs2.2360>.

- Pearse, Ian S., Walter D. Koenig, and Dave Kelly. 2016. "Mechanisms of Mast Seeding: Resources, Weather, Cues, and Selection." *New Phytologist* 212: 546–62. <https://doi.org/10.1111/nph.14114>.
- Pearse, Ian S., Walter D. Koenig, and Johannes M.H. Knops. 2014. "Cues versus Proximate Drivers: Testing the Mechanism behind Masting Behavior." *Oikos* 123 (2): 179–84. <https://doi.org/10.1111/j.1600-0706.2013.00608.x>.
- Pearse, Ian S., Andreas P. Wion, Angela D. Gonzalez, and Mario B. Pesendorfer. 2021. "Understanding Mast Seeding for Conservation and Land Management." *Philosophical Transactions of the Royal Society B: Biological Sciences* 376 (1839). <https://doi.org/10.1098/rstb.2020.0383>.
- Pearson, G. A. 1923. *Natural Reproduction of Western Yellow Pine in the Southwest / . Natural Reproduction of Western Yellow Pine in the Southwest /*. Washington, D.C. : U.S. Dept. of Agriculture,. <https://doi.org/10.5962/bhl.title.64666>.
- Pesendorfer, Mario B., Michał Bogdziewicz, Jakub Szymkowiak, Zbigniew Borowski, Władysław Kantorowicz, Josep M. Espelta, and Marcos Fernández-Martínez. 2020. "Investigating the Relationship between Climate, Stand Age, and Temporal Trends in Masting Behavior of European Forest Trees." *Global Change Biology* 26 (3): 1654–67. <https://doi.org/10.1111/gcb.14945>.
- Redmond, Miranda D., Katharine C. Kelsey, Alexandra K. Urza, and Nichole N. Barger. 2017. "Interacting Effects of Climate and Landscape Physiography on Piñon Pine Growth Using an Individual-Based Approach." *Ecosphere* 8 (3). <https://doi.org/10.1002/ecs2.1681>.
- Redmond, Miranda D., Peter J. Weisberg, Neil S. Cobb, Catherine A. Gehring, Amy V. Whipple, and Thomas G. Whitham. 2016. "A Robust Method to Determine Historical Annual Cone Production among Slow-Growing Conifers." *Forest Ecology and Management* 368: 1–6. <https://doi.org/10.1016/j.foreco.2016.02.028>.
- Rodman, Kyle C., Thomas T. Veblen, Robert A. Andrus, Neal J. Enright, Joseph B. Fontaine, Angela D. Gonzalez, Miranda D. Redmond, and Andreas P. Wion. 2020. "A Trait-based Approach to Assessing Resistance and Resilience to Wildfire in Two Iconic North American Conifers." *Journal of Ecology*, no. December 2019: 1–14. <https://doi.org/10.1111/1365-2745.13480>.
- Rodman, Kyle C., Thomas T. Veblen, Teresa B. Chapman, Monica T. Rother, Andreas P. Wion, and Miranda D. Redmond. 2020. "Limitations to Recovery Following Wildfire in Dry Forests of Southern Colorado and Northern New Mexico, USA." *Ecological Applications* 30 (1): e02001. <https://doi.org/10.1002/eap.2001>.
- Rodman, Kyle C., Thomas T. Veblen, Sara Saraceni, and Teresa B. Chapman. 2019. "Wildfire Activity and Land Use Drove 20th Century Changes in Forest Cover in the Colorado Front Range." *Ecosphere* 10 (February): e02594. <https://doi.org/10.1002/ecs2.2594>.

- Roland, Carl A., Joshua H. Schmidt, and Jill F. Johnstone. 2014. "Climate Sensitivity of Reproduction in a Mast-Seeding Boreal Conifer across Its Distributional Range from Lowland to Treeline Forests." *Oecologia* 174 (3): 665–77. <https://doi.org/10.1007/s00442-013-2821-6>.
- Schubert, Gilbert H. 1974. "Silviculture of Southwestern Ponderosa Pine: The Status of Our Knowledge. Res. Paper RM-123."
- Sharma, Shubhi, Robert Andrus, Yves Bergeron, Michal Bogdziewicz, Don C Bragg, Dale Brockway, Natalie L Cleavitt, et al. 2022. "North American Tree Migration Paced by Climate in the West , Lagging in the East." *Proceedings of the National Academy of Sciences* 119 (3): 1–8. <https://doi.org/10.1073/pnas.2116691118/-/DCSupplemental>.Published.
- Shepperd, Wayne D, Carleton B Edminster, and Stephen A Mata. 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. https://www.fs.fed.us/rm/pubs_exp_forests/manitou/rmrs_2006_shepperd_w001.pdf.
- Stephenson, Nathan. 1998. "Actual Evapotranspiration and Deficit: Biologically Meaningful Correlates of Vegetation Distribution across Spatial Scales." *Journal of Biogeography* 25 (5): 855–70. <https://doi.org/10.1046/j.1365-2699.1998.00233.x>.
- Stephenson, Nathan L. 1990. "Climatic Control of Vegetation Distribution: The Role of the Water Balance." *Source: The American Naturalist* 135 (5): 649–70. <http://www.jstor.org/stable/2462028>.
- Stephenson, Nathan L., Adrian J. Das, Nicholas J. Amperssee, Beverly M. Bulaon, and Julie L. Yee. 2015. *Which Trees Die during Drought? The Key Role of Insect Host-tree Selection.* *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13176>.
- Stevens, Jens T., Matthew M. Kling, Dylan W. Schwilk, J. Morgan Varner, and Jeffrey M. Kane. 2020. "Biogeography of Fire Regimes in Western U.S. Conifer Forests: A Trait-Based Approach." *Global Ecology and Biogeography* 29 (5): 944–55. <https://doi.org/10.1111/geb.13079>.
- Stevens, Jens T, Collin M Haffey, Jonathan D Coop, Paula J Fornwalt, Larissa Yocom, Craig D Allen, Anne Bradley, et al. 2021. "Postfire Landscape Management in Frequent-Fire Conifer Forests of the Southwestern United States." *Forest Ecology and Management* 502 (June): 119678. <https://doi.org/10.1016/j.foreco.2021.119678>.
- Talluto, Matthew V., and Craig W. Benkman. 2014. "Conflicting Selection from Fire and Seed Predation Drives Fine-Scaled Phenotypic Variation in a Widespread North American Conifer." *Proceedings of the National Academy of Sciences* 111 (26): 9543–48. <https://doi.org/10.1073/pnas.1400944111>.

Vacchiano, Giorgio, Mario B Pesendorfer, Marco Conedera, Georg Gratzer, Lorenzo Rossi, Davide Ascoli, and Giorgio Vacchiano. 2021. “Natural Disturbances and Masting : From Mechanisms to Fitness Consequences.” *Phil Trans Roy Soc B*.

Wion, Andreas P., Peter J. Weisberg, Ian S. Pearse, and Miranda D. Redmond. 2020. “Aridity Drives Spatiotemporal Patterns of Masting across the Latitudinal Range of a Dryland Conifer.” *Ecography* 42: 1–12. <https://doi.org/10.1111/ecog.04856>.

Wion, Andreas P, Ian S Pearse, Kyle C Rodman, Thomas T Veblen, Miranda D Redmond, and Andreas P Wion. 2021. “The Effects of ENSO and the North American Monsoon on Mast Seeding in Two Rocky Mountain Conifer Species.” *Phil Trans Roy Soc B*.

CHAPTER 3

³THE EFFECTS OF ENSO AND THE NORTH AMERICAN MONSOON ON MAST SEEDING IN TWO ROCKY MOUNTAIN CONIFER SPECIES

OVERVIEW

We aimed to disentangle the patterns of synchronous and variable cone production (i.e., masting) and its relationship to climate in two conifer species native to dry forests of western North America. We used cone abscission scars to reconstruct ca. 15 years of recent cone production in *Pinus edulis* and *Pinus ponderosa*, and used redundancy analysis to relate time series of annual cone production to climate indices describing the North American monsoon and the El Niño Southern Oscillation (ENSO). We show that the sensitivity to climate and resulting synchrony in cone production varies substantially between species. Cone production among populations of *P. edulis* was much more spatially synchronous and more closely related to large-scale modes of climate variability than were populations of *P. ponderosa*. Large-scale synchrony in *P. edulis* cone production was associated with the North American monsoon and we identified a dipole pattern of regional cone production associated with ENSO phase. In *P. ponderosa*, these climate indices were not strongly associated with cone production, resulting in asynchronous masting patterns among populations. This study helps frame our understanding of mast seeding as a life history strategy and has implications for our ability to forecast mast years in these species.

INTRODUCTION

³ By Andreas P. Wion, Ian S. Pearse, Kyle C. Rodman, Thomas T. Veblen, and Miranda D. Redmond. Formatted for and accepted in the *Philosophical Transactions of the Royal Society B*.

Masting is the synchronous and irregular production of episodic seed crops by plant populations [1]. Variable seed production is a life history strategy common among many different plant families, which may have evolved as a mechanism to cope with nutrient or resource limitations [2, 3], satiate seed predators [4], or increase pollination efficiency [5]. In conifers and other long-lived species, synchronized mast years (such years of large, synchronized seed crops) occurring across large geographic areas are likely driven by broad-scale similarities in weather (i.e., Moran effects, [6, 7]). The effects of weather on seed production often occur during key phenological periods of the seed and cone development process which, for many species, take place over multiple years [8, 9]. Such lagged relationships between the consecutive stages of seed development and broad-scale weather patterns present opportunities for ecological forecasts of mast years, which would aid in the management of plant regeneration, animal population dynamics, and zoonotic disease outbreaks [10]. Yet it remains unclear how much of the interannual variability in seed production can be attributed to broad-scale weather patterns, and how much variability arises from local or regional factors. Disentangling these patterns and their relationship to climate is a prerequisite to future forecasts of masting.

Resource matching is the null hypothesis of masting, which posits that plant investment in annual reproduction is a linear function of the available resources or nutrients each year [2, 11]. While intuitive, empirical observations of seed production at large-scales and over long time periods are often noisy and complex. Synchrony in seed production among populations is commonly reported across many hundreds, sometimes thousands, of kilometers [9, 12, 13], but populations may also be unsynchronized at local-scales (e.g., < 100 kilometers; [8, 14]) or anti-synchronous at continental-scales (i.e., an ecological dipole; [15, 16]). Broadly synchronous mast years occur infrequently, while seed production is highly localized or region-specific during

most years, across many species [9, 12, 13, 14]. Individual-level factors like size and age [17, 18], endogenous resource budgets [19], density-dependent dynamics like competition and pollen availability [20, 21], and local climate differences [9, 22] may all lead to a decoupling of seed production and interannual climate variability among individual trees. Divergent sensitivities of forest populations may lead to complex patterns of asynchronous seed production that are ultimately unrelated to similarities in weather.

Water is the primary limiting resource for plant physiological processes in dry and seasonally dry ecosystems [23]. Climate conditions that alleviate water stress, such as cool temperatures (via reduced evaporative demand due to lower saturation vapor pressure) and abundant precipitation (via increased soil moisture) drive forest productivity in most dry ecosystems [24]. Moisture constraints on tree demography are apparent in dry conifer forests of western North America, where regional pulses of tree recruitment and growth follow infrequent years of above average precipitation and cool temperatures [25, 26, 27, 28], and likely also drive masting in several forest species native to this region [8, 9, 29]. Cool temperatures and abundant precipitation may be a “cue” to synchronize phenological events like cone initiation or pollen dispersal, but weather also has direct, proximate effects on seed production [2]. Drought and hot temperatures can “veto” mast crops [2, 30], leading to infrequent but highly synchronous mast crops during years of widespread moisture availability. In this study, we hypothesized that large scale modes of climate variability which influence tree water stress would drive the patterns of synchronous masting in dry forests of western North America.

Large-scale modes of climate variability, like the El Niño Southern Oscillation (ENSO) and the North American monsoon, shape recurring continental-scale patterns of moisture availability throughout western North America [31, 32, 33]. These climate modes are highly

pronounced in southwestern North America (portions of the southwestern United States and western Mexico) where precipitation is strongly bimodal- i.e., peaking in the winter and summer, with little or no precipitation in the intervening months [34]. The North American monsoon is strongly associated with increased summer precipitation in this region [33], whereas ENSO is associated with cool season (winter and spring) temperature and precipitation [31, 32, 35]. Notably, below-average temperatures and above-average precipitation in southwestern North America often cooccur with below-average precipitation and above-average temperatures in northwestern North America (portions of the northern US and western Canada [35]). This climate-dipole is characteristic of the El Niño phase of ENSO (La Niña describes the inverse of this pattern), which tends to develop over several months and peak in the boreal winter [36]. Climate dipoles can reinforce negative spatial autocorrelation, or anti-synchrony, among populations over large distances- driving see-saw patterns of boom-and-bust population dynamics across geographically disparate regions [16]. A growing body of evidence suggests that there are links between mast years and large-scale modes of climate variability in some tree species [37, 38, 39], but there has yet been little exploration of the synchronizing effect of climate modes on masting across species in North America.

We aimed to disentangle the patterns of synchronous cone production and their relationship to these large-scale modes of climate variability in two tree species native to dry forests of western North America (Rocky Mountain ponderosa pine, *Pinus ponderosa* var. *scopulorum*; and Colorado piñon pine, *Pinus edulis*). Cone abscission scars [40] were used to reconstruct 14-16 years of annual cone production in 470 individual trees from 76 sites. We then identified the variation in annual cone production across sites that could be explained by the interannual variation in climate modes during key phenological periods of cone development

using redundancy analysis. The results carry implications for our ability to forecast future mast years, which can aid in management of cascading ecosystem processes arising from the availability of seeds [10] and illuminate our understanding of mast seeding as a life history strategy in these conifer species.

METHODS

Natural History

Piñon pine and ponderosa pine are widespread conifer species found throughout dry forests, woodlands, and savannas of western North America [41]. Both species require at least two years to produce a single crop of cones. Cone production is initiated during the growing season, two years before cones are fully mature and seeds are released. Cone initiation in ponderosa pine occurs earlier in the growing season (June or July [42]) than piñon pine cone initiation, which occurs in late August or early September [43]. Unfertilized conelets overwinter and are pollinated the following spring, April or May, one year prior to cone maturation. During this time, a small structure forms between the cone and the branch, leaving a conspicuous scar at the point of attachment when a cone is abscised. These ‘cone scars’ can then be recorded in relation to the annual growth whorls of branches to reconstruct cone production in these species [40].

Previous research has linked masting in both species to periods of above average moisture and below average temperatures, primarily during cone initiation and pollen dispersal [8, 9, 29]. This motivated our expectation that the North American monsoon would have a positive relationship with subsequent cone production- specifically, summer precipitation falling

two years prior to cone maturation (i.e., the months preceding and during cone initiation). We also expected ENSO would impact cone production one year prior to cone maturation, preceding and during pollen dispersal. Cool temperatures and abundant moisture may prime resource uptake overwinter between initiation and pollination, or stable spring weather may cue synchronous pollen release among populations [44]. Alternatively, winter and spring drought may lead to desiccation of unfertilized conelets, or unstable spring weather (e.g., late frosts) may damage pollen cones or lead to asynchronous pollen dispersal among populations.

Study Area

We quantified annual cone production at 76 sites (*P. edulis* – 28 sites, 188 trees; *P. ponderosa* – 48 sites, 282 trees; Appendix 3 Figure A.3.1) located in the Black Hills, the central and southern Rocky Mountains, the Colorado Plateau, and the mountains of Arizona and New Mexico. Each site contained cone production data on one of the two focal species. The study area is bounded by 32° and 44° north latitude and -112° and -103° longitude. The study sites ranged in elevation from 1,400 and 2,800 meters above sea level and from 265 mm to 675 mm in mean (1981-2010) annual precipitation (using 800-m resolution 30-year climate averages from PRISM [45]).

Individual sites were combined from several different research projects, and the site selection criteria differed slightly between each project (see [9, 20] for full details). In addition, 17 ponderosa pine sites were sampled that were adjacent to recent wildfires or within unburned or low-severity fire refugia (see [20] for details). However, all sites conformed to the following criteria: 1) sites were located on public federal lands within 1 km of an accessible road, and 2) each site contained a minimum of 5 reproductively and healthy trees of the focal species within

50 meters of a randomly placed plot center. At each site, trees were randomly selected within stands for cone production sampling. Most often, this was achieved by sampling the nearest tree from a fixed point (or otherwise nearest opportunity) along a randomly placed or oriented belt transect (see Appendix 3: *Sampling criteria of individual trees* for more details).

Cone Production Data

We reconstructed recent historical cone production using the cone abscission scar method [40]. This method has been statistically validated against records of cone production in piñon pine [46], and used previously in other species [47, 48, 49], including ponderosa pine [20]. Results from a previous study suggest that stand-level estimates of the mean annual cone abundance stabilize after sampling 4-5 branches per tree, and 4-6 individuals per site [46]. We surveyed 5-7 trees at each site, and 4-8 branches per tree, and then recorded the total number of cone-bearing branches per tree to scale the estimates of cones per branch to annual cones per tree (see Appendix A1 for more details). The estimates of annual cone production are expressed as the mean cone production $\text{tree}^{-1} \text{ year}^{-1}$ (aligned to reflect the year of cone maturation) at each site. We compiled time series of annual cone production at each site into a matrix with years as rows and sites as columns for each species. Data were scaled and centered (i.e., z-score transformation) within each site using the series-wide means and standard deviations to equalize variance across sites.

Large-scale modes of climate variability

Interannual climate variability across the study area is shaped by two large-scale forces (the North American monsoon and ENSO) operating in different seasons (the warm season and

cool season, respectively; [34]). We aimed to capture this interannual variability using two climate indices, one describing the annual intensity of the North American monsoon across our study sites, and the other describing the annual magnitude of ENSO, which is associated with interannual variability in winter and spring precipitation and temperature (Figure 3.1). We aligned these indices to correspond with the matrices of annual cone production at two- and one-year lags, respectively, corresponding to the year of cone initiation for the North American monsoon (*year -2* relative to cone maturation) and cone pollination for ENSO (*year -1* relative to cone maturation) in both species.

