DIRECT EFFECTS OF SEASONAL PRECIPITATION AND TEMPERATURE ON THE DEMOGRAPHY OF TWO DOMINANT BUNCHGRASSES IN NORTHERN ARIZONA

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ABSTRACT

DIRECT EFFECTS OF SEASONAL PRECIPITATION AND TEMPERATURE ON THE DEMOGRAPHY OF TWO DOMINANT BUNCHGRASSES IN NORTHERN ARIZONA

TYLER ANNETTS

Understanding plant population responses to climate and land-use change is fundamental to conservation and land management. Here, we focus on two dominant, perennial, bunchgrasses in northern Arizona: *Festuca arizonica* (Arizona fescue) and *Muhlenbergia montana* (mountain muhly). We used data from 68 annually remapped quadrats (2002-2018) to examine the effects of precipitation and temperature on the survival and growth of each species. We constructed life tables to examine their vital rates and then made population projections using an Integral Projection Model (IPM) framework to quantify the direct effects of seasonal precipitation and temperature on vital rates. We predicted that survival and growth of *F. arizonica* (a cool-season, C3 species) would be greater with increased spring precipitation and increased spring temperatures, and *M. montana* (a warm-season, C4 species) would be greater with increased summer precipitation and increased summer temperatures. First year survival probabilities were 0.17 and 0.07 and mean life expectancies were 1.19 and 1.07 years for *F. arizonica* and *M. montana*, respectively. Both species had lambda values less than 1 (0.90 for *F. arizonica*, and 0.88 for *M. montana*) indicating decreased population growth over the 17-year time period, however, neither plant recruitment nor fecundity were analyzed in this study. Plant size was the most important predictor for survival and growth of each species. Spring precipitation influenced survival and growth for *F. arizonica* while summer monsoon precipitation influenced survival and growth for *M. montana*. Growth of both species increased with warmer spring temperatures. Given their dominance in this system, understanding the controls on demographic parameters of these bunchgrass species is critical for predicting community response to changing environmental conditions.

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PREFACE:

This thesis is presented in the format of the journal of *Population Ecology* and consists of one manuscript with extended introduction and conclusion chapters. Redundancy between the manuscript and supporting information in the introduction and conclusion is due to the fact that Chapter 2 is presented as a self-contained manuscript. Throughout this thesis, I use a collective "we" when presenting this work in order to represent the collaborative effort of my co-authors and I in carrying out this research.

CHAPTER 1:
INTRODUCTION

Predicting responses of plant and animal communities to anthropogenic climate change is the impetus behind much of today's ecological research. While global circulation models continue to exhibit varying levels of uncertainty at local and regional scales (Reichler & Kim, 2008), a general consensus is that change is on the horizon, and in many cases has already arrived. In the southwestern United States, temperatures are predicted to change between 2-8 ˚C, and frequency of "megadroughts" are predicted to increase, despite uncertainty surrounding changes in total precipitation (Seager et al., 2007; IPCC AR5 WGII, 2014; Williams et al., 2020). Much of this uncertainty results from unknown future responses in policy reform (Dufresne et al., 2013) as governments attempt to balance scientific insight with societal aspirations. The role of ecological research is pivotal in quantifying and mitigating risks to biodiversity and ecosystem functions and services. Although the magnitude of environmental changes are uncertain, understanding the mechanisms that currently govern ecological communities will help to forecast imminent changes in species distribution and community composition.

Plant communities that we observe on the landscape are the result of ecological mechanisms including dispersal, competition, and environmental filtering (Grinnell, 1917; Clements, 1936; MacArthur & Wilson, 1963; Odum, 1969). These mechanisms define a species' niche (Grinnell, 1917; Grinell, 1924; Vandermeer, 1972), which refers to a set of habitat conditions (abiotic and biotic interactions) that are suitable for the occupation of a particular species; this set of conditions drives community assembly by selecting for species that are capable of surviving and reproducing within that ecosystem (Tilman, 2004). The set of conditions and resulting functionality of these systems may change as a result of management and climate change, but the underlying mechanisms that drive community assembly will remain the same.

Just as observation under current conditions can be used to infer past processes, discerning variation in individual vital rates can be used to infer processes that occur on population and community levels (Easterling, Ellner, & Dixon, 2000). Demographic analyses have proven useful at linking individual vital rates such as survival, growth, and life expectancy to population dynamics (Harper, 1980). By understanding how environmental conditions such as temperature and precipitation relate to population dynamics under current conditions, it is possible to model population responses under future projected climate conditions (Jongejans, de Kroon, Tuljapurkar, & Shea, 2010).