We used principal component analysis (PCA) to decompose the variability in summer precipitation across all study sites to develop an index of annual monsoon intensity. This index was developed using monthly PRISM data, which are gridded climate series based on interpolated weather station data and regression models to account for physiographic effects of slope and elevation, developed at a 4-kilometer resolution for the conterminous United States [45]. Monthly precipitation totals for June - September were extracted at the site's center-point location and summed by site and year for the period 2001-2016 (corresponding to the year of cone initiation, or two years prior to the last available year of cone production data). Next, precipitation anomalies within each time series were transformed to z-scores. PCA was then performed on the transformed site-level time series. The first principal component explained 52.3% of the overall variability in precipitation, with positive values describing years of abundant monsoon precipitation across a large proportion of study sites. This index, which provides a simplified representation of the effects of the North American monsoon, was retained for use in subsequent redundancy analyses (below).

We used the bimonthly December/January average of the Multivariate ENSO Index (MEI v.2 [50]) to describe the magnitude of ENSO events at an annual resolution from 2002-2017 (corresponding to the year of cone pollination, or one year prior to the last available year of cone production data). The MEI is the first principal component of a series of measurements associated with ENSO magnitude, including sea surface temperature, atmospheric pressure, wind speed, and outgoing longwave radiation in the tropical Pacific [50]. This index is standardized relative to a 1980-2018 reference period such that positive phases of ENSO ($MEI > 0.5$) are considered El Niño events and are associated with cool and wet winters and springs in the US Southwest - the southern portion of our study area. Impacts from ENSO are strongest in this southern portion of our study area, and this relationship decays and ultimately reverses north of approximately 40 degrees north latitude (Figure 3.1). Negative phases of ENSO ($MEI < -0.5$) are considered La Niña events and are associated with hot and dry winters and springs in this region. We focused on the December/January period because ENSO events typically peak in strength during this time, and thus are commonly used as a benchmark of annual ENSO magnitude [36]. ENSO is also known to interact with other climate modes, like the Pacific Decadal Oscillation [51] or Atlantic Multidecadal Oscillation [52, which may influence summer precipitation and temperature across large portions of the central United States [52, 53]. Importantly, the two climate indices examined here were not correlated ($r = 0.16$, $p = 0.55$), and therefore we interpret each as an independent variable describing the general climate patterns during winter/spring (ENSO) and summer (the North American monsoon).

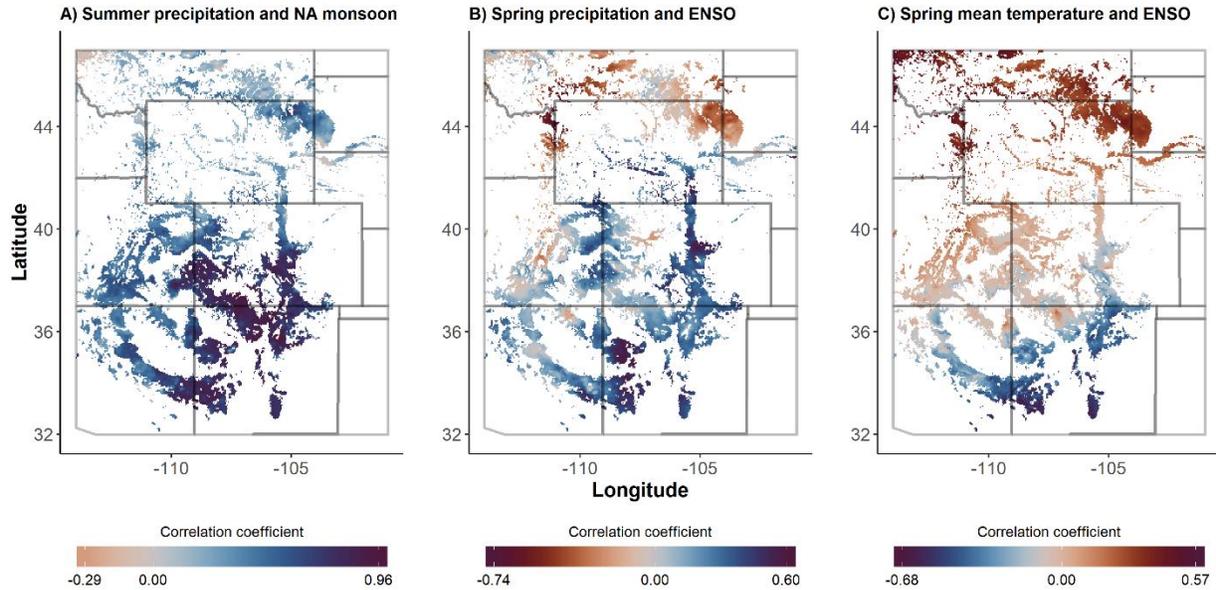


Figure 3.1) Large-scale modes of climate variability across the study area, masked to the combined distribution of piñon pine and ponderosa pine in this region (distribution from [54]). Colors represent the Pearson correlation between the climate index of interest and weather during key periods of cone development. Panel A shows the correlation between the index of annual North American (NA) monsoon intensity and a gridded series of summer precipitation (June – September) between 2001-2016. Panels B and C show the correlation between the December/January average of the Multivariate ENSO Index (MEI), spring precipitation (March-May, B), and temperature (C) between 2002-2017. See Appendix 3 for maps of correlation between ENSO (El Niño Southern Oscillation) and winter (December-March) precipitation and temperature, which were largely identical.

Redundancy Analysis

We performed redundancy analyses (RDA) to identify and describe the variation in annual cone production that was shared among (i.e., redundant with) the two climate indices of interest: ENSO and the North American monsoon. Redundancy analysis is an extension of constrained principal components analysis and multiple regression, where two or more datasets are summarized by the linear relationships between a set of multivariate response and predictor variables [55]. This approach allows us to identify commonalities between many time series of cone production and a limited number of explanatory variables. The response variable in each RDA was a matrix of annual cone production across all sites for each focal species, and the

predictor variables were the two climate indices describing annual monsoon intensity and ENSO magnitude. We report the proportion of constrained variability (i.e., shared with the predictor variables) for each species, as well as the adjusted R^2 of the full RDA model. The statistical significance of predictor variables and RDA axes was assessed individually using permutational multivariate analysis of variance (PERMANOVA) on a constrained ordination with 999 iterations.

All statistical analyses were performed using the software R [56]. Data carpentry was performed using the `data.table` [57] package, RDA analysis was conducted in `vegan` [58], spatial analyses were conducted using the `raster` package [59], and figures were produced using the `ggplot2` [60], `scico` [61], and `patchwork` [62] packages.

RESULTS

The North American monsoon and ENSO were strongly related to time series of piñon pine cone production, but such relationships were weak or absent in ponderosa pine. These two climate indices – the first describing intensity of the monsoon during cone initiation, and the other the magnitude of winter ENSO prior to cone pollination, captured 40% of the overall interannual variability (i.e., constrained variability) in piñon pine cone production, but only 15.2% of interannual variability in ponderosa pine cone production. PERMANOVA tests indicated that both climate indices were significant model terms (i.e., having non-zero effect sizes) in our RDA model for piñon pine (Table 3.1), but these terms were marginally significant or not significant in ponderosa pine. Similarly, both RDA1 and 2 were statistically significant (i.e., explained a proportion of variation greater than what would be expected by random chance) in piñon pine but not ponderosa pine (Table 3.2). The first axis of unconstrained variability in

ponderosa pine explained a greater proportion than the first axis of the constrained variability, indicating a low signal to noise ratio between these climate indices and masting in ponderosa pine.

Table 3.1) Coefficients for piñon pine (top) and ponderosa pine (bottom) redundancy analysis (RDA) models, describing the impact of large-scale modes of climate variability during key phenological events (noted in parentheses) on annual cone production in both species. MEI = Multivariate ENSO Index; ENSO = El Niño Southern Oscillation.

<i>Piñon pine RDA</i>	<i>Variance</i>	<i>F statistic</i>	<i>P value</i>
North American monsoon (<i>cone initiation</i> ; yr-2)	7.24	4.73	0.002
Dec/Jan MEI (<i>cone pollination</i> ; yr-1)	3.95	2.58	0.018
<i>Adj. R² = 0.29</i>			
<i>Ponderosa pine RDA</i>			
North American monsoon (<i>cone initiation</i> ; yr-2)	4.53	1.45	0.087
Dec/Jan MEI (<i>cone pollination</i> ; yr-1)	2.75	0.88	0.643
<i>Adj. R² = 0.02</i>			

Table 3.2) Summary of the individual axes from the piñon pine (top) and ponderosa pine (bottom) redundancy analysis (RDA) models. In both species, RDA1 was associated with the North American monsoon, and RDA2 was associated with ENSO (Appendix 3 Figure A.3.2). The proportion of constrained variability described by each axis is included in parentheses.

<i>Piñon pine RDA</i>	<i>Variance</i>	<i>F statistic</i>	<i>P value</i>
RDA1 (25.9%)	7.25	4.73	0.002

RDA2 (14%)	3.93	2.58	0.011
<i>Ponderosa pine</i>			
<i>RDA</i>			
RDA1 (9.4%)	4.53	1.45	0.265
RDA2 (5.7%)	2.75	0.88	0.632

The two climate indices had similar effects on the constrained ordination in both species (Appendix 3 Figure A.3.2), but in ponderosa pine, these relationships explain a very small proportion of variability in the overall dataset (Adj. $R^2 = 0.02$), and therefore statistical relationships were either marginal or insignificant (Tables 3.1 and 3.2). For this reason, descriptions of climate-masting relationships below focus primarily on piñon pine.

The first axis of the RDA (RDA1) was a time series that captured the greatest proportion of variability which was shared between the climate indices and matrices of annual cone production (Figure 3.2, left panels). RDA1 was positively associated with monsoon intensity (Appendix 3 Figure A.3.2), and site scores exhibited largely positive scores (Figure 3.2, center and right panels). In other words, a large proportion of piñon pine sites exhibited positive associations between monsoon precipitation during cone initiation and subsequent mast years two years later, a finding that supports previous research in this species [9, 32]. This indicates that the North American monsoon is a strong driver of the variability in annual piñon pine cone production. High values of RDA1 occurred in 2008 and 2015, describing years of both abundant monsoon precipitation and widespread mast years in piñon pine (Figure 3.2).

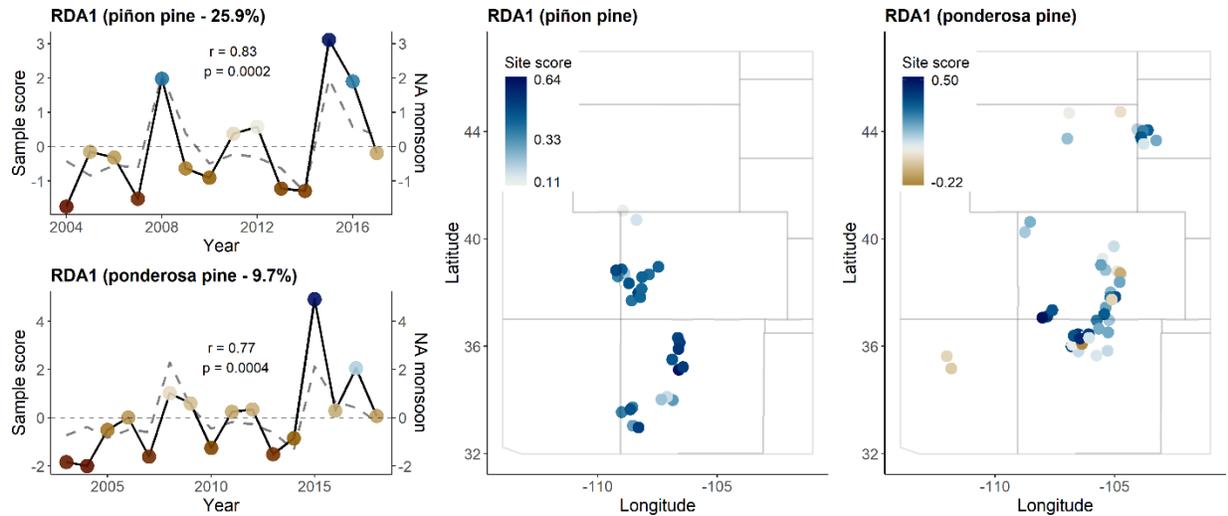


Figure 3.2) The axes of variability shared among the North American monsoon and cone production, or RDA1, in piñon pine (top left and center panel) and ponderosa pine (bottom left and right panel). Left panels show time series of the sample scores (solid black line) which are the weighted average of RDA1 site scores for each year (colored circles). Dashed lines show the index of the North American monsoon (during cone initiation, or two years prior to cone maturation) across all study sites. Both time series are aligned to reflect the year of cone maturation. Values of sample scores and the monsoon index are unitless and were scaled to equalize variance between the series. In-panel text reports the Pearson correlation coefficient and associated p-value between RDA1 and the North American monsoon. Center and right panels show maps of the site scores, or the weighted sum of RDA1 sample scores across all years at each site for each species. The North American monsoon was a strong driver of piñon pine cone production (explaining 25.9% of the overall variability in piñon pine cone production), but did not explain a statistically significant amount of variability in ponderosa pine cone production (9.7%).

The axis of shared variability among ENSO and annual cone production (RDA2) described regional patterns where cone production was abundant in one region and absent in another (Figure 3.3). In both species, RDA2 was associated with ENSO during the year of cone pollination (Appendix 3 Figure A.3.2), but this relationship only explained a significant portion of the overall variability in cone production in piñon pine (Table 3.2). In ponderosa pine, RDA2 only explained 5.7% of the shared variability between ENSO and cone production, and PERMANOVA tests indicated this was not a significant proportion of the total variability in cone production.

Maps of the RDA2 site scores revealed a dipole pattern in piñon pine (Figure 3.3), where positive values of RDA2 were associated with cone production at southern sites (largely in New Mexico) and negative values of RDA2 were associated cone production at northern sites (in western Colorado). Because RDA2 is positively associated with ENSO, El Niño years (positive values of the MEI) are associated with mast years in the southwestern portion of the study area. This pattern is flipped during La Niña years, where negative values (La Niña years) are associated with mast crop failures in the southwestern portion of the study area. We did not observe regional-scale spatial structuring in RDA2 for ponderosa pine. Sites with high and low RDA2 site scores were often in close proximity and were distributed evenly throughout the latitudinal gradient, making it highly unlikely that RDA2 reflects a consistent regional-scale climate signal.

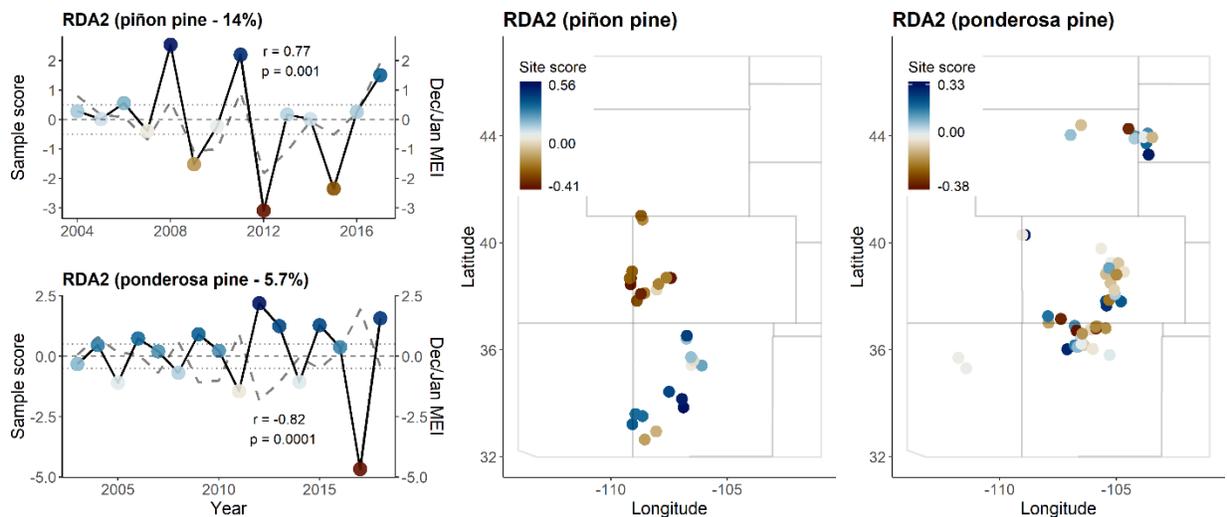


Figure 3.3: The axes of variability shared among the El Niño Southern Oscillation (ENSO) and cone production, or RDA2, in piñon pine (top left and center panel) and ponderosa pine (bottom left and right panel). Left panels show time series of the sample scores (solid black line) which are the weighted average of RDA2 site scores for each year (colored circles). Dashed lines show the December/January average of the Multivariate ENSO Index (MEI) during cone pollination,

one year prior to cone maturation. Values of the MEI are unitless, years greater than 0.5 are considered El Niño years and less than -0.5 are considered La Niña years (dotted horizontal lines). Both time series are aligned to reflect the year of cone maturation. In-panel text reports the Pearson correlation coefficient and associated p-value between RDA2 and the MEI. Center and right panels show maps of the site scores, or the weighted sum of RDA2 sample scores across all years at each site for each species. RDA2 in piñon pine described an ecological dipole, where El Niño years are associated with masting at southern sites and crop failures at northern sites, and La Niña years are associated with the opposite pattern. Despite a strong correlation between the MEI and RDA2 in ponderosa pine, this relationship did not explain a significant proportion of the overall variability in cone production (5.7%).

DISCUSSION

Mast years are bottom-up resource pulses in forest ecosystems that drive processes such as plant regeneration [28], animal population dynamics [63], and zoonotic disease outbreaks [64]. This study disentangled regionally synchronous patterns of masting and related these to two large-scale modes of climate variability. The results demonstrate that climate sensitivity and synchrony in cone production vary substantially between two co-occurring dry pine species in western North America. Masting in piñon pine was highly synchronous among populations and exhibited stronger relationships to large-scale modes of climate variability in comparison to ponderosa pine. Our *a priori* expectations about the timing of moisture in relation to key phenological periods were also supported for piñon pine, but climate modes during these same time periods had little effect on ponderosa pine. Specifically, piñon pine showed strong positive responses in cone production following above average monsoon precipitation, and regional anti-synchrony in association with ENSO. In contrast, ponderosa pine populations had highly variable patterns of seed production, ultimately leading to complex patterns of asynchronous reproduction that were unrelated to the climate indices studied here. Below we explore some potential reasons for these differences, and the implications they have for forecasts of masting and our understanding of masting as a life history strategy.