This study utilizes a data-driven ecological population model to link seasonal weather effects and demographic parameters to population dynamics in two long-lived, perennial bunchgrasses. The species selected for this study are Arizona fescue (*Festuca arizonica)*, a cool-season C_3 species (Fletcher et al., 2004; Allred, 2005,), and mountain muhly (*Muhlenbergia montana*), a warm-season C_4 species (Arnold, 1950). The motivation behind the selection of these two species was due to their difference in photosynthetic pathway (C_3 vs. C_4), as well as their dominance in the Arizona fescue – mountain muhly bunchgrass community that characterizes the ponderosa pine understory of northern Arizona.

Throughout this investigation, I explore the relationship between temperature, precipitation, and size-class on variation of individual vital rates using 68 annually-mapped 1-m^2 quadrats over a 17-year period. Life tables for each species were constructed for individual survival probability, growth, and life expectancy using demographic scripts created by Lauenroth and Adler (2008). Then, using an integral projection model (IPM) framework, I used individual vital rates along with local weather data to project population growth rates over time for both species (Figure 1.1).

The remainder of this chapter is as a literature review in order to scientifically justify the placement of this study in an ecological context. The complexity of quantifying ecological community shifts to anthropogenic climate change dictates a multi-disciplinary understanding of various fields of research. The sections that follow will serve as a comprehensive introduction for the self-contained manuscript in chapter 2.