Divergent climate-masting relationships between species

Temporal variation in ponderosa pine cone production was not associated with ENSO or the North American Monsoon, the two climate indices widely considered to be important climatic drivers of growth and recruitment in our study area [26, 27, 65]. This result stands in contrast to the patterns exhibited by piñon pine, which displayed higher synchrony in cone production among populations and stronger responses to modes of climate variability. We suspect that this may be tied to differences in life history strategies between species or reflect the different ecological settings that these species inhabit. For example, piñon pine produces fewer, larger seeds that are highly vulnerable to predation and attract seed consumers with large home range sizes, such as birds, in contrast to ponderosa pine [41]. The evolutionary pressures of predator satiation may select for stronger regional synchrony in species that are highly vulnerable to predation especially in those species that are dispersed by highly mobile seed predators [11], as seen in piñon pine; however, previous research has shown that ponderosa pine also experiences some fitness benefits related to the economies of scale associated with predator satiation [66]. Piñon pine also occupies drier habitats (e.g., lower elevations and latitudes) than ponderosa pine, and as such may experience more frequent reproductive vetoes related to drought and hot temperatures or lack the resources necessary to produce smaller crops in non-mast years. These explanations are not mutually exclusive, as the larger seed mass in piñon pine (and other animal dispersed species) may also incur higher resource costs. In other words, it may require a greater relative investment of resources to produce larger seeds in drier environments and could explain the stronger relationship to climate seen here.

The high degree of asynchrony in ponderosa pine aligns with a previous study of climate-masting relationships in this species on the Colorado Front Range. Mooney et al. [8] documented a rapid decay of synchrony among ponderosa pine populations greater than 30 kilometers apart. Such asynchrony might be attributed to the high heterogeneity in local water balance or soils across topographically complex areas like the Rocky Mountains. They also described a relationship between cone production and antecedent spring temperature and precipitation in several populations near Boulder, Colorado, however; these relationships were not consistent in a separate population 100 kilometers to the south. High levels of genetic variability among populations may drive different degrees of climate sensitivity, as has been suggested in *Fagus crenata* [67]. The prevalence of ‘super producers,’ or trees that do not exhibit a strong masting habit and instead produce large levels of cones each year [68], has a genetic component and appears to be somewhat common in ponderosa pine [69, 70]. Super producers are by definition largely asynchronous from other trees within a shared stand and exhibit little to no relationship with climate. The role of genetic variability in regulating the sensitivity of trees to climate and the production of seeds remains an intriguing and understudied question [71].

Piñon pine populations on drier sites tend to produce smaller and less frequent cone crops than populations on wetter sites, suggesting that water balance plays an important role in regulating the size and frequency of mast years [9]. But it is unclear from this study whether water balance plays a similar role in ponderosa pine cone production. Cone production in ponderosa pine was not strongly associated with the direct effects of moisture availability during cone initiation or pollination; however, cone production may instead be more strongly associated with factors like temperature, or other environmental factors not examined in this study. Ponderosa pines are generally fast-growing, shade intolerant trees capable of reaching relatively

tall heights, whereas piñon pines are generally shade tolerant and slow growing, attaining much older ages but reaching much smaller statures [41]. Individual-level factors such as tree size, age, and stand structure may influence climate sensitivity and cone abundance [20, 72], and thus may play a relatively greater role in the individual-level variability of ponderosa pine cone production than in piñon pine. Density dependent factors like competition [20] or pollination limitations [21] also likely play important roles in regulating the interannual variability of ponderosa pine cone production.

An ecological dipole associated with ENSO

We identified a dipole relationship between ENSO and regional cone production in piñon pine. A mechanistic explanation for this pattern is that warm and dry springs in the southwestern United States, associated with La Niña, veto subsequent cone production by disrupting pollen dispersal [2, 44]. Alternatively, El Niño brings moisture that may prime resource uptake and sustain pollen cone development through the typically hot and dry spring months in this area [34]. Asynchrony in pollen release may also disrupt the cone development process independent of the direct effects of weather, as has been documented in some oak (*Quercus*) species [44]. Previous research using these same piñon pine sites found increased sensitivity to spring climate during cone pollination in southern populations of piñon pine [9]. In contrast, populations further north were more sensitive to late summer climate during the period of cone initiation. The northern portion of the ecological dipole observed in this study typically experiences dry summers, receiving most of the mean annual precipitation during winter, fall, and spring, while the southern portion where precipitation is highly bimodal [34]. Precipitation falling during the cool season is generally not subject to intense evaporative demand, which allows water to

percolate into deep soil storage [73]. Piñon pine radial growth is sensitive to antecedent winter precipitation [74], and this relationship is stronger on sites that have greater soil available water capacity [75]. This suggests that interactions between summer and winter water balance may play an important role in regulating cone production in piñon pine.

The relationship between large scale modes of climate variability and masting may also act as a cue to synchronize reproduction across large geographic areas. Synergistic interactions between broad-scale climate modes and plant reproduction may bridge evolutionary and mechanistic hypotheses explaining masting [39]. Climate modes can align weather across the multiple consecutive stages of cone development and can manifest as lagged environmental conditions that are favorable to tree recruitment in this region [39]. Timing mast years to climate modes like ENSO could benefit the fitness of seedlings, but we did not detect such a relationship in ponderosa pine. A recent study demonstrated that ponderosa pine recruitment between the northwest and southwest United States followed a dipole pattern similar to that reported here for piñon pine [76]. However, our ponderosa pine sites are concentrated in areas where the effects of ENSO are highly variable (near 40 degrees latitude), and further sampling at the extreme margins of our study area may illuminate yet undiscovered patterns.

Infrequent, broad-scale masting events operate as a keystone process that influences community and ecosystem dynamics across trophic levels. The lagged relationships between cone production and climate described in this study and many others indicate that near-term ecological forecasts of mast years may be within reach, at least for some species. Mast forecasts may eventually be leveraged to time ecosystem management activities related to the management of plant and animal populations, including in shelterwood forestry, ecosystem restoration [77], and endangered species management [78, 79], which are often intertwined with boom-and-bust

cycles of seed availability [10]. Piñon pine has experienced extensive tree mortality associated with recent hotter droughts [80, 81], documented declines in cone production [82], and limited recruitment following these recent die-off events [83]. Forecasts of piñon pine masting may thus help manage the balance between supply and demand for piñon pine seeds for research, management, cultural, and commercial purposes [10]. The present study suggests that a deeper understanding of the interaction between ENSO and North American monsoon will be a useful indicator when developing regional forecasts of masting in piñon pine.

Linking the patterns of synchronous reproduction to large-scale climate modes can help improve forecasts of mast years and reveal the underlying mechanisms that drive masting. The lack of a regional climate signal driving ponderosa pine cone production requires further exploration into whether a broader array of potential climatic variables can predict seed production in this species. Future work on this topic should also be focused on resolving individual-level variability in masting, including how stand structure, size, and age affect cone production, and how these factors scale up to drive the variability in seed production at stand- and ecosystem-levels. This information will be critical to accurately parameterize demographic processes in predictive models, and project future changes in forest ecosystems across broad biophysical gradients.

REFERENCES

1. Koenig WD, Knops JMH. 2000 Patterns of annual seed production by northern hemisphere trees: A global perspective. *Am. Nat* **155**, 59–69.
2. Pearse IS, Koenig WD, Kelly D. 2016 Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytol.* **212**, 546–562.
3. Fernández-Martínez M *et al.* 2019 Nutrient scarcity as a selective pressure for mast seeding. *Nat. Plants.* **5**, 1222–1228.
4. Bogdziewicz M, Szymkowiak J, Tanentzap AJ, Calama R, Marino S, Steele MA, Seget B, Piechnik Ł, Żywiec M. 2020 Seed predation selects for reproductive variability and synchrony in perennial plants. *New Phytol.*
5. Kelly D, Hart DE, Allen RB. 2001 Evaluating the wind pollination benefits of mast seeding. *Ecology* **82**, 117–126.
6. Moran AP. 1953 The statistical analysis of the Canadian lynx cycle II. Synchronization and meteorology. *Aust. J. Zool.* **1**, 291–298.
7. Liebhold A, Koenig WD, Bjørnstad ON. 2004 Spatial synchrony in population dynamics. *Annu. Rev. Ecol. Evol. Syst.* **35**, 467–90.
8. Mooney KA, Linhart YB, Snyder MA. 2011 Masting in ponderosa pine: Comparisons of pollen and seed over space and time. *Oecologia* **165**, 651–661.
9. Wion AP, Weisberg PJ, Pearse IS, Redmond MD. 2020 Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography.* **42**, 1–12.
10. Pearse IS, Wion AP, Gonzalez AD, Pesendorfer MB. Understanding mast seeding for conservation and land management. *Proceedings. Biol. Sci.* This issue.
11. Kelly D, Sork VL. 2002 Mast Seeding in Perennial Plants: Why, How, Where? *Annu. Rev. Ecol. Syst.* **33**, 427–27.
12. Koenig WD, Knops JMH. 2013 Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology* **94**, 83–93.
13. Nussbaumer A *et al.* 2016 Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. *For. Ecol. Manage.* **363**, 237–251.
14. Lamontagne JM, Boutin S. 2007 Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. *J. Ecol.*

15. LaMontagne JM, Pearse IS, Greene DF, Koenig WD. 2020 Mast seeding patterns are asynchronous at a continental scale. *Nat. Plants* **6**, 1–6.
16. Zuckerberg B, Strong C, Lamontagne JM, George SS, Betancourt JL, Koenig WD. 2020 Climate dipoles as continental drivers of plant and animal populations. *Trends Ecol. Evol.* 1–14.
17. Bogdziewicz M *et al.* 2020 Does masting scale with plant size? High reproductive variability and low synchrony in small and unproductive individuals. *Ann. Bot.* **126**, 971–979.
18. Pesendorfer MB, Bogdziewicz M, Szymkowiak J, Borowski Z, Kantorowicz W, Espelta JM, Fernández-Martínez M. 2020 Investigating the relationship between climate, stand age, and temporal trends in masting behavior of European forest trees. *Glob. Chang. Biol.* **26**, 1654–1667.
19. Crone EE, Rapp JM. 2014 Resource depletion, pollen coupling, and the ecology of mast seeding. *Ann. N. Y. Acad. Sci.* 1322, 21–34.
20. Rodman KC, Veblen TT, Andrus RA, Enright NJ, Fontaine JB, Gonzalez AD, Redmond MD, Wion AP. 2020 A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *J. Ecol.* 1–14.
21. Moreira X, Abdala-Roberts L, Linhart YB, Mooney KA. 2014 Masting promotes individual- and population-level reproduction by increasing pollination efficiency. *Ecology* **95**, 801–807.
22. Bogdziewicz M, Szymkowiak J, Fernández-Martínez M, Peñuelas J, Espelta JM. 2019 The effects of local climate on the correlation between weather and seed production differ in two species with contrasting masting habit. *Agric. For. Meteorol.* **268**, 109–115.
23. Grossiord C *et al.* 2017 Precipitation, not air temperature, drives functional responses of trees in semi-arid ecosystems. *J. Ecol.* **105**, 163–175.
24. Knowles JF, Scott RL, Biederman JA, Blanken PD, Burns SP, Dore S, Kolb TE, Litvak ME, Barron-Gafford GA. 2020 Montane forest productivity across a semiarid climatic gradient. *Glob. Chang. Biol.* , 1–14.
25. Adams HD, Kolb TE. 2005 Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *J. Biogeogr.* **32**, 1629–1640.
26. Peltier DMP, Ogle K. 2019 Legacies of La Niña: North American monsoon can rescue trees from winter drought. *Glob. Chang. Biol.* **25**, 121–133.
27. Brown PM, Wu R. 2005 Climate and Disturbance Forcing of Recruitment in a Southwestern Ponderosa Pine Landscape. *Ecology* **86**, 3030–3038.

28. Savage M, Brown PM, Feddema J. 1996 The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience* **3**, 310–318.
29. Parmenter RR, Zlotin RI, Moore DI, Myers OB. 2018 Environmental and endogenous drivers of tree mast production and synchrony in piñon-juniper-oak woodlands of New Mexico. *Ecosphere* (doi:10.1002/ecs2.2360)
30. Bogdziewicz M, Steele MA, Marino S, Crone EE. 2018 Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytol.* **219**, 98–108.
31. Baek SH, Smerdon JE, Coats S, Williams AP, Cook BI, Cook ER, Seager R. 2017 Precipitation, temperature, and teleconnection signals across the combined North American, monsoon Asia, and old world drought atlases. *J. Clim.* **30**, 7141–7155.
32. Kurtzman D, Scanlon BR. 2007 El Niño-Southern Oscillation and Pacific Decadal Oscillation impacts on precipitation in the southern and central United States: Evaluation of spatial distribution and predictions. *Water Resour. Res.* **43**, 1–12.
33. Adams DK, Comrie AC. 1997 The North American Monsoon. *Bull. Am. Meteorol. Soc.* **78**, 2197–2213.
34. Sheppard PR, Comrie AC, Packin GD, Angersbach K, Hughes MK. 2002 The climate of the US Southwest. *Clim. Res.* **21**, 219–238.
35. Brown DP, Comrie AC. 2004 A winter precipitation ‘dipole’ in the western United States associated with multidecadal ENSO variability. *Geophys. Res. Lett.* **31**, 1–4.
36. Stein K, Timmermann A, Schneider N, Jin FF, Stuecker MF. 2014 ENSO seasonal synchronization theory. *J. Clim.* **27**, 5285–5310.
37. Ascoli D, Vacchiano G, Turco M, Conedera M, Drobyshev I, Maringer J, Motta R, Hacket-Pain A. 2017 Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nat. Commun.* **8**, 1–9.
38. Ascoli D, Hacket-Pain A, LaMontagne JM, Cardil A, Conedera M, Maringer J, Motta R, Pearse IS, Vacchiano G. 2020 Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: Evidence for a fire-related form of environmental prediction. *J. Ecol.* **108**, 1186–1198.
39. Ascoli, D, Hacket-Pain, A, Pearse, IS, Vacchiano, G, Corti, S, Davini, P. 2021 Modes of climate variability bridge proximate and evolutionary mechanisms of masting. *Proceedings. Biol. Sci.* This issue.
40. Forcella, F. 1981 Estimating pinyon cone production in New Mexico and Western Oklahoma. *The Journal of Wildlife Management*, 45(2), 553-557.

41. Burns RM, Honkala BH. 1990 *Silvics of North America: Volume 1. Conifers. Silvics North Am.*, 877.
42. Krannitz PG, Duralia TE. 2004 Cone and seed production in *Pinus ponderosa*: A review. *West. North Am. Nat. West. North Am. Nat.* **64**, 208–218.
43. Little EL. 1938 The earliest stages of pinyon cones. Research Note 46, Southwestern Forest and Range Experiment Station, Tucson, Arizona, USA.
44. Koenig WD, Knops JMH, Carmen WJ, Pearse IS. 2015 What drives masting? The phenological synchrony hypothesis. *Ecology* **96**, 184–192.
45. PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, data accessed Jul 2020.
46. Redmond MD, Weisberg PJ, Cobb NS, Gehring CA, Whipple A V., Whitham TG. 2016 A robust method to determine historical annual cone production among slow-growing conifers. *For. Ecol. Manage.* **368**, 1–6.
47. Crone EE, McIntire EJB, Brodie J. 2011 What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. *J. Ecol.* **99**, 438–444.
48. Peters VS, Gelderman MS, Visscher DR. 2017 Resiliency in masting systems: Do evolved seed escape strategies benefit an endangered pine? *Ecosphere* *8(9):e01928*.
49. Bouchard M, Pernot C. 2020 Climate and size of previous cone crops contribute to large-scale synchronous cone production in balsam fir. *Can. J. For. Res.* 1–33.
50. Wolter K, Timlin MS. 2011 El Niño/Southern Oscillation behaviour since 1871 as diagnosed in an extended multivariate ENSO index (MEI.ext). *Int. J. Climatol.* **31**, 1074–1087.
51. Tamaddun KA, Kalra A, Bernardez M, Ahmad S. 2017 Multi-Scale Correlation between the Western U.S. Snow Water Equivalent and ENSO/PDO Using Wavelet Analyses. *Water Resour. Manag.* **31**, 2745–2759.
52. Hu Q, Feng S. 2012 AMO- and ENSO-driven summertime circulation and precipitation variations in North America. *J. Clim.* **25**, 6477–6495.
53. Castro CL, McKee TB, Pielke Sr. RA. 2001 The Relationship of the North American Monsoon to Tropical and North Pacific Sea Surface Temperatures as Revealed by Observational Analyses. *J. Clim.* **14**, 4449–4473.
54. Wilson BT, Lister AJ, Riemann RI, Griffith, DM. 2013 Live tree species basal area of the contiguous United States (2000-2009). Newtown Square, PA: USDA Forest Service, Rocky Mountain Research Station.

55. Legendre P, Legendre L. Numerical ecology. Elsevier; 2012 Jul 21.
56. R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
57. Dowle M, Srinivasan A. (2019). data.table: Extension of `data.frame`. R package version 1.12.8. <https://CRAN.R-project.org/package=data.table>
58. Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). vegan: Community ecology package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
59. Hijmans RJ. (2020). raster: Geographic data analysis and modeling. R package version 3.0-12. <https://CRAN.R-project.org/package=raster>
60. Wickham H. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York, 2016.
61. Pedersen TL, Cramer F. (2020). scico: Colour palettes based on the scientific colour-Maps. R package version 1.2.0. <https://CRAN.R-project.org/package=scico>
62. Pedersen TL. (2019). patchwork: The composer of plots. R package version 1.0.0. <https://CRAN.R-project.org/package=patchwork>
63. Bogdziewicz M, Zwolak R, Crone EE. 2016 How do vertebrates respond to mast seeding? *Oikos*. 125, 300–307.
64. Ostfeld RS, Keesing F. 2000 Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *TREE* 15, 232–237.
65. League K, Veblen T. 2006 Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. *For. Ecol. Manage.* **228**, 98–107.
66. Linhart YB, Moreira X, Snyder MA, Mooney KA. 2014 Variability in seed cone production and functional response of seed predators to seed cone availability: Support for the predator satiation hypothesis. *J. Ecol.* 102, 576–583.
67. Masaki T, Oka T, Osumi K, Suzuki W. 2008 Geographical variation in climatic cues for mast seeding of *Fagus crenata*. *Popul. Ecol.* 50, 357–366.
68. Minor DM, Kobe RK. 2017 Masting synchrony in northern hardwood forests: super-producers govern population fruit production. *J. Ecol.* 105, 987–998.

69. Linhart YB, Mitton JB, Bowman DM, Sturgeon KB, Hamrick JL. 1979 Genetic aspects of fertility differentials in ponderosa pine. *Genet. Res.* 33, 237–242.
70. Shepperd WD, Edminster CB, Mata SA. 2006 Long-Term Seedfall, Establishment, Survival, and Growth of Natural and Planted Ponderosa Pine in the Colorado Front Range. *West. J. Appl. For.* 21, 19–26.
71. Satake A, Kelly, D. Studying the genetic basis of masting. *Proceedings. Biol. Sci.* This issue.
72. Fritts HC. 1976 *Tree rings and climate*. Academic Press.
73. Notaro M, Liu Z, Gallimore RG, Williams JW, Gutzler DS, Collins S. 2010 Complex seasonal cycle of ecohydrology in the Southwest United States. *J. Geophys. Res. Biogeosciences* 115.
74. Barger NN, Adams HD, Woodhouse C, Neff JC, Asner G.P (2009) Influence of livestock grazing and climate on piñon pine (*Pinus edulis*) dynamics. *Rangel. Ecol. Manag.* 62:531–539.
75. Redmond MD, Kelsey KC, Urza AK, Barger NN. 2017 Interacting effects of climate and landscape physiography on piñon pine growth using an individual-based approach. *Ecosphere*
76. Littlefield CE, Dobrowski SZ, Abatzoglou JT, Parks SA. 2020 A climatic dipole drives short- and long-term patterns of postfire forest recovery in the western United States. *Proc. Natl. Acad. Sci.* , 6–13.
77. Pesendorfer MB, Baker CM, Stringer M, McDonald-Madden E, Bode M, McEachern AK, Morrison SA, Sillett TS. 2018 Oak habitat recovery on California’s largest islands: Scenarios for the role of corvid seed dispersal. *J. Appl. Ecol.* 55, 1185–1194.
78. Pease CM, Mattson DJ. 2017 Demography of the Yellowstone Grizzly Bears. *Ecology* 80, 957–975.
79. Elliott GP, Eason DK, Jansen PW, Merton DV, Haprer GA. 2006 Productivity of kakapo (*Strigops habroptilus*) on offshore island refuges. *Notornis* 53, 138–142.
80. Breshears DD *et al.* 2005 Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci.* 102, 15144–15148.
81. Floyd ML, Clifford M, Cobb NS, Hanna D, Delph R, Ford P, Turner D. 2009 Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands. *Ecol. Appl.* 19, 1223–1230.
82. Redmond MD, Forcella F, Barger NN. 2012 Declines in pinyon pine cone production associated with regional warming. *Ecosphere* 3(12):120.

83. Redmond MD, Weisberg PJ, Cobb NS, Clifford MJ. 2018 Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. *J. Ecol.* **106**, 625–639.

SECTION 2

CHAPTER 4

⁴DEAD AGAIN: PREDICTIONS OF REPEAT TREE DIE-OFF UNDER HOTTER DROUGHTS CONFIRM TIPPING POINTS FOR A DRYLAND CONIFER SPECIES

OVERVIEW

Tree die-off, driven by extreme drought and exacerbated by a warming climate, is occurring rapidly across every wooded continent - threatening carbon sinks and other ecosystem services provided by forests and woodlands. Forecasting the spatial patterns of tree die-off in response to drought is a priority for the management and conservation of forested ecosystems under projected future hotter and drier climates. Several thresholds derived from drought-metrics have been proposed to predict mortality of *Pinus edulis*, a model tree species in many studies of drought-induced tree die-off. To improve future capacity to forecast tree mortality, we used a severe drought as a natural experiment. We compared the ability of existing mortality thresholds derived from four drought metrics (the Forest Drought Severity Index, the Standardized Precipitation Evapotranspiration Index, and raw values of precipitation and vapor pressure deficit, calculated using 4km PRISM data) to predict areas of *P. edulis* die-off following an extreme drought in 2018 across the southwestern US. Using aerial detection surveys of tree mortality in combination with gridded climate data, we calculated the agreement between these four proposed thresholds and the presence and absence of regional-scale tree die-off using sensitivity, specificity, and the area under the curve (AUC). Overall, existing mortality thresholds tended to over predict the spatial extent of tree die-off across the landscape, yet some retain moderate skill in discriminating between areas that experienced and did not experience

⁴ By Andreas P. Wion, David D. Breshears, Charles J. Carroll, Neil S. Cobb, Sarah J. Hart, Darin J. Law, Nashelly Meneses, and Miranda D. Redmond.

tree die-off. The simple precipitation threshold had the highest AUC score (71%) as well as fair sensitivity and specificity, but the Forest Drought Severity Index had the greatest sensitivity to die-off (85.9%). We highlight that empirically derived climate thresholds may be useful forecasting tools to identify vulnerable areas to drought induced die-off, allowing for targeted responses to future droughts and improved management of at-risk areas.

INTRODUCTION

Tree die-off (or mass-mortality events of trees) driven by extreme drought, exacerbated by a warming climate, and frequently associated with forest pests and pathogens, presents a global-scale challenge to maintaining forested ecosystems under accelerating climate warming (Breshears et al. 2005, Allen et al. 2010, 2015). Forecasting tree die-off has the potential to inform management goals like the provisioning of ecosystem services, developing treatments to increase forest resiliency during or prior to drought, and planning recovery efforts following drought, as well as scientific questions like carbon sink-source dynamics, global climate circulation, and species distributions (e.g., Bradford et al. 2018, Anderegg et al. 2013, Swann et al. 2018, Jackson 2021). But forecasting tree die-off remains a major challenge, as tree die-off events are relatively infrequent, long-lasting, and slow developing in comparison to many other forest disturbances like fires or hurricanes (Redmond et al. 2019). Thus, while the study of tree mortality is often a retrospective exercise, advancing forecasts of tree die-off requires iteratively testing existing hypotheses to refine future predictions, highlight areas of uncertainty, and evaluate our understanding of ecological processes (Dietze 2017).

“Hotter droughts” or “hot droughts” (Allen et al. 2015; originally “global-change-type-droughts”, Breshears et al. 2005) are major drivers of tree die-off, due to the positive exponential

relationship between maximum temperature and saturation vapor pressure (Breshears et al. 2013, Groissord et al. 2020). Hotter temperatures exponentially increase the water stress experienced by plants during periods of drought (e.g., Vapor Pressure Deficit [VPD], Anderson 1953, Groissord et al. 2020), therefore continued and accelerating climate warming greatly increases the vulnerability of trees to bark beetles, pathogens, hydraulic failure of the xylem, and carbon starvation (Adams et al. 2009, McDowell et al. 2008, 2011, Breshears et al. 2013, Gaylord et al. 2013). Identifying temperature and moisture thresholds associated with tree die-off (i.e., mortality thresholds) has been the focus of much recent research (e.g., Huang et al. 2015, Clifford et al. 2013, Hammond et al. 2019) in part because this would allow scientists and managers to better predict how, when, and where trees are most likely to die following hotter droughts. However, the wide variation in physiological vulnerability and drought exposure makes individual-tree mortality exceedingly difficult to predict (Trugman et al. 2021). Ultimately, it is unclear whether empirically derived threshold responses, often retrospectively identified from a single drought event, produce transferrable and repeatable results in future drought events of differing severity, or whether such predictions are consistent across large geographic areas.

One of the best-documented examples of tree die-off occurred in the southwestern United States during the early 2000s (Breshears et al. 2005, Meddens et al. 2015, Floyd et al. 2009). An outbreak of piñon *Ips* beetles (*Ips confusus*), occurring in combination with a hot drought event, resulted in high levels of regional-scale mortality of piñon pine (*Pinus edulis*), an iconic conifer species in dry woodlands and forests of the region. This event motivated a substantial amount of research on drought and warming-driven die-off. In the last twenty years, over a dozen metrics and their associated thresholds have been proposed as predictors of piñon pine die-off (reviewed

in Breshears et al. 2018). Many of these metrics require detailed ecophysiological and hydraulic data to predict individual-level mortality (Breshears et al. 2018), though such data are not widely available, especially over long periods of time or across broad spatial areas. However, four of these metrics are amenable to broad-scale forecasting efforts: the Forest Drought Severity Index (FDSI), the Standardized Precipitation Evaporation Index (SPEI), and absolute values of precipitation and VPD (Breshears et al. 2018). Yet, the applicability of these metrics and their associated thresholds to predict piñon pine mortality have not been field-tested in subsequent droughts. Such metrics also share similarities with those available for other species of *Pinus* (e.g., Williams et al. 2013, Breshears et al. 2018) and field-validating such relationships will improve our ability to forecast forest die-off in other systems and species.

We used a recent hot drought as a natural experiment to evaluate our ability to predict areas experiencing piñon pine die-off using these four existing mortality thresholds. Our primary objective was to assess whether thresholds derived from these four regional-scale drought metrics could successfully predict the spatial patterns of piñon pine die-off in advance of aerial surveys of tree die-off the following year. We also explore the repeatability of these empirically derived thresholds' ability to predict tree die-off across events with different historical contingencies by comparing tree die-off following the 2018 drought to a benchmark year for tree die-off (2002). Finally, we highlight the importance of testing previously developed mortality thresholds discuss how these results bear on our ability to develop future forecasts of tree die-off.

Methods and Materials

Study species and area

Piñon pine occupies low elevation, semi-arid forests and woodlands of the southwestern United States and Mexico. The study area comprised the distribution of piñon pine (from Little 1971) in the US states of Colorado, New Mexico, Utah, and Arizona (hereafter the southwestern US). Trees of the genus *Pinus* are some of the most commercially important species worldwide, and piñon pine specifically has been used in a large majority of studies examining hotter drought driven die-off, making it a model species (Breshears et al. 2018). It has been estimated that half of a million hectares of piñon pine woodlands and forests in the southwestern US (14% of the total area of the species) have been affected by tree die-off between 2000-2018 (Hicke et al. 2020), with some areas experiencing near total loss of mature piñon pine trees (Breshears et al. 2005, Floyd et al. 2009, Clifford et al. 2013).

The climate of the southwestern US is characterized by cold winters, warm summers, and highly seasonal precipitation. Annual precipitation averages around 400 mm per year (PRISM Climate Group, 1981-2010) and is highly seasonal. In the north and western portion of the study area, precipitation falls mostly as snow during the cool-season (October – April) and the warm-season is dry. Heading south and east, precipitation is more strongly influenced by the North American monsoon (Notaro et al. 2010). In these areas, half or more of the annual precipitation may fall during the summer months of July, August, and September (which are usually the driest months in the north and west portions of the study area, PRISM Climate Group, 2021).

Much of this area has experienced a persistent hydrological drought for two decades, the driest such period since in at least 1200 years (Williams et al. 2022), and climate models predict continued warming and drying trends in the future (Bradford et al. 2020, Cook et al. 2021). The 2018 hot drought in the southwest US was an acute event that was overlaid on this extended hydrological drought. About half of the study area experienced precipitation deficits greater than

50% of the climatological normal (e.g., 1981-2010), and annual mean temperatures in 2018 across the region were on average 0.5 - 2° C warmer relative to 1981-2010 climate averages (PRISM Climate Group, 2021). Despite several drought events that occurred between 2002-2018, the 2018 drought event was at the time the most severe drought since 2002 (Figure 4.1).

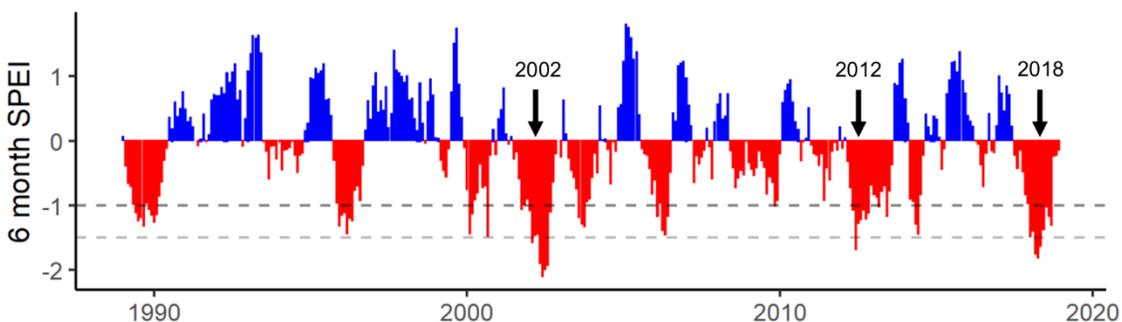


Figure 4.1) Running six-month standardized precipitation-evapotranspiration index (SPEI) values between Jan 1, 1989, and December 1, 2018 averaged across all piñon pine woodlands in the southwestern US. Each bar represents the difference in precipitation and evapotranspiration for the prior 6-month period, standardized to the long-term mean (since 1901). Positive values (blue) indicate cooler and wetter than average conditions, and negative values (red) indicate hotter and drier than average conditions. SPEI was calculated with a Thornwaite type water balance using PRISM derived precipitation and mean temperature at a 4km resolution, and the distribution of piñon pine woodlands was described by Little (1971). Dashed line indicates 1 standard deviation below the average (fainter line, -1.5) as benchmarks of drought stress. Drought conditions in 2018 (minimum 6-month SPEI value = -1.81) were the most severe in this area since 2002 (minimum 6-month SPEI value = -2.10). A long-term drought in 2012 briefly reached a minimum 6-month SPEI value of -1.69, but overall, the 2012 event was less severe than the 2002 or 2018 droughts.

Quantifying tree-die off – Aerial Detection Surveys

To quantify tree die-off across the study area, we used Aerial Detection Surveys (ADS; USDA Forest Service 2019). These surveys are flown by the United States Forest Service each year, usually in mid-summer, and are widely used in studies of tree mortality at coarse spatial

grains (ca. 1 km²) and at regional extents (Coleman et al. 2018, Hicke et al. 2020, Meddens et al. 2012, Preisler et al. 2017, Masek et al. 2013, Hart et al. 2017). Trained surveyors sketch polygons of areas affected by tree mortality, representing stand-level mortality at spatial scales greater than 0.4 ha, and then estimate the attributes of these polygons including the approximate area, severity category (5 categories based on the percentage of dead or dying trees), tree species, and mortality agent. Detection of mortality often lags at least a year behind drought; therefore, we examined ADS surveys flown in summer 2019 to assess the impacts of the 2018 hotter drought (similar to Hicke et al. 2020 and Meddens et al. 2012). Previous work also suggests that the background rate of mortality in these systems is 1-3% annually (van Mantgem et al. 2009); therefore, to be confident that we were describing mortality events that exceeded background mortality rates, we excluded observations where fewer than 15 trees died in areas < 0.4 ha in size (point observations) and stand-level observations labeled as < 10% mortality severity (ADS severity classes 1-2). Finally, we masked all data surveyed by ADS teams in 2019 to the extent of piñon pine (Little, 1971). All analyses were carried out in R 4.1.0 (R Core Team 2021) using functions from the raster (Hilman 2021) and sf (Pebesma 2018) packages. Data visualizations were made in ggplot2 (Wickham 2016) with scico, PNWcolors, and patchwork packages (Pedersen and Cramer 2020, Lawlor 2020, Pedersen 2020), and data carpentry was performed using data.table (Dowle and Srinivasan, 2021).

We calculated the total number of acres affected by tree die-off by summing the area of all polygons in each severity class. However very few of these polygons were in the most severe mortality class (i.e., > 50% mortality of live trees, n = 9). Therefore, summing the total area affected would overestimate the total area directly affected by tree die-off. To account for this, we multiplied each polygon by a constant corresponding to the upper, middle, and lower bounds

of each severity class. For example, the acreage of polygons described as experiencing 11-29% mortality (the lowest severity class included in this study, “Severity class 3 – Moderate”) were multiplied by 11% (lower bound), 29% (upper bound), and 20% (middle estimate). For comparison with gridded climate data (below) we transformed ADS polygon data to a 4-kilometer resolution raster of presence/absence and aligned with the gridded climate data (Figure 4.2). We then calculated the total acres affected by tree die-off in each pixel to visualize the spatial patterns of mortality across the region.

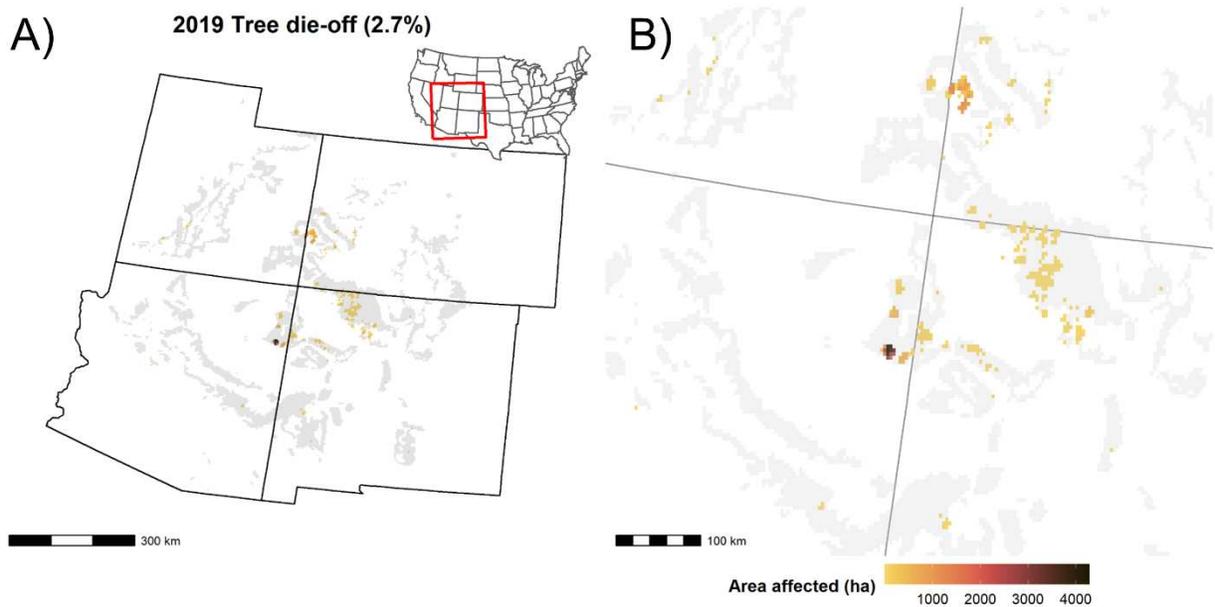


Figure 4.2) Panel A shows tree die-off (i.e., observations of mortality exceeding 10% of the affected area) of piñon pine in 2019 as quantified by aerial detection surveys (ADS). Gray shading shows the distribution of piñon pine across the U.S. states of Colorado, New Mexico, Arizona, and Utah (southwest US), and darker colors indicate greater amounts of tree die-off in each pixel. Total area affected was estimated by multiplying the size of each polygon by the middle estimate of each ADS severity class. Panel B is zoomed to the extent of tree die-off observations in the study area. Tree-die off in 2019 was not spatially widespread across the area and was only present in 2.7% of the areas surveyed by ADS teams.