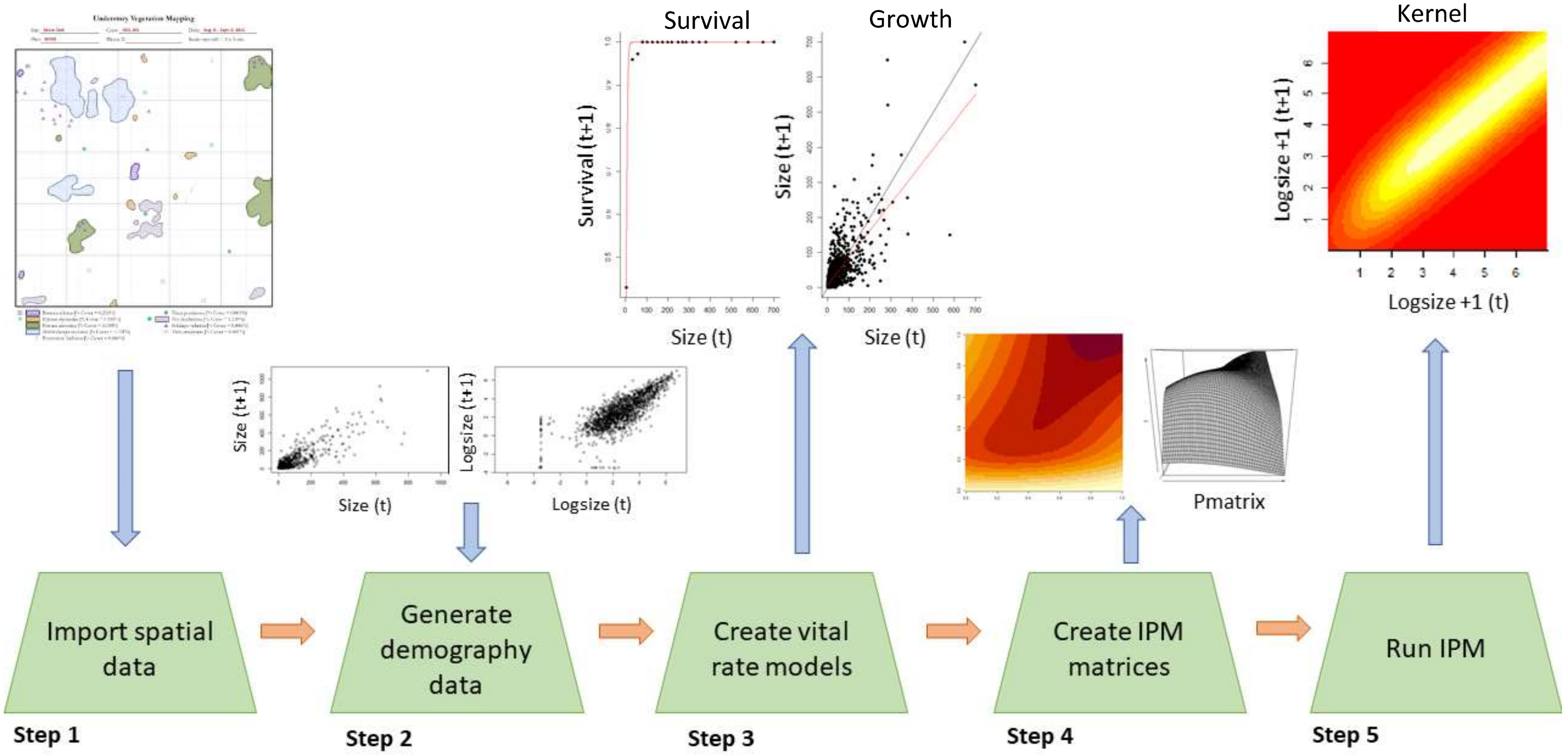


Figure 1.1 | IPM flow-chart

Step 1: Permanent 1-m^2 quadrats were sampled annually and digitized using ARCGIS.

Step 2: Using a demography program designed by Lauenroth and Adler (2008), life tables containing individual vital rates (survival, growth, life expectancy) were generated.

Step 3: Seasonal weather data (temperature & precipitation) was imported and generalized linear models were created for survival and growth. Model selection determines model fitness.

Step 4: A p-matrix was created for survival and growth using vital rate models.

Global climate change

As evidence of anthropogenic climate change continues to build, the advancement of climate models is increasing the capacity to predict future climate scenarios (IPCC, 2014); however, uncertainty continues to persist in forecasting the magnitude of change, extreme events, and regional variability (Easterling et al., 2000; Reichler & Kim, 2008). Sources of this uncertainty are a result of complex feedback systems in Earth's climate (Dessler, 2010) as well as unpredictable political responses to climate mitigation strategies (Shackley & Wynne, 1996). These uncertainties lead to the formulation of multiple potential trajectories known as Representative Concentration Pathways (RCP) in which the IPCC (2014) created projections based on multiple emission scenarios. In association with uncertainty surrounding feedbacks in Earth's global climate system, projection models such as the 5th phase of the Coupled Model Intercomparison Project (CMIP5) struggle with parameterization of regional variability such as the El Niño Southern Oscillation (ENSO) (Dufrense et al., 2013). Variation in regional processes such as ENSO lead to unforeseen implications in future climate projections in places such as the American Southwest. However, while magnitude of change is difficult to predict, a move to more arid conditions is generally accepted (Sheppard et al., 2002).

Climate change in the Southwestern United States

While global circulation models contain levels of uncertainty when determining sensitivity to feedbacks and regional climate variability (Reichler & Kim, 2008), projections are able to predict general trends on a regional scale. For example, according to IPCC AR5 WGII (2014), climate models and observations both show an increase in annual mean temperatures between 2-8° C in the American Southwest; this holds true for all emission projections (RCP 2.6-RCP 8.5). ENSO plays an important role in the Southwest by increasing eastern equatorial

Pacific Ocean surface temperatures as impacting precipitation and temperature in the southwest (Sheppard et al., 2002). In conjunction with these expected regional climate shifts, it is also likely that associated extreme weather events could result in severe droughts in portions of the Southwest (Cayan et al., 2010; Cook, Ault, & Smerdon, 2015). Although projection models continue to struggle with predicting ENSO's temporal circulation, future La Niña events will likely result in "megadroughts" more severe than previously recorded due to preexisting climate perturbations in this region (Seager et al., 2007; Williams et al., 2020). An example of one of these megadroughts in currently ongoing in the southwestern United States, beginning in 2000, and has been described as the second most severe drought in 1200 years (Williams et al., 2020).

Predicting changes in precipitation has proven to be a continued source of challenge among regional and global climate modelling. For example, a study by Harding et al. (2012) predicted high amounts of variation throughout the Colorado River basin ranging from 30% increases to 30% decreases. Emission scenarios and disagreement among projection scales leads to high levels of uncertainty, however, a reoccurring trend shows temporal shifts in spring snowmelt as well as more precipitation falling as rain and less as snow throughout much of the western United States (Harding et al., 2012; Wi et al., 2012). According to Mote et al. (2018), this has resulted in dramatic reductions in April 1st snowpack throughout the West, amounting to a 15-30% reduction when compared to mid-century averages.

Despite levels of uncertainty and disagreement surrounding changes in precipitation, increasing mean temperatures have been shown to lead to higher evapotranspiration rates and dryer soil conditions (Cook et al., 2015). Following extended dry periods, this can result in soil moisture debts (Eng et al., 2016), and reduce plant-available water.