Quantifying drought intensity – Climatic thresholds

We compared published thresholds of four climate metrics hypothesized to predict regional conifer die-off in the southwestern US (reviewed in Breshears et al. 2018, Table 4.1; Figure 4.3): the Forest Drought Severity Index (FDSI, Williams et al. 2013), the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010, Huang et al. 2015), and absolute precipitation (PPT) and vapor pressure deficit (VPD; described by Clifford et al. 2013). Gridded 4 km monthly climate data from PRISM (PRISM Climate Group 2020) were used to calculate the pixel value of all metrics across the study area.

Table 4.1) Descriptions of four published metrics and the hypothesized thresholds of *Pinus edulis* die-off.

Metric	Description	Threshold
FDSI ¹	Mean Forest Drought Severity Index of the current year and the year prior. FDSI is calculated as the combination of winter (Nov - Mar) precipitation, May - July VPD of the current year, and Aug-Oct VPD of the year prior, and is standardized by applying a ratio of the current conditions to the long-term mean.	-1.41
SPEI ²	Negative Standardized Precipitation Evapotranspiration Index values for the 11-month period of September (during the year prior) through July (of the current year). SPEI is calculated as difference between precipitation and potential evapotranspiration, standardized to the long-term mean.	-1.64
PPT ³	Total precipitation of the current water year (September – previous October) and the year prior.	< 600 mm

VPD ³	Mean warm-season (May-August) vapor pressure deficit (VPD), averaged over the current year and the year prior.	> 17 hPa
------------------	--	----------

¹Williams et al. 2013, ²Huang et al. 2015, ³Clifford et al. 2013

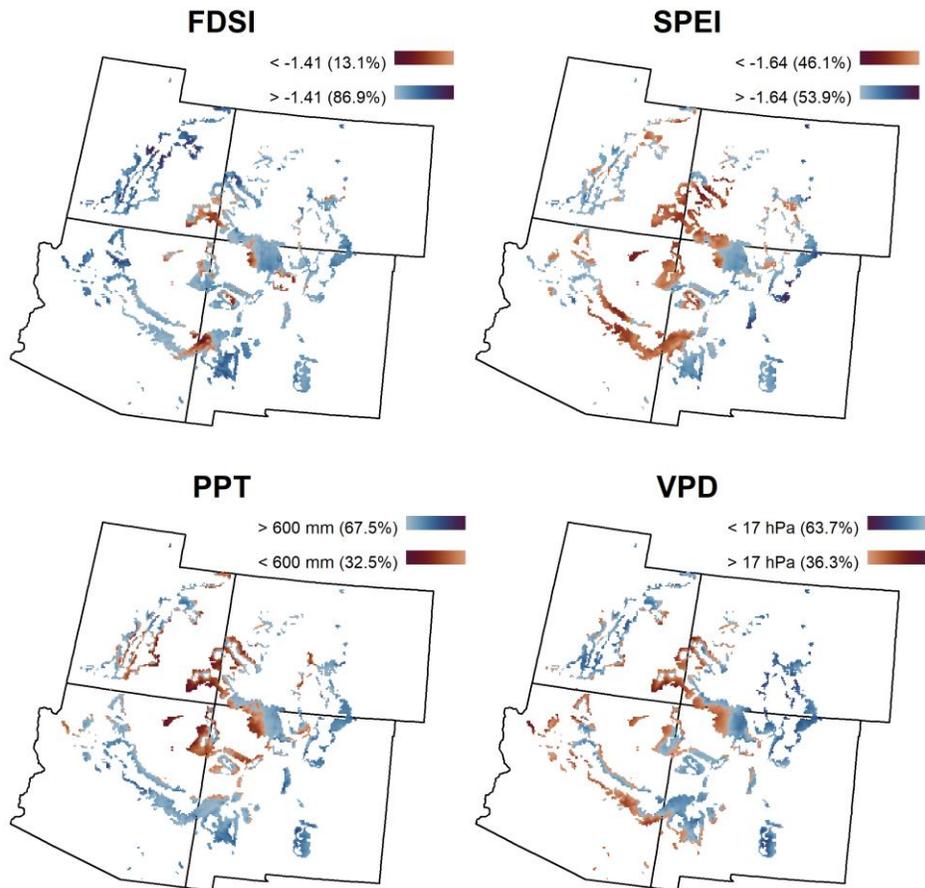


Figure 4.3) Spatial patterns of tipping points hypothesized to be predictors of tree die-off during the 2018 hotter drought across the range of *Pinus edulis* that was surveyed by Aerial Detection Surveys in 2019 (all pixels). Gridded climate data were classified as either beyond (red colors) or below (blue colors) the tipping points. The proportion of pixels above or below tipping points are included in parentheses.

Using tree ring chronologies that span 1000 years from the southwest US, Williams et al. (2013) identified years with FDSI values below -1.41 as benchmark years of severe drought stress, where tree die-off was likely widespread across this region. Williams et al. (2013) also showed a strong negative correlation between FDSI and the area affected by bark beetles as observed by ADS data. However, some authors have cautioned against using FDSI as a point-based metric, stating that FDSI was intended to capture the regionally coherent variability in tree growth of multiple tree species across the entire southwest US (McDowell et al. 2016; Williams et al. 2013). Nevertheless, FDSI (and the -1.41 threshold) has been used as a benchmark of severe drought stress in other studies of tree mortality and drought (Flake and Weisberg 2018, McDowell et al. 2013); thus, its utility as a point-based metric of drought severity and mortality likelihood warrants explicit testing. We calculated FDSI following the equations in Williams et al. (2013). Specifically, we calculated the two-year average of FDSI values (i.e., 2017-2018) relative to the period between 1896 – 2018.

The SPEI is a multiscalar index that is calculated as the difference between precipitation and potential evapotranspiration, integrated over time, and standardized to the long-term mean. During the 2002 drought, 11-month SPEI values (≤ -1.64) were associated with a cessation of tree growth and subsequent die-off following the 2002 event (Huang et al. 2015; Table 1). SPEI was calculated using a Thornwaithe type water balance model for the period 1901-2018, using PRISM derived mean temperature and precipitation, and the SPEI package (Begueria and Vicente-Serrano 2017) in R.

Both FDSI and SPEI were standardized at the pixel-level to the 122-year and 118-year (respectively) average, with negative values indicating more severe drought stress relative to the long-term average. On the other hand, the precipitation and VPD thresholds are absolute values,

and thus are not standardized at the pixel-level to a long-term mean. We summed monthly precipitation over the previous two water years (2017-2018; the period from October 1 – September 30) to calculate the precipitation threshold from Clifford et al. (2013). We used monthly maximum and minimum temperature, and average dew-point temperature from the prior two years to calculate mean warm-season (May-August) VPD following Clifford et al.'s (2013) approach, which also followed the equations for VPD provided in Williams et al. (2013; above).

Because 2002 was a benchmark year for tree die-off in this region, we compared the intensity of the 2018 and 2002 droughts as characterized by these four metrics (Figure 4). These two events were nearly equivalent in terms of their two-year precipitation totals and warm-season VPD averages, with 2002 being slightly warmer and drier than 2018 overall (Figure 4). This is likely because PPT and VPD are based on the raw climate values, which vary greatly across the region in relation to topography, rather than standardized to the long-term mean. However, FDSI and SPEI, which are standardized indices, clearly differentiate these two events in terms of drought severity, with both FDSI and SPEI being more negative (i.e., hotter and drier) in 2002 than in 2018 (Figure 4). Near-uniformly negative values of these metrics reflect the pervasive nature of hot drought conditions throughout the study area.

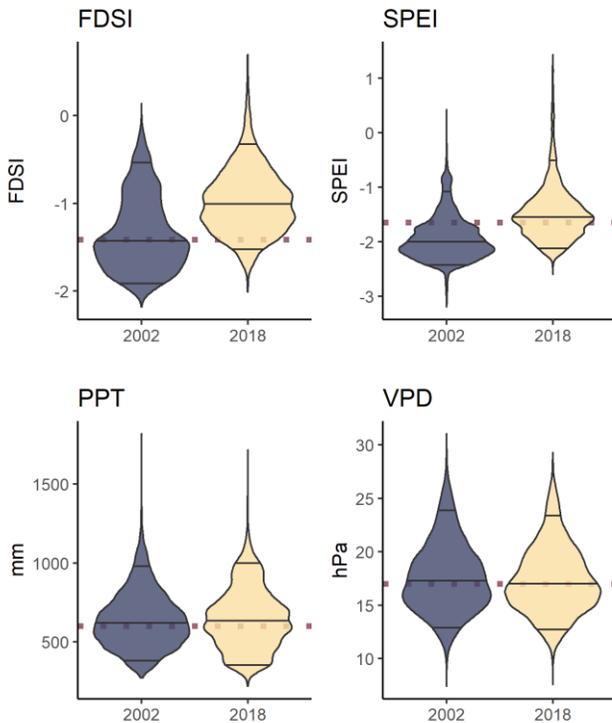


Figure 4.4) Comparison of 2002 and 2018 hotter droughts. Violin plots show the continuous distribution of the four drought metrics of interest: two-year average of the Forest Drought Severity Index (FDSI), and 11-month Standardized Precipitation Evapotranspiration Index (SPEI), two-year precipitation total (PPT), and two-year mean warm-season vapor pressure deficit (VPD), in 2002 (blue, left) and 2018 (yellow, right). Red dotted lines denote proposed threshold values for each metric. Horizontal solid lines indicate the 5%, median, and 95% percentiles of the data. Although the drought events are nearly equivalent in terms of PPT and VPD values, both standardized drought metrics (FDSI and SPEI) were more negative in 2002, indicating hotter and drier conditions.

Agreement between climatic thresholds and tree die-off

We extracted continuous values of the drought metrics for each pixel with and without observations of tree die-off, and then plotted the distribution of all pixels for each individual metric in relation to their proposed threshold to visualize the skill of the threshold in discriminating areas that experienced die-off. Climate data were transformed to binary variables (0 – below threshold, or 1 – beyond threshold) and compared to presence/absence maps of tree die-off with confusion matrices using in the caret package in R (Khun 2021). We evaluated

metrics based on their sensitivity (i.e., true positive rate, or the proportion of correct predictions containing tree die-off), specificity (i.e., true negative rate, or the proportion of correct predictions not containing tree die-off), and the area under the curve (AUC; a metric of overall predictive power that balances the trade-off between sensitivity and specificity using a receiver's operating characteristic curve, Marzban 2004). Values are constrained from 0 – 1, with values of 0.5 indicating predictions no better than chance, and higher values indicating a higher proportion of correct predictions (both presence and absence).

RESULTS

Can empirically derived thresholds predict the spatial patterns of tree die-off?

We estimate that between 5,621.1– 10,950.4 ha (middle estimate = 8,285.9 ha) were directly affected by tree die-off (i.e., tree mortality > 10%) in 2019. Tree die-off was not spatially extensive and was found in only 2.7% of the pixels within the study area (Figure 4.1). The area of mortality observations (n =313) ranged from 0.4 – 2,354.4 ha, with a median polygon area of 5.2 ha. Simple comparisons of the total area beyond the climate threshold relative to the total area that experienced tree die-off would suggest that overall, these metrics tended to overestimate the amount of tree die-off anticipated in 2019 (ranging from 13.1% to 46.1% of the study area predicted to experience die-off, Figure 4.3).

The FDSI threshold had the greatest true-positive rate (sensitivity = 86.9%, Figure 4.5) indicating that this metric was highly skilled at correctly predicting locations where tree mortality was most likely to occur across the landscape. However, the FDSI threshold also had the lowest true-negative rate (specificity = 15.8%, Figure 4.5), indicating that a substantial amount of mortality occurred in areas that FDSI predicted it would not (i.e., below the -1.41

threshold, Figure 4.6). Overall, the FDSI threshold had the lowest AUC score (51%). When accounting for both sensitivity and specificity, the precipitation threshold better balanced predictions of both presence and absence, with the highest AUC score (71%), highest true negative rate (specificity = 73.2%) and the second highest true positive rate (sensitivity = 68.6%). Based on visual assessments, the value of the VPD threshold was roughly consistent with the location proposed by Clifford et al. (2013; Figure 4.6); however, the VPD threshold was less specific than the precipitation threshold, (sensitivity = 64.3%, specificity = 57.9%, AUC = 61.1%; Figures 4.5 and 4.6). Observations of tree-die off were skewed towards the hotter and drier side of SPEI values, although mortality was also observed across a wide range of SPEI values, indicating relatively low specificity (Figure 4.5). The SPEI threshold also predicted the most amount of tree die-off relative to the other metrics (46.4% of all pixels were expected to contain die-off, Figure 4.3) and classification accuracy metrics hovered near 54% (sensitivity = 54.3%, specificity = 54% and AUC = 54.6%).

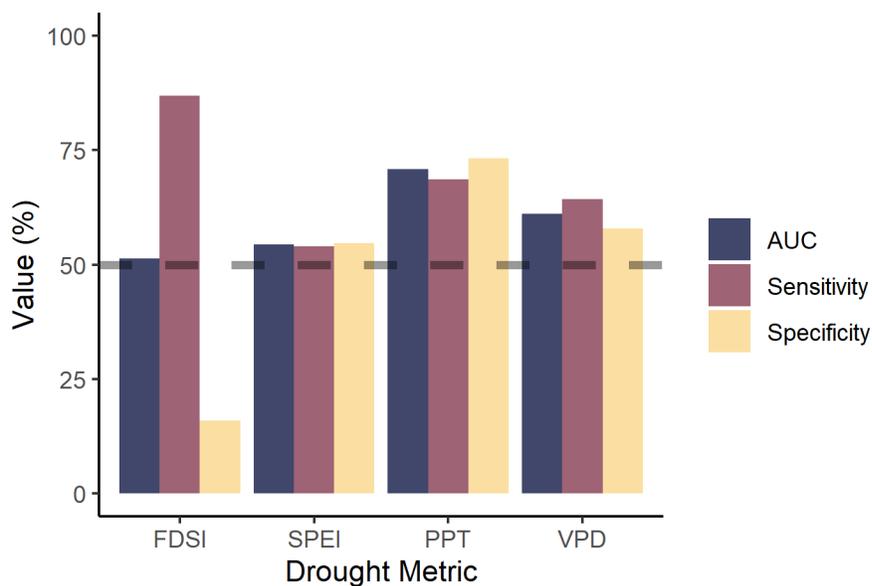


Figure 4.5) Results of confusion matrices classifying the agreement between all pixels surveyed by ADS in 2019 within the distribution of *P. edulis* that experienced tree die-off (>10 % mortality) and those pixels that exceeded die-off tipping points of the four metrics. Sensitivity is the true positive rate, specificity is the true negative rate, and AUC balances the overall proportion of correction predictions (balancing sensitivity and specificity).

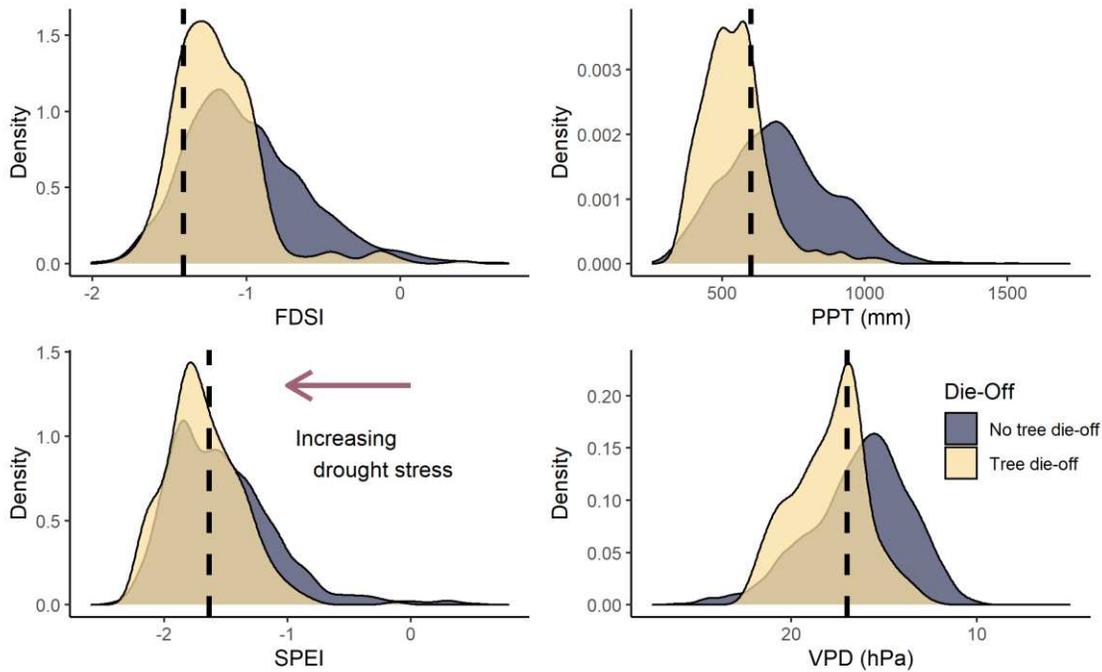


Figure 4.6) Distribution of drought metric values for all pixels that were surveyed by ADS in 2019 that either had evidence of tree die-off (yellow) or had no tree die off (blue). Distribution of metric values for all pixels are plotted on the x axis, and the location of the tipping point is shown by a dashed line. The y axis shows the cumulative density (unitless) of all pixels in each category. Drought stress increases from right to left along the x axis of each panel, denoted by direction of red arrows.

DISCUSSION

This study was a key first step in advancing future forecast models of tree die-off. By field-testing multiple pre-existing mortality thresholds (specifically those which can be easily calculated from readily available climate data), we can begin to evaluate our understanding of regional-scale tree die-off, refine future predictions under repeat drought events, highlight areas of potential uncertainty, and point to areas of growing confidence where these results may be

translated into action. In the southwest US, droughts are projected to increase in frequency, intensity, and duration in step with a warmer climate, portending continued tree die-off events that will have major impacts on society and ecosystems alike (Overpeck and Udall 2017, Chiang et al. 2021, McDowell et al. 2016, Williams et al. 2010, 2013). Yet significant uncertainties remain about when and where these droughts will ultimately occur, and which trees are the most likely to die following drought. Thus, managing for forest and woodland persistence in a hotter future will require the capacity to respond to extreme climate events as they are developing, and to rapidly implement targeted interventions that increase ecosystem resiliency to drought or aid in the recovery of ecosystems following droughts (Bradford et al. 2018, 2020, Redmond et al. 2019).

Tree mortality is notoriously difficult to accurately predict (Trugman et al. 2021). Recent research has used hydraulic data, forest inventories, remote sensing, and climate data to predict tree mortality in many different species with mixed success (Venturas et al. 2021, Rogers et al. 2018, Preisler et al. 2017, Das et al. 2013). Ecophysiological approaches to understanding drought-driven mortality may provide a mechanistic understanding of the processes that proximately lead to tree death (McDowell et al. 2013). Yet individual-level factors can confound hydraulic predictions, and such models often contain many parameters that vary continuously and can be difficult to estimate precisely. In this study, we bypass the variability in drought responses at the individual level and instead take a top-down approach to predicting tree mortality at regional scales. Our results suggest that simple metrics derived from readily available climate data may provide broadly useful generalizations about the spatial patterns of tree mortality across large spatial extents and lay the groundwork for refining future forecasts of drought-driven tree die-off. Such information can help rapidly identify areas of priority for

implementing adaptive management decisions, including managing for understory vegetation responses, future fire risk, public fuelwood sources, wildlife habitat, and the provisioning of other ecosystem services.

Tree die-off following repeat hotter drought events

Following the 2018 drought, tree die-off was less severe compared to the 2002 drought. Though the estimates are not directly comparable, Hicke et al. (2020) estimated that across approximately 300,000 ha impacted by hotter drought and piñon *Ips* beetles (*Ips confusus*), 400 million trees died following the 2002 hotter drought. For comparison, these estimates are an order of magnitude greater than what we estimate died following the 2018 event (middle estimate of tree die-off = 8,286 ha). We also estimate that the highest severity class of tree die-off (i.e., > 50% mortality) accounted for only 20% of the total area experiencing die-off in 2019 (middle estimate = 1,643 ha, minimum estimate = 1,095.5 ha, maximum estimate = 2,191 ha). A lack of highly susceptible trees following the 2002 hotter drought could explain the discrepancy in die-off severity between droughts. Many of the regions affected during the 2018 hotter drought were also affected by the 2002 event (Meddens et al. 2015, Hicke et al. 2020). Though ADS data does not characterize size and age distributions of surveyed forests, the absence of widespread and severe mortality may reflect the lack of large and old trees remaining on these landscapes (Floyd et al. 2015), which are preferred hosts of piñon ips beetles (Negron and Wilson, 2003).

Repeat tree die-off events may also increase the relative abundance of drought adapted genotypes in surviving populations, which can shape the susceptibility of populations to future drought at the landscape level (Kuparinen et al. 2010). Trees likely exhibit some capacity to adapt to repeated exposure to drought, possibly through temporarily reducing structural growth or the remobilization of stored carbon (Ovenden et al. 2021, Peltier et al. 2021), though damage incurred from past droughts can also influence mortality responses in subsequent droughts (Macalady and Buggman 2014, Trugman et al. 2018). It remains unclear whether any such adaptive capacity or phenotypic plasticity will maintain pace with the velocity of climate change (Kuparinen et al. 2010, Jump and Peneulas 2005).

The 2002 drought also followed several decades of cool and wet weather, particularly during the 1970's and 1980's, which may have promoted structural overshoot of canopy growth (Jump et al. 2017, Zhang et al. 2021) or facilitated establishment of trees into marginal microsites, i.e., areas that can support young trees during cool and wet periods but lack the buffer from drought to support older trees during hot and dry periods (Greenwood and Weisberg 2008). The 16-year period between 2002 and 2018 was notably much drier and hotter than the long-term average (Williams et al. 2022), and since piñon pine can take decades to reach maturity, there have been few opportunities for episodic recruitment or structural overshoot during the historically dry conditions that have characterized the early 21st century (Floyd et al. 2015). The 2002 drought lasted several years - notably longer than the 2018 drought, which was also punctuated by a small number of heavy summer rainfall events in part of the region, relieving short-term drought stress in a field experiment (Redmond et al., 2019). The reduced regional mortality response of piñon pine to subsequent hotter drought events may have important

implications for forecasting and may bias these thresholds towards overpredicting mortality across the landscape.

Differences among drought metrics

While some of these metrics showed promise in predicting tree die-off, they varied in their predictive power and the context when each may be most useful. The FDSI mortality threshold was the most sensitive of the four metrics, correctly predicting the areas that experienced tree die-off more than 85% of the time. This suggests that the FDSI mortality threshold could be most useful for identifying locations that are the most likely to experience mortality during drought. For example, in situations where resources may be limited, managers or scientists may choose to selectively target only a subset of the areas likely to experience future mortality, and FDSI could be used to prioritize those locations. However, the low specificity of FDSI may limit its ability to accurately capture more detailed, spatial patterns of tree die-off at regional extents. The FDSI metric was initially developed as a region-wide indicator of annualized forest drought stress as measured by tree rings. In other words, widespread tree die-off is only predicted to occur in years when region-wide FDSI reaches below -1.41 (Williams et al., 2013), which was not achieved in 2018 (Figure 3). For this reason, the authors of this index have argued that it may not be appropriate as a point-based metric (e.g., McDowell et al. 2016), because FDSI at any given point may not be indicative of FDSI across the entire southwest. This may explain the poor specificity of the metric in discriminating tree die-off from tree survival at point locations. Nevertheless, our study suggests that FDSI may still retain a high degree of

sensitivity as a point-based metric and in some cases may be useful in identifying priority areas for targeted actions.

The precipitation mortality threshold proposed by Clifford et al. (2013) was better able to discriminate both true-positives and true-negatives, providing a more balanced picture of tree die-off at the regional level. This was somewhat surprising, given the wide range of mean annual precipitation across the study area relative to the extent this mortality threshold was originally developed at (i.e., 100 km transect in central New Mexico, Clifford et al. 2013), but also because responses to reduced precipitation are implicitly constrained by temperature (i.e., VPD; Adams et al. 2009, Williams et al. 2013). Yet its simplicity provides significant practical value to land managers concerned about tree die-off in the face of increasing hot drought. Absolute precipitation totals do not require data transformation (like FDSI) or software packages (like SPEI) to calculate, and precipitation is widely and easily monitored by numerous individuals and agencies. Clear paths to refining this relationship include the use of weather station data and real time monitoring of tree die-off events. Furthermore, understanding how this relationship varies across individuals of different size and age classes, along topographic and climatic gradients, and in the presence and absence of pathogens and other biotic agents of tree mortality, will greatly improve future forecasting efforts as well.

Differences in predictive power among these metrics may arise from the different extents and scales that these metrics were originally developed at (i.e., range-wide extent for FDSI and SPEI, regional-extent for PPT and VPD), or the different data sources originally used to parameterize these thresholds. It should be noted here that the grain-size of our climate data (4 km²) did not always align with the mortality observations (ranging in size from 0.4 – 2,354.4 ha or approximately 20 km²), and uncertainty in our relatively coarse-grained maps of piñon

presence could also introduce error in these analyses. Within the relatively coarse-grained resolution of this climate data, there are many fine-scale biophysical attributes that likely also modulate mortality responses, including stand density, topographic exposure, and soil depth and texture (Trugman et al. 2021). Tree mortality often arises from cross-scale phenomena among these drivers (i.e., individual-level resistance, stand- or landscape-level vulnerability, and regional-scale climate drivers), and thus accounting for these different variables and their interactions in future models will be a key to producing more accurate forecasts of tree mortality.

Near term ecological forecasting requires a learn-by-doing approach, with close collaboration between scientists and managers to supply an iterative cycle of adaptive management (Dietze et al. 2018). We show that empirically derived thresholds show promise in predicting the spatial patterns of tree die-off in the future, although such relationships must continue to be tested, validated, and refined to develop accurate forecasts. Nevertheless, regional-scale forecasts of tree die-off, similar to semi-seasonal forecasts of fire activity or extreme weather, may soon be within reach for this species and other species at risk from hotter drought.

CONCLUSION

By building the capacity to forecast future tree die-off, we can inform efforts to manage and restore forested ecosystems following hotter droughts. This research highlights areas of both agreement and uncertainty in our predictive understanding of tree die-off from drought, and we suggest that simple forecasts using readily available climate data may soon be within reach for this widely studied conifer species. Yet numerous avenues remain to improve these predictions

of tree die-off, including accounting for biophysical characteristics like stand density, soil properties, tree size, and topographic exposure, which are known to influence mortality in many species. The thresholds evaluated here should continue to be tested in a forward-facing manner, including with independent field observations and local weather station data, to further refine our predictive understanding of tree survival and die-off in an increasingly hotter world.

REFERENCES

- Adams H D, Zeppel M J B, Anderegg W R L, Hartmann H, Landhäusser S M, Tissue D T, Huxman T E, Hudson P J, Franz T E, Allen C D, Anderegg L D L, Barron-Gafford G A, Beerling D J, Breshears D D, Brodribb T J, Bugmann H, Cobb R C, Collins A D, Dickman L T, Duan H, Ewers B E, Galiano L, Galvez D A, Garcia-Forner N, Gaylord M L, Germino M J, Gessler A, Hacke U G, Hakamada R, Hector A, Jenkins M W, Kane J M, Kolb T E, Law D J, Lewis J D, Limousin J M, Love D M, Macalady A K, Martínez-Vilalta J, Mencuccini M, Mitchell P J, Muss J D, O'Brien M J, O'Grady A P, Pangle R E, Pinkard E A, Piper F I, Plaut J A, Pockman W T, Quirk J, Reinhardt K, Ripullone F, Ryan M G, Sala A, Sevanto S, Sperry J S, Vargas R, Vennetier M, Way D A, Xu C, Yezpez E A and McDowell N G 2017 A multi-species synthesis of physiological mechanisms in drought-induced tree mortality *Nat. Ecol. Evol.* **1** 1285–91 Online: <http://dx.doi.org/10.1038/s41559-017-0248-x>
- Adams H D, Guardiola-Claramonte M, Barron-Gafford G A, Villegas J C, Breshears D D, Zou C B, Troch P A, Huxman T E and Mooney H A 2009 Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought *Proc. Natl. Acad. Sci.* **106** 7063–6 Online: <http://www.pnas.org/content/pnas/106/17/7063.full.pdf>
- Allen C D, Breshears D D and McDowell N G 2015 On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene *Ecosphere* **6** art129 Online: <http://doi.wiley.com/10.1890/ES15-00203.1>
- Allen C D, Macalady A K, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears D D, Hogg E H (Ted., Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J H, Allard G, Running S W, Semerci A and Cobb N 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *For. Ecol. Manage.* **259** 660–84
- Anderegg W R L, Kane J M and Anderegg L D L 2013 Consequences of widespread tree mortality triggered by drought and temperature stress *Nat. Clim. Chang.* **3** 30–6 Online: <http://www.nature.com/articles/nclimate1635>
- Beguería S. and Vicente-Serrano S.M. (2017). SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index. R package version 1.7. <https://CRAN.R-project.org/package=SPEI>
- Bradford J B, Andrews C M, Robles M D, McCauley L A, Woolley T J and Marshall R M 2020 Landscape-scale restoration minimizes tree growth vulnerability to 21st century drought in a dry forest *Ecol. Appl.* **0** 1–16
- Bradford J B, Betancourt J L, Butterfield B J, Munson S M and Wood T E 2018 Anticipatory natural resource science and management for a changing future *Front. Ecol. Environ.* **16** 295–303

- Bradford J B, Schlaepfer D R, Lauenroth W K and Palmquist K A 2020 Robust ecological drought projections for drylands in the 21st century *Glob. Chang. Biol.* **26** 3906–19
- 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, Myers O B and Meyer C W 2005 Regional vegetation die-off in response to global-change-type drought *Proc. Natl. Acad. Sci.* **102** 15144–8
- Breshears D D, Carroll C J W, Redmond M D, Wion A P, Allen C D, Cobb N S, Meneses N, Field J P, Wilson L A, Law D J, McCabe L M and Newell-Bauer O 2018 A Dirty Dozen Ways to Die: Metrics and Modifiers of Mortality Driven by Drought and Warming for a Tree Species *Front. For. Glob. Chang.* **1** 4 Online: <https://www.frontiersin.org/articles/10.3389/ffgc.2018.00004/abstract>
- Breshears D D, Adams H D, Eamus D, McDowell N G, Law D J, Will R E, Williams A P and Zou C B 2013 The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off *Front. Plant Sci.* **4** 266 Online: <http://www.ncbi.nlm.nih.gov/pubmed/23935600>
- Chiang F, Mazdiyasn O and AghaKouchak A 2021 Evidence of anthropogenic impacts on global drought frequency, duration, and intensity *Nat. Commun.* **12** 1–10 Online: <http://dx.doi.org/10.1038/s41467-021-22314-w>
- Choat B, Jansen S, Brodribb T J, Cochard H, Delzon S, Bhaskar R, Bucci S J, Feild T S, Gleason S M, Hacke U G, Jacobsen A L, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell P J, Nardini A, Pittermann J, Pratt R B, Sperry J S, Westoby M, Wright I J and Zanne A E 2012 Global convergence in the vulnerability of forests to drought *Nature* **491** 752–5
- Clifford M J, Royer P D, Cobb N S, Breshears D D and Ford P L 2013 Precipitation thresholds and drought-induced tree die-off: insights from patterns of *Pinus edulis* mortality along an environmental stress gradient *New Phytol.* **200** 413–21 Online: <http://doi.wiley.com/10.1111/nph.12362>
- Coleman T W, Graves A D, Heath Z, Flowers R W, Hanavan R P, Cluck D R and Ryerson D 2018 Accuracy of aerial detection surveys for mapping insect and disease disturbances in the United States *For. Ecol. Manage.* **430** 321–36 Online: <https://doi.org/10.1016/j.foreco.2018.08.020>
- Cook B I, Mankin J S, Williams A P, Marvel K D, Smerdon J E and Liu H 2021 Uncertainties, Limits, and Benefits of Climate Change Mitigation for Soil Moisture Drought in Southwestern North America *Earth's Futur.* **9**
- Das A J, Stephenson N L, Flint A, Das T and van Mantgem P J 2013 Climatic Correlates of Tree Mortality in Water- and Energy-Limited Forests ed G Bohrer *PLoS One* **8** e69917 Online: <http://dx.plos.org/10.1371/journal.pone.0069917>

- Dietze M C 2017 Prediction in ecology: a first-principles framework *Ecol. Appl.* 27 2048–60
Online: <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1002/eap.1589>
- Dowle M and Srinivasan A 2021. data.table: Extension of `data.frame`. R package version 1.14.0. <https://CRAN.R-project.org/package=data.table>
- Flake S W and Weisberg P J 2018 Fine-scale stand structure mediates drought-induced tree mortality in pinyon–juniper woodlands *Ecol. Appl.* eap.1831 Online: <https://onlinelibrary.wiley.com/doi/abs/10.1002/eap.1831>
- Floyd M L, Clifford M, Cobb N S, Hanna D, Delph R, Ford P and Turner D 2009 Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands *Ecol. Appl.* **19** 1223–30
- Floyd M L, Romme W H, Rocca M E, Hanna D P and Hanna D D 2015 Structural and regenerative changes in old-growth piñon-juniper woodlands following drought-induced mortality *For. Ecol. Manage.*
- Gaylord M L, Kolb T E, Pockman W T, Plaut J A, Yezpe E A, Macalady A K, Pangle R E and McDowell N G 2013 Drought predisposes piñon-juniper woodlands to insect attacks and mortality *New Phytol.* **198** 567–78
- Greenwood D L and Weisberg P J 2008 Density-dependent tree mortality in pinyon-juniper woodlands *For. Ecol. Manage.* **255** 2129–37 Online: <https://www.sciencedirect.com.ezproxy2.library.colostate.edu/science/article/pii/S0378112707009619>
- Grossiord C, Buckley T N, Cernusak L A, Novick K A, Poulter B, Siegwolf R T W, Sperry J S and McDowell N G 2020 Plant responses to rising vapor pressure deficit *New Phytol.* **226** 1550–66
- Hammond W M, Yu K, Wilson L A, Will R E, Anderegg W R L and Adams H D 2019 Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality *New Phytol.* **223** 1834–43
- Hart S J, Veblen T T, Schneider D and Molotch N P 2017 Summer and winter drought drive the initiation and spread of spruce beetle outbreak *Ecology* **98** 2698–707
- Hicke J A, Xu B, Meddens A J H and Egan J M 2020 Characterizing recent bark beetle-caused tree mortality in the western United States from aerial surveys *For. Ecol. Manage.* **475**
- Hijmans R J 2021 raster: Geographic Data Analysis and Modeling. R package version 3.4-13. <https://CRAN.R-project.org/package=raster>
- Huang K, Yi C, Wu D, Zhou T, Zhao X, Blanford W J, Wei S, Wu H, Ling D and Li Z 2015 Tipping point of a conifer forest ecosystem under severe drought *Environ. Res. Lett.* **10**