Current state of forests in the southwestern U.S.

As climate scientists attempt to increase the accuracy of their models, a key component of both climate and ecological research is the ability to quantify the effects of climate change and land management decisions on plant communities, ecosystem functions, and ecosystem services. A recent tree-ring analysis by Peltier et al. (2016) analyzed legacy effects of drought on tree species throughout the Southwest. Their findings suggest varying degrees of drought sensitivity by species, including low resistance and slow recovery of *Pinus ponderosa* (ponderosa pine) for up to 5 years following a period of sustained drought (Peltier et al., 2016). These drought conditions are not only affecting the overstory; higher soil temperatures negatively impact grass seedling establishment as well. Modelling efforts in the Great Basin suggest that temperature increases of 2˚C in the coming decades could result in a 30% decrease in germination and establishment (James et al., 2019).

Land management decisions such as historical forest fire suppression have led to changes in the Southwest, such as increased forest stand density (Parsons & DeBenedetti, 1979; Swetnam & Baisan, 1996; Fulé, Covington, & Moore, 1997). According to Brown et al. (1997), arid ecosystems of the Southwest have begun to show signs of reorganization, characterized by a 3-fold increase in woody shrub density. While the woody encroachment documented by Brown et al. (1997) took place at lower elevations (1300-1500m), a study by Laughlin et al. (2011) identified a decline in understory species richness (by 21%) in the higher elevation (~2100m) ponderosa pine ecosystem in response to elevated forest stand densities and resulting canopy closure.

Because the Southwest is comprised of a mosaic of landscapes, localized effects of climate and land management decisions may vary; however, a general decrease in fire return intervals (Cooper, 1960; Bataineh et al., 2006) has led to communities that are structurally and functionally different than what would be historically typical of the region (Moore et al., 1999). In a review Cooper (1960) concludes that extensive overgrazing along with fire suppression contributed to increased forest densities and fuel loads in the ponderosa pine communities of northern Arizona. Although implications of these management decisions have been well-documented in the literature, effects on understory and associated ecosystem function are less-studied. However, a study by Strahan et al. (2016) suggests that both overstory and understory communities have experienced changes in plant functional traits such as higher specific leaf area (SLA) and leaf nitrogen. This functional adaptation may result in higher establishment of species that are less fire-prone, creating a more functionally-homogenous community (Bond and Keeley 2005; Cavender-Bares and Reich 2012). In addition to wildlife forage, bunchgrass species play an important role in controlling seedling establishment of ponderosa pine (Pearson, 1942; Arnold 1950; Bakker & Moore, 2007), particularly in park-like settings (Rietveld, 1975).

In order to better understand how the compounding effects of climate and management decisions have influenced understory function, we can utilize long-term data sets to link demographic parameters and corresponding population dynamics.