- Jackson S T 2021 Transformational ecology and climate change *Science* **373** 1085–6
- Johnson E W and Wittwer D 2006 Aerial Detection Surveys in the United States *USDA Forest Service Proceedings RMRS-P-42CD* pp 809–11
- Jump A S and Peñuelas J 2005 Running to stand still: Adaptation and the response of plants to rapid climate change *Ecol. Lett.* **8** 1010–20
- Jump A S, Ruiz-Benito P, Greenwood S, Allen C D, Kitzberger T, Fensham R, Martínez-Vilalta J and Lloret F 2017 Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback *Glob. Chang. Biol.* **23** 3742–57
- Kuhn M 2021 caret: Classification and Regression Training. R package version 6.0-88. <https://CRAN.R-project.org/package=caret>
- Kuparinen A, Savolainen O and Schurr F M 2010 Increased mortality can promote evolutionary adaptation of forest trees to climate change
- Lawlor J 2020. PNWColors: Color Palettes Inspired by Nature in the US Pacific Northwest. R package version 0.1.0. <https://CRAN.R-project.org/package=PNWColors>
- Little E L 1971 *Atlas of United States trees*. (Washington, D.C. : U.S. Dept. of Agriculture, Forest Service,) Online: <http://www.biodiversitylibrary.org/bibliography/130546>
- Macalady A K and Bugmann H 2014 Growth-Mortality Relationships in Piñon Pine (*Pinus edulis*) during Severe Droughts of the Past Century: Shifting Processes in Space and Time ed H BassiriRad *PLoS One* **9** e92770 Online: <http://dx.plos.org/10.1371/journal.pone.0092770>
- McDowell N G, Williams A P, Xu C, Pockman W T, Dickman L T, Sevanto S, Pangle R, Limousin J, Plaut J, Mackay D S, Ogee J, Domec J C, Allen C D, Fisher R A, Jiang X, Muss J D, Breshears D D, Rauscher S A and Koven C 2016 Multi-scale predictions of massive conifer mortality due to chronic temperature rise *Nat. Clim. Chang.* Online: <http://www.nature.com.ezproxy2.library.colostate.edu/articles/nclimate2873.pdf>
- McDowell N G, Beerling D J, Breshears D D, Fisher R A, Raffa K F and Stitt M 2011 The interdependence of mechanisms underlying climate-driven vegetation mortality *Trends Ecol. Evol.* 523–32
- McDowell N G, Fisher R A, Xu C, Domec J C, Hölttä T, Mackay D S, Sperry J S, Boutz A, Dickman L, Gehres N, Limousin J M, Macalady A, Martínez-Vilalta J, Mencuccini M, Plaut J A, Ogee J, Pangle R E, Rasse D P, Ryan M G, Sevanto S, Waring R H, Williams A P, Yezzer E A and Pockman W T 2013 Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework *New Phytol.* **200** 304–21

- McDowell N, Pockman W T, Allen C D, Breshears D D, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams D G and Yezpez E A 2008 Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* **178** 719–39 Online: <http://doi.wiley.com/10.1111/j.1469-8137.2008.02436.x>
- Meddens A J H, Hicke J A and Ferguson C A 2012 Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States *Ecol. Appl.* **22** 1876–91
- Meddens A J H, Hicke J A, Macalady A K, Buotte P C, Cowles T R and Allen C D 2015 Patterns and causes of observed piñon pine mortality in the southwestern United States *New Phytol.*
- Negrón J F and Wilson J L 2003 Attributes associated with probability of infestation by the pinon ips, *Ips confusus* (Coleoptera: Scolytidae), in piñon pine, *Pinus edulis* West. *North Am. Nat.* **63** 440–51
- Ovenden T S, Perks M P, Clarke T K, Mencuccini M and Jump A S 2021 Life after recovery: Increased resolution of forest resilience assessment sheds new light on post-drought compensatory growth and recovery dynamics *J. Ecol.* 1–14
- Overpeck J T and Udall B 2020 Climate change and the aridification of North America *Proc. Natl. Acad. Sci.* **117** 202006323 Online: <http://www.pnas.org/lookup/doi/10.1073/pnas.2006323117>
- Pebesma E 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10 (1), 439-446, <https://doi.org/10.32614/RJ-2018-009>
- Pedersen T L 2020 patchwork: The Composer of Plots. R package version 1.1.1. <https://CRAN.R-project.org/package=patchwork>
- Pedersen T L and Cramer F 2020 scico: Colour Palettes Based on the Scientific Colour-Maps. R package version 1.2.0. <https://CRAN.R-project.org/package=scico>
- Peltier D M P, Guo J, Nguyen P, Bangs M, Wilson M, Samuels-Crow K, Yocom L L, Liu Y, Fell M K, Shaw J D, Auty D, Schwalm C, Anderegg W R L, Koch G W, Litvak M E and Ogle K 2021 Temperature memory and non-structural carbohydrates mediate legacies of a hot drought in trees across the southwestern US *Tree Physiol.* 1–15
- Preisler H K, Grulke N E, Heath Z and Smith S L 2017 Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California *For. Ecol. Manage.* **399** 166–78 Online: <http://dx.doi.org/10.1016/j.foreco.2017.05.039>
- PRISM Climate Group. PRISM Climate data accessed September 25, 2021.

- Redmond M D, Law D J, Field J P, Meneses N, Carroll C J W, Wion A P, Breshears D D, Cobb N S, Dietze M C and Gallery R E 2019 Targeting Extreme Events: Complementing Near-Term Ecological Forecasting With Rapid Experiments and Regional Surveys *Front. Environ. Sci.* **7** 183 Online:
<https://www.frontiersin.org/article/10.3389/fenvs.2019.00183/full>
- Rogers B M, Solvik K, Hogg E H, Ju J, Masek J G, Michaelian M, Berner L T and Goetz S J 2018 Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data *Glob. Chang. Biol.* **24** 2284–304 Online:
<http://doi.wiley.com/10.1111/gcb.14107>
- Schnitzer S A and Carson W P 2016 Would Ecology Fail the Repeatability Test ? *Bioscience* **66** 98–9
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J and Naik N 2007 Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America *Science (80-.)*. **316** 1181–4
- Swann A L S, Laguë M M, Garcia E S, Field J P, Breshears D D, Moore D J P, Saleska S R, Stark S C, Villegas J C, Law D J and Minor D M 2018 Continental-scale consequences of tree die-offs in North America: Identifying where forest loss matters most *Environ. Res. Lett.* **13**
- Trugman A T, Detto M, Bartlett M K, Medvigy D, Anderegg W R L, Schwalm C, Schaffer B and Pacala S W 2018 Tree carbon allocation explains forest drought-kill and recovery patterns *Ecol. Lett.* 1552–60 Online: <http://doi.wiley.com/10.1111/ele.13136>
- Trugman A T, Anderegg L D L, Anderegg W R L, Das A J and Stephenson N L 2021 Why is Tree Drought Mortality so Hard to Predict? *Trends Ecol. Evol.* 1–13 Online:
<https://doi.org/10.1016/j.tree.2021.02.001>
- Udall B and Overpeck J 2017 The twenty-first century Colorado River hot drought and implications for the future *Water Resour. Res.* **53** 2404–18
- USDA Forest Service, Forest Health Protection. 2019. Mapping and Reporting.
<https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/detection-surveys.shtml> (accessed July 31 2020).
- van Mantgem P J, Stephenson N L, Byrne J C, Daniels L D, Franklin J F, Fule P Z, Harmon M E, Larson A J, Smith J M, Taylor A H and Veblen T T 2009 Widespread Increase of Tree Mortality Rates in the Western United States *Science (80)*.
- Venturas M D, Todd H N, Trugman A T and Anderegg W R L 2020 Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage *New Phytol.*

- Vicente-Serrano S M, Beguería S and López-Moreno J I 2010 A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index *J. Clim.* **23** 1696–718 Online: <http://journals.ametsoc.org/doi/abs/10.1175/2009JCLI2909.1>
- Wickham H 2016 *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York
- Williams, A. Park, Benjamin I. Cook, and Jason E. Smerdon. 2022. “Rapid Intensification of the Emerging Southwestern North American Megadrought in 2020–2021.” *Nature Climate Change* 12 (3): 232–34. <https://doi.org/10.1038/s41558-022-01290-z>.
- Williams A P, Cook E R, Smerdon J E, Cook B I, Abatzoglou J T, Bolles K, Baek S H, Badger A M and Livneh B 2020 Large contribution from anthropogenic warming to an emerging North American megadrought *Science* (80). **368** 314–8
- Williams P A, Allen C D, Macalady A K, Griffin D, Woodhouse C A, Meko D M, Swetnam T W, Rauscher S A, Seager R, Grissino-Mayer H D, Dean J S, Cook E R, Gangodagamage C, Cai M and McDowell N G 2013 Temperature as a potent driver of regional forest drought stress and tree mortality *Nat. Clim. Chang.* **3** 292–7
- Zhang Y, Keenan T F and Zhou S 2021 Exacerbated drought impacts on global ecosystems due to structural overshoot *Nat. Ecol. Evol.* 2021 1–9 Online: <https://www.nature.com/articles/s41559-021-01551-8>

CONCLUSION

This dissertation was an exploration into the drivers of mast seeding and mortality in piñon and ponderosa pine ecosystems of the Rocky Mountains and Colorado Plateau. I employed a combination of field surveys and empirical modeling to describe the variation in two key demographic processes across a large portion of these species' distributions in the western US. I describe divergent masting behavior in these two species and explore how this may affect future resilience and recovery under warmer climates and altered disturbance regimes. I also provide the first, field-based comparison of several climate thresholds expected to predict pinyon pine die-off and provide a simple framework for evaluating mortality risk at regional scales.

Part 1 of this dissertation highlights contrasting masting behavior between these two dry pine species. Masting in pinyon pine was strongly associated with climate factors, synchronous across large distances (up to 500 kilometers), and cone production was more variable at hotter and drier sites. This suggests that ongoing changes in climate may have significant impacts on future pinyon pine seed production (e.g., Redmond et al. 2012). However, I found a contrasting masting pattern in ponderosa pine, in which cone production was not strongly associated with climate, highly asynchronous across sites, and more strongly influenced by individual and neighborhood-scale factors like tree size and density. This suggests that ponderosa pine may be less sensitive to future changes in climate than pinyon pine, and that we may be able to manage ponderosa pine ecosystems for increased seed production by conserving large trees and reducing stand density. Forecasts of mast years may also soon be within reach for piñon pine, but further work likely needs to be undertaken to develop a stronger, predictive understanding of ponderosa pine cone production.

In part two of this dissertation, I compared four climate thresholds based on their ability to correctly predict piñon pine die-off. All metrics overpredicted mortality to some degree, suggesting that these climate thresholds may overestimate the severity of future die-off events. However, I also highlight that these relatively simple climate metrics can be generally useful indicators of tree die-off a year or more in advance of its detection by aerial surveys by the US Forest Service. This research also lays the groundwork for future forecasts of tree die-off following ongoing, hotter drought events.

This dissertation represents several significant advances in our understanding of dry forest and woodland demography, how it varies across space and time, and how we may be able to leverage forecasts of demography to improve management and conservation. Much work remains to be done – key remaining questions include how seed production translates to seedling recruitment, particularly how the timing of seed production interacts with climate and disturbance events shape the patterns of ecosystem recovery. Long term collection of demographic data across broad geographic regions will be most useful for the parameterization of future population models to predict future forest distributions, map species refugia, and to identify bottlenecks to population growth. Every seed harbors the potential for a thousand future forests, and the answers to many key questions in forest ecology may be found by better understanding them.

\

APPENDICES

APPENDIX 1

Table A.1.1) Site level summary statistics. Mean cones is the average number of seed cones produced per tree, across all years. CV_p is the ratio of the standard deviation to the long term mean of seed cone production at each site, with higher values indicating more variable cone production. Within site r is the degree of synchrony (mean pairwise Spearman correlation) between all trees and across all years at a site. Within cluster r is calculated in the same manner but is measured between sites within each cluster (representing how synchronous a site is with others in the identified cluster). Monsoonality is the 30-year mean of July, August, and September precipitation- reported in both absolute quantities (millimeters) and percent of annual precipitation. Climatic water deficit (CWD) was calculated using the CWD and AET function in R (Redmond 2018) and is the 30-year average of the difference between potential and actual evapotranspiration at 800-meter resolution. Mean live canopy area was included as a scalar to account for differences between stands across sites and is the average area of live canopy of all trees within a site.

Cluster	Latitude	Longitude	Mean cones	CV _p	Within site <i>r</i>	Within cluster <i>r</i>	Monsoonality (mm / % annual ppt)	CWD (mm)	Mean live canopy area (m ²)
A	40.87	106.14	26	1.81	0.88	0.85	107 23.2%	288	18.78
A	40.59	108.67	38	1.85	0.79	0.85	114 23.6%	311	19.49
B	39.00	108.89	10	1.77	0.42	0.49	111 24.1%	562	12.27
B	38.94	108.91	15	1.68	0.6	0.53	119 25.3%	402	19.35
B	38.74	107.61	30	1.29	0.59	0.54	121 26.4%	438	21.38
B	38.64	109.01	28	1.62	0.49	0.54	160 30.5%	439	13.37
B	38.62	107.59	36	1.3	0.44	0.52	143 29.2%	223	17.86
B	38.62	109.05	46	1.39	0.59	0.59	175 30.1%	316	21.4
B	38.45	108.02	21	1.85	0.52	0.44	118 35.0%	447	15.29
C	38.38	108.07	42	1.04	0.45	0.72	167 34.1%	243	16.72
B	38.13	108.57	30	1.31	0.54	0.54	153 33.8%	352	16.59
B	38.12	108.50	28	1.45	0.41	0.51	148 34.5%	366	21.86
C	37.88	108.59	37	1.32	0.69	0.64	136 31.6%	422	20.97
C	37.86	108.63	53	1.13	0.63	0.54	135 30.8%	297	24.79
C	36.49	106.46	46	1.31	0.52	0.60	187 38.2%	176	22.21
C	36.39	106.49	45	1.27	0.67	0.65	163 40.4%	307	15.33
C	35.71	106.62	36	1.18	0.48	0.63	215 41.7%	246	17.25
C	35.68	106.66	39	1.12	0.52	0.59	193 46.3%	533	13.55
D	35.28	106.48	20	2.38	0.73	0.53	186 42.0%	604	18.64
D	35.25	106.36	16	2.2	0.75	0.68	214 40.9%	435	11.83
D	34.20	107.21	59	1.24	0.64	0.68	178 52.9%	754	27.37
D	34.06	107.23	50	1.35	0.78	0.58	322 56.1%	278	18.24
C	34.04	107.13	40	1.44	0.54	0.43	223 54.7%	561	18.66
D	33.44	108.84	39	1.56	0.77	0.73	233 41.4%	345	26.27
D	33.39	108.82	53	1.38	0.56	0.72	248 42.2%	347	25.23
D	33.30	108.88	36	1.64	0.68	0.74	217 43.7%	529	27.57
B	32.83	108.36	46	1.16	0.51	0.28	297 46.8%	255	37.77
B	32.81	108.15	42	1.52	0.73	0.36	256 53.1%	598	32.87

Table A.1.2) Spearman's correlation (1st quartile [25%], median [50%], and 3rd quartile [75%]) between annual seed cone production and monthly weather for the three years prior to seed maturation. Bold shows the strongest correlations, which was used in subsequent analyses.

VPD				PPT			
Month	1 st quartile	median	3 rd quartile	Month	1 st quartile	median	3 rd quartile
J (yr-3)	-0.129	0.084	0.240	J (yr-3)	-0.008	0.099	0.210
F	-0.193	-0.004	0.258	F	-0.189	-0.048	0.154
M	-0.015	0.149	0.307	M	-0.295	-0.182	-0.002
A	0.044	0.136	0.252	A	-0.357	-0.169	-0.097
M	-0.158	0.134	0.314	M	-0.198	-0.057	0.102
J	0.003	0.147	0.297	J	-0.407	-0.259	-0.073
J	-0.225	-0.038	0.128	J	-0.160	-0.056	0.107
A	-0.018	0.136	0.199	A	-0.403	-0.273	-0.072
S	-0.211	-0.113	-0.010	S	0.017	0.123	0.300
O	-0.265	-0.081	0.087	O	-0.181	-0.114	0.040
N	0.126	0.209	0.384	N	-0.329	-0.189	-0.009
D	-0.194	0.064	0.344	D	-0.374	-0.206	-0.052
J (yr-2)	-0.142	0.160	0.343	J (yr-2)	-0.373	-0.132	0.090
F	-0.082	0.189	0.459	F	-0.368	-0.103	0.172
M	-0.230	-0.054	0.097	M	-0.189	0.000	0.208
A	-0.215	-0.018	0.093	A	-0.188	-0.046	0.130
M	-0.180	0.000	0.152	M	-0.143	0.011	0.130
J	-0.156	-0.043	0.075	J	-0.097	0.130	0.239
J	-0.200	-0.080	0.058	J	0.163	0.262	0.407
A	-0.552	-0.448	-0.176	A	0.170	0.281	0.536
S	-0.399	-0.153	-0.033	S	0.014	0.240	0.391
O	-0.219	-0.119	0.049	O	-0.076	0.147	0.302
N	-0.389	-0.138	-0.071	N	-0.046	0.148	0.339
D	-0.318	-0.178	-0.060	D	-0.038	0.134	0.222
J (yr-1)	-0.326	-0.242	-0.090	J (yr-1)	-0.136	0.086	0.273
F	-0.160	0.046	0.258	F	-0.128	-0.026	0.232
M	-0.260	-0.079	0.163	M	-0.049	0.185	0.427
A	-0.539	-0.399	-0.324	A	0.240	0.423	0.525
M	-0.553	-0.448	-0.390	M	0.285	0.354	0.460
J	-0.334	-0.233	-0.042	J	-0.022	0.112	0.274
J	-0.198	-0.147	-0.023	J	-0.035	0.102	0.238
A	-0.158	-0.075	0.055	A	-0.095	-0.007	0.179
S	0.004	0.170	0.230	S	-0.290	-0.083	0.003
O	-0.153	-0.029	0.152	O	-0.146	-0.077	0.053
N	-0.110	-0.029	0.078	N	-0.225	-0.044	0.144
D	-0.288	-0.103	0.134	D	-0.098	0.085	0.214

Table A.1.3) Spearman’s correlation (1st quartile [25%], median [50%], and 3rd quartile [75%]) between annual seed cone production and monthly weather for the three years prior to seed maturation. Bold shows the strongest correlations, which was used in subsequent analyses.

VPD				PPT			
Month	1 st quartile	median	3 rd quartile	Month	1 st quartile	median	3 rd quartile
JF (yr-3)	-0.116	0.033	0.245	JF (yr-3)	-0.100	0.095	0.177
FM	-0.142	0.056	0.350	FM	-0.260	-0.092	0.002
MA	-0.037	0.197	0.391	MA	-0.334	-0.207	-0.080
AM	0.022	0.155	0.354	AM	-0.308	-0.176	-0.001
MJ	-0.025	0.147	0.222	MJ	-0.244	-0.163	-0.088
JJ	0.082	0.217	0.302	JJ	-0.213	-0.095	0.020
JA	-0.042	0.107	0.277	JA	-0.296	-0.157	-0.011
AS	-0.147	-0.015	0.163	AS	-0.203	-0.042	0.108
SO	-0.222	-0.136	0.039	SO	-0.065	0.139	0.241
ON	-0.121	0.019	0.205	ON	-0.257	-0.111	0.004
ND	0.124	0.229	0.386	ND	-0.365	-0.209	-0.067
DJ	-0.278	0.317	0.421	DJ	-0.411	-0.236	-0.008
JF (yr-2)	-0.058	0.297	0.466	JF (yr-2)	-0.445	-0.077	0.225
FM	-0.048	0.071	0.358	FM	-0.320	-0.040	0.179
MA	-0.248	-0.064	0.113	MA	-0.170	-0.065	0.176
AM	-0.169	-0.084	0.092	AM	-0.211	0.001	0.157
MJ	-0.074	-0.004	0.079	MJ	-0.031	0.069	0.230
JJ	-0.253	-0.107	-0.003	JJ	0.097	0.300	0.431
JA	-0.496	-0.345	-0.270	JA	0.252	0.352	0.521
AS	-0.527	-0.437	-0.245	AS	0.181	0.441	0.549
SO	-0.403	-0.182	0.004	SO	0.125	0.253	0.369
ON	-0.295	-0.180	0.067	ON	-0.099	0.101	0.392
ND	-0.394	-0.237	-0.033	ND	-0.120	0.194	0.292
DJ	-0.391	-0.280	-0.155	DJ	-0.008	0.123	0.314
JF (yr-1)	-0.286	-0.059	0.073	JF (yr-1)	-0.159	0.017	0.287
FM	-0.221	-0.130	0.235	FM	-0.098	0.076	0.346
MA	-0.484	-0.355	-0.053	MA	0.135	0.352	0.497
AM	-0.659	-0.564	-0.453	AM	0.307	0.499	0.616
MJ	-0.512	-0.383	-0.262	MJ	0.213	0.336	0.403
JJ	-0.431	-0.251	-0.160	JJ	-0.114	0.070	0.247
JA	-0.240	-0.089	0.031	JA	-0.052	0.087	0.223
AS	-0.078	-0.014	0.151	AS	-0.227	-0.099	0.028
SO	-0.066	0.042	0.205	SO	-0.365	-0.053	-0.001
ON	-0.123	-0.063	0.097	ON	-0.268	-0.116	0.024
ND	-0.169	-0.055	0.123	ND	-0.085	0.011	0.145
DJ	-0.249	-0.104	0.173	DJ	-0.169	-0.011	0.258

Table A.1.4) To identify which tree size variable is most strongly associated with seed cone production, we performed linear mixed effect modeling to assess the relationship between mean cone production (number of cones per tree) at the tree-level (n=185) and three metrics of tree size: mean live canopy area, height, and basal area (measured at root collar). We scaled predictor variables to a mean of zero and a standard deviation of one to facilitate interpretation between coefficients. Because our metrics of tree size were correlated with one another, we built three separate linear mixed models and included site as a random intercept. Our analyses indicated that live canopy area was the strongest tree-level correlate with mean seed cone production, based on AICc.

Variable	β	SE	T value	AICc
Live Canopy Area	8.59	0.63	7.19	1540.25
Basal Area	4.84	1.27	3.80	1571.89
Height	4.95	1.41	3.50	1573.92
Intercept-only	35.97	2.31	15.55	1586.13

Table A.1.5) Multiple regression on distance matrices (MRM) model of synchrony between sites. Significance of individual terms and full model determined using permutation tests (n=999).

Variable	MRM Coefficient	<i>P</i> value
April/May VPD _{yr-1}	0.052	0.014
August VPD _{yr-2}	0.053	0.025
Geographic Distance	0.000	0.496
$R^2 = 0.29$	$F=51.4$	$P = 0.001$

Table A.1.6) All model subsets within 4 AICc units of top model of annual seed cone production. Model was fit to a negative binomial distribution and included site as a random intercept. The average of these models are presented in Table 1.2 in the main text. Results are presented as standardized regression coefficients, scaled to a mean of zero and a standard deviation of one. Canopy (mean canopy area in tables) is a scalar that describes differences in stand structures across sties. CWD is climatic water deficit and Monsoonality is the proportion of summer precipitation (July, August, September) relative to the mean annual precipitation expressed as a percentage. VPD yr-1 is vapor pressure deficit at the time of cone pollination (April/May yr-1) and VPD yr-2 is the during the time of cone initiation. Cones yr-1 is the previous years cone production at a site. Interactions are indicated with an x. Delta represents the change in AICc units between the top model and subsequent models, and the weight is the relative importance of this model of all possible subsets expressed as a percentage.

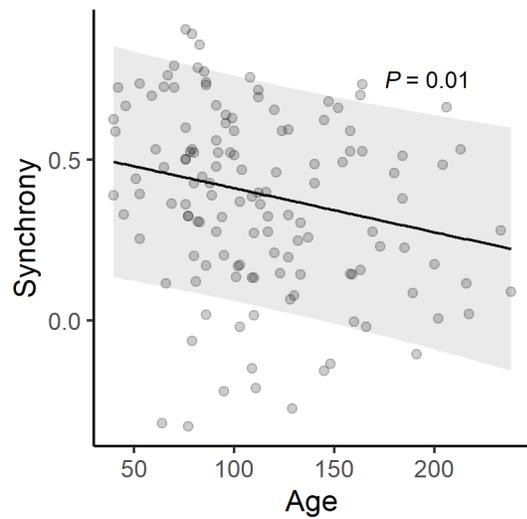
Canopy	CWD	VPD yr-1	VPD yr-2	Monsoonality	Cones _{yr-1}	VPD _{yr-1} x CWD	VPD _{yr-2} x CWD	VPD _{yr-1} x Monsoon	VPD _{yr-2} x Monsoon	AICc	weight
0.21	-0.28	-0.53	-0.23	0.28	-0.34	-	-	-0.19	0.29	3215.69	0.32
0.21	-0.29	-0.54	-0.22	0.29	-0.34	-	-0.08	-0.19	0.32	3215.93	0.28
0.21	-0.28	-0.53	-0.23	0.29	-0.34	-0.03	-	-0.18	0.29	3217.45	0.13
0.21	-0.29	-0.54	-0.22	0.29	-0.34	0.00	-0.08	-0.19	0.32	3218.08	0.10
NA	-0.32	-0.54	-0.23	0.38	-0.32	-	-	-0.19	0.29	3219.52	0.05

APPENDIX 2

Table A.2.1) Model selection table of the weather variables associated with ponderosa pine cone production. Monthly weather data (precipitation = PPT, vapor pressure deficit = VPD) were aggregated into three month means, denoted by either JJA (June, July, August) or JAS (July, August, September). Analyses covered the three year period prior to seed cone maturation, and years of variables (T) are identified relative to the year of cone maturation (T-0). Cone initiation occurs in T-2. Δ VPD is calculated as the difference between VPD in T-2 and T-3. All models included cone production in the year prior to maturation (T-1) as a covariate. Models were fit with an observation-level random intercept, and a random intercept of tree nested within site, and a negative binomial error distribution. The Δ VPD model best explained patterns of annual cone production in ponderosa pine, though a model of precipitation and VPD was equally supported based on AIC.

Model	AIC	Δ AIC from top
T-3 VPD JJA + T-2 PPT JJA	24,987.3	0
Δ VPD	24,994.49	-7.2
T-3 VPD JJA + T-2 VPD JJA	24,997.87	-10.56
T-3 VPD JJA + T-2 PPT JAS	25,009.57	-22.27
T-2 VPD JJA + T-2 PPT JAS	25,012.16	-24.86
T-3 VPD JJA + T-2 VPD JAS	25,031.32	-44.013
T-2 VPD JAS + T-2 PPT JAS	25,045.12	-57.82
T-2 PPT JAS	25,049.67	-62.37
T-2 VPD JAS + T-2 PPT JJA	25082.12	-94.91
T-2 VPD JJA + T-2 PPT JJA	25,085.4	-98.01
T-2 PPT JJA	25090.06	-102.76
T-2 VPD JAS	25,117.37	-130.10
T-2 VPD JJA	25,131.9	-144.60
T-3 VPD JJA	25,133.17	-145.87
Random Intercepts-Only	25,234.12	-246.81

Figure A.2.1) Marginal prediction of the effect of age on tree-level synchrony. Age was only a significant predictor of tree synchrony, after accounting for the effects of tree size (diameter at breast height) climate (30 yr CWD and AET), and neighborhood competition (measured with a basal area prism). Older trees were on average less synchronous than younger trees, in other words, old trees produced cones more often than the population-level average in a site.



APPENDIX 3

Figure A.3.1) Map of the sites used in this study with the distribution of focal species in the study area. Distribution mapped using data from Wilson et al. 2014. Darker colors indicate higher basal area (measured in m^2/ha) of the focal species. Piñon pine sites are indicated by circles and the distribution of piñon pine is colored brown. Ponderosa pine sites are indicated by triangles and the distribution is colored blue.

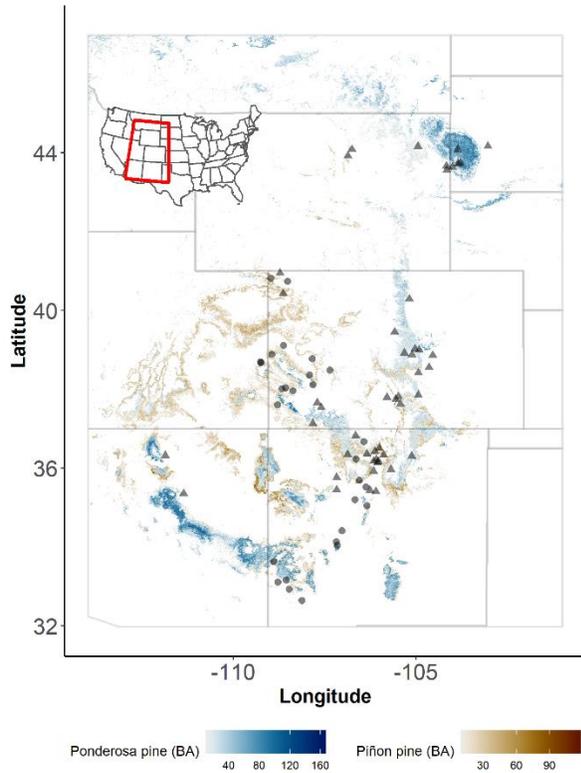


Figure A.3.2) Ordination plots showing redundancy analysis axes RDA1 and RDA2 for both species. Blue arrows indicate the strength and direction of the relationships between RDA axes and the constraining variables. Site scores are plotted in red and the sample scores are black circles and labeled by year.

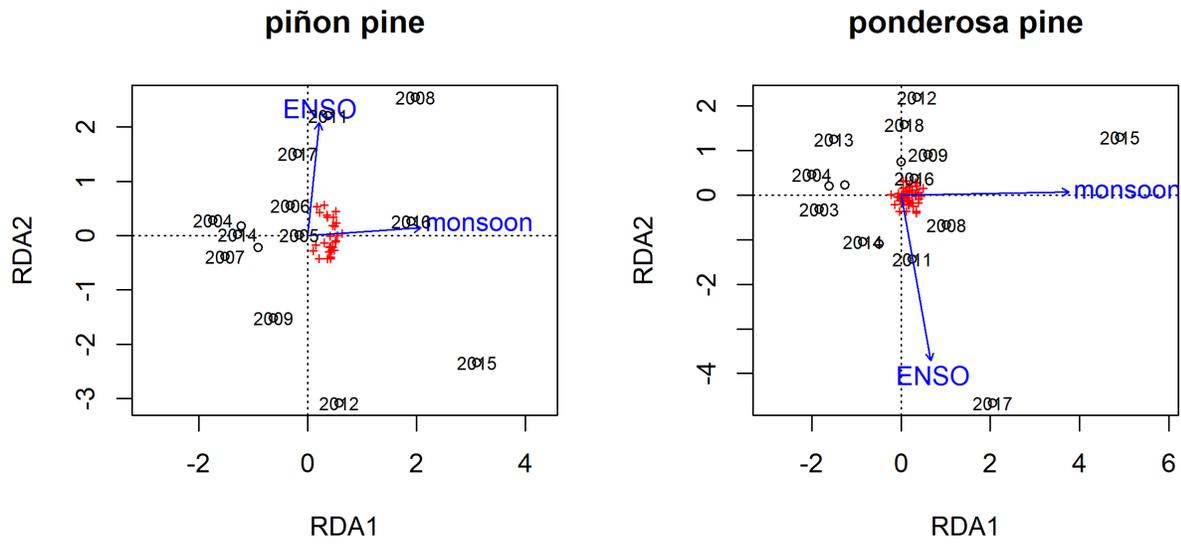
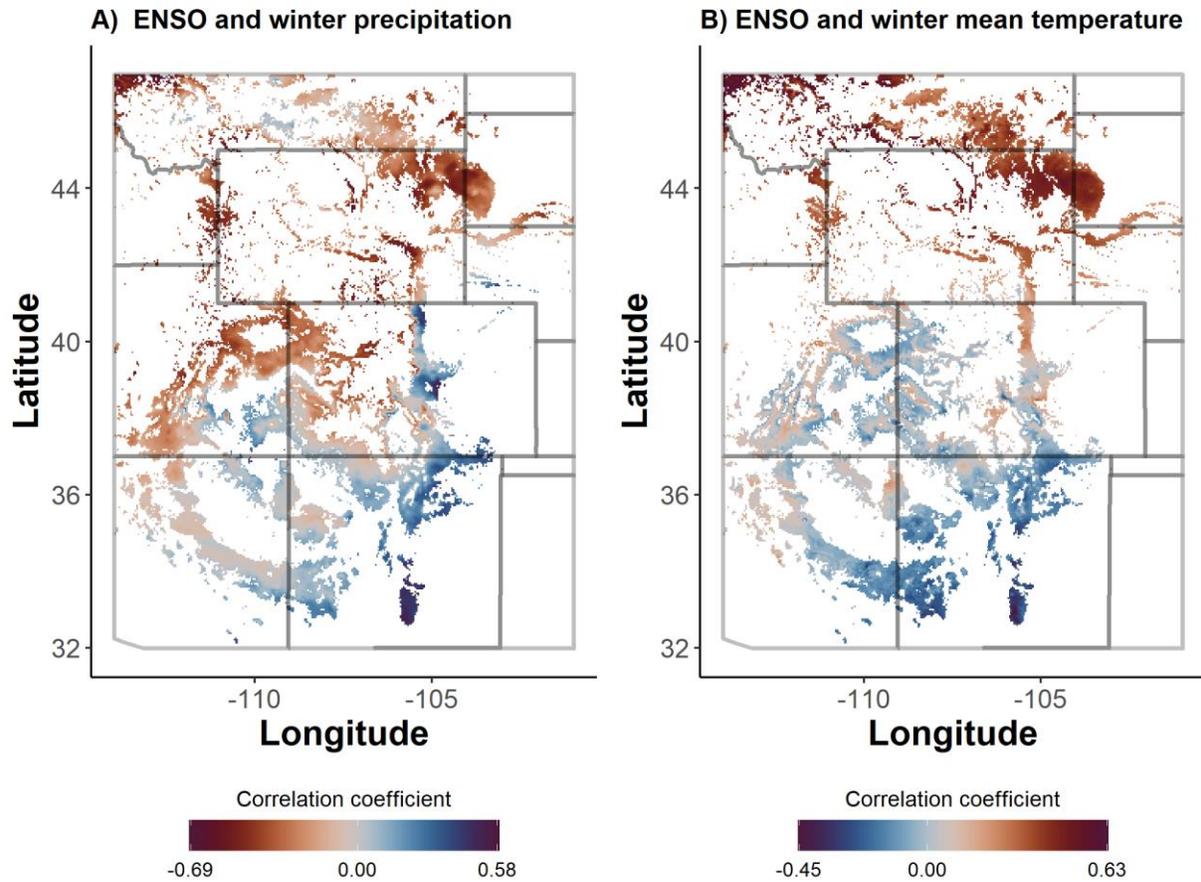


Figure A.3.3) Maps showing the correlation coefficient between the December/January average of the Multivariate ENSO Index (MEI) and winter precipitation and mean temperature (December-February). ENSO = El Niño Southern Oscillation.



Appendix 3 - *Sampling criteria of individual trees*

Trees that were selected for cone scar sampling were required to be greater than 20 cm in diameter at the root collar in piñon pine or at breast height (140 cm) in ponderosa pine. We sampled trees that were open-grown to minimize the effects of competition or climate buffering from overstory trees, and we avoided sampling trees with significant crown or trunk damage from defoliators, bark beetles, fire, or mechanical damage. Tree branches with broken tips, or those that have been previously damaged by herbivores, prevent the reliable dating of bud scale scars (which are used to separate annual growth segments) and thus were excluded. In addition, trees with crown base heights exceeding the maximum height of the sampling tool (> 8m) were

excluded by necessity. Sites were also sampled in different years (2017-2020), therefore sites sampled in 2017 lacked data in 2018, 2019, and 2020. To control for variability in sample depth across years, we limited the ponderosa analysis to 2003-2018, as all ponderosa sites had complete or nearly complete data for these years, and the piñon analyses were limited to 2004-2017. Comparisons between species were therefore restricted to 2004-2017.