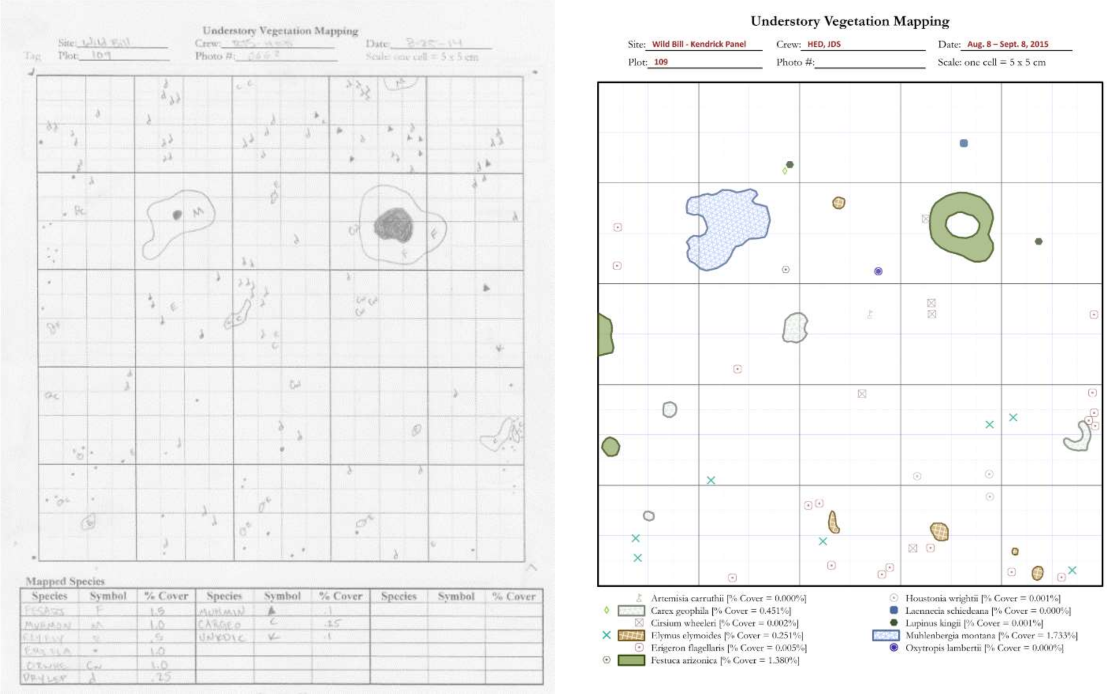
Study Site

The history of forest and range ecology in the Coconino National Forest is among the richest in the American West. The legacy of ecological inquiry begins in 1908 with G.A. Pearson, US Forest Service scientist and director of Fort Valley Experimental Forest and in 1910 with Robert R. Hill, grazing examiner with the US Forest Service (Bakker et al., 2008; Oblerding, 2018). Hill began a long-term range study near Flagstaff, Arizona (within a 40 km) to document the effects of livestock grazing on ponderosa pine seedling regeneration and on dominant graminoids following intense grazing practices (Hill, 1917). By 1912, Hill and his team had established fifty 1-m^2 quadrats inside and out five 0.6-ha grazing exclosures. The 1-m^2 quadrats were permanently marked with stakes and tags. These sites became locally known as the "Hill Plots" (Bakker et al., 2008).

In addition to the Hill Plots, Fort Valley Experimental Forest established what is known as the "Cooperrider-Cassidy study" in 1927. This study included 1-m^2 quadrats as well as larger 0.005 - 0.01-acre overstory plots in which ponderosa pine seedlings were mapped and tagged (Laughlin & Moore, 2008). The goal of this study was similar to that of the Hill Plots, but occurred on range allotments to the northwest of Flagstaff, known as Wild Bill and Willaha; this study took place until 1938, and the plots that still exist are referred to by their range allotment names ("Wild Bill and Willaha") in contemporary studies (Laughlin & Moore, 2008).

Within these 1-m^2 quadrats, basal area of the vegetation was mapped using the quadrat method, which was a common method used in the early 1900s (Clements, 1905; Weaver & Clements, 1929). Mapping was done by hand and also using a pantograph (Hill, 1920). Graminoids were recorded as polygons, while shrubs and forbs were marked as points Hill, 1920; Weaver &Clements, 1929), therefore the exact location and species of each individual plant within the quadrat is known. This protocol is still used on these plots today.

Despite a multitude of challenges including budget cuts and fires, many of the permanent 1-m^2 quadrats and overstory plots still exist today. Adopting the nomenclature of the past, the plots are referred to as the "Hill & Wild Bill" plots. Despite a series of different studies being carried out on these plots, most research faded away by the 1940s, with the exception of a small subset of repeated photography ending in 1956 (Bakker et al., 2008). This is not the end of the legacy of Hill & Wild Bill, however. Between 2002 and 2006, Margaret Moore, Jon Bakker, and



Understory Vegetation Mapping

Site: Wild Bill
Crew: [illegible]
Date: 8-25-14
Tag
Plot: 109
Photo #: [illegible]
Scale: one cell = 5 x 5 cm

Mapped Species

Species	Symbol	% Cover	Species	Symbol	% Cover	Species	Symbol	% Cover
FESARI	F	1.5	MUHMIN	▲	.1			
MUHMON	M	1.0	CARGEO	C	.25			
ELYELY	X	.5	UNKDIC	K	.1			
ERIFLA	•	1.0						
CIRWHE	Cw	1.0						
ARTCAR	∂	.25						

Understory Vegetation Mapping

Site: Wild Bill - Kendrick Panel
Crew: HED, JDS
Date: Aug. 8 – Sept. 8, 2015
Plot: 109
Photo #:
Scale: one cell = 5 x 5 cm

Artemisia carruthii [% Cover = 0.000%]	Houstonia wrightii [% Cover = 0.001%]
Carex geophila [% Cover = 0.451%]	Laennecia schiedeana [% Cover = 0.000%]
Cirsium wheeleri [% Cover = 0.002%]	Lupinus kingii [% Cover = 0.001%]
Elymus elymoides [% Cover = 0.251%]	Muhlenbergia montana [% Cover = 1.733%]
Erigeron flagellaris [% Cover = 0.005%]	Oxytropis lambertii [% Cover = 0.000%]
Festuca arizonica [% Cover = 1.380%]	

Figure 1.2 | Quadrat datasheets

The hand-mapped datasheet on the left (2014) and the digitized version on the right (2015) show large Arizona fescue (green, right) and mountain muhly (blue, left) individuals surviving and growing from one year to the next.

Daniel Laughlin carried on the legacy with the rediscovery of many of the original quadrats and overstory plots. Starting with the discovery of the first plots in 2002, a series of studies have been carried out under Moore as her team began to annually remap and digitize (Figure 1.2) the original quadrats (Bakker & Moore, 2007; Bakker et al., 2008; Laughlin & Moore, 2008; Laughlin et al., 2011; Strahan et al., 2015). In addition to an annual census, the original data sheets were recovered from the USFS Fort Valley Experimental Forest Archives and digitized. By ensuring a consistent protocol between historic and contemporary data collection, it is possible to compare the community of the past to that of today. In a tip of the hat to founders of these studies, this rich data set continues to provide valuable ecological insight into the ponderosa pine ecosystem of northern Arizona.

Other studies using 1-m^2 quadrat data

The quadrat method of mapping basal area has been used to study changes in plant composition and demography in other locations in the western U.S. In a study similar to those carried on Hill & Wild Bill, Adler et al. (2006) used a historical data set located at Hays, Kansas to analyze the stabilizing effects of climate variability on the coexistence of prairie grasses. The dataset used by Adler et al. (2006) was used in a mid-grass prairie community analysis by Albertson & Tomanek (1965) over a 30-year period from 1932 to 1961. Albertson and Tomanek's (2006) study concluded that two drought periods resulted in a plant community composition shift that led to dominance by *Bouteloua gracilis* in one community, and *Andropogon gerardi* in two others; all three communities were co-dominated prior to drought conditions from 1933-1939 and 1959-1956.

Adler et al. (2010) used a 22-year dataset of 26 1-m^2 quadrats located on a sagebrush-steppe system north of Dubois, Idaho to study the coexistence of communities in relation to niche differences. Adler et al. (2010) determined that there was an "excess of niche differences" in which mechanisms that stabilized the sagebrush community were strong enough to maintain diversity; extinction of inferior competitors took 300-400 years

The dataset compiled from 1-m^2 quadrats has resulted in a multitude of ecological research including multiple dissertations from Bakker (2005), Laughlin (2009), and Strahan (2013), as well as a thesis by Dowling (2015). Strahan's dissertation included a life table for *F. arizonica* and *M. montana*, while Dowling's thesis included a life table and integral projection model (for seasonal precipitation) on *F. arizonica*. Dowling (2015) determined that *F. arizonica* population was decreasing over time, using an integral projection model that utilized seasonal precipitation but did not include seasonal temperature. Strahan (2013) determined that shade was the only significant factor determining relative abundance of *F. arizonica*, underscoring the species shade-tolerant behavior.

In addition to the academic achievements that the Hill & Wild Bill dataset is responsible for, a long list of publications has also been generated. These publications include Arnold (1955), Clary and Kruse (1979), Moore et al. (2004), Bakker et al. (2010), Laughlin et al. (2010), and Strahan et al. (2015), among many others. This long-term dataset continues to be of immeasurable importance in the study of plant communities in Northern Arizona and the framing of overarching ecological questions that help us better understand population and community-level processes.

Species Selection: C_3 vs C_4

The motivation behind the selection of Arizona fescue and mountain muhly for this study relates to their differing photosynthetic pathways. By selecting one C_3 and one C_4 species, we were able to start comparing physiologic adaptations and whether or not one was better adapted to the study site. The competitive advantage of C_3 versus C_4 plants is a highly-contested topic, the results of which are often is dependent upon a series of biotic and abiotic conditions. In order to better understand the environmental conditions that would favor one photosynthetic pathway over another it is important to first outline how these two strategies differ. Although there exist three different photosynthetic pathways (C_3, C_4, and CAM), this section will only focus on C_3 and C_4 because CAM is largely found in cactus species and is outside the scope of this study. C_3 and C_4 photosynthetic pathways are named based on the primary output that is created from each form of photosynthesis. In C_3 photosynthesis, a 3-carbon molecule is the first product that is produced, while C_4 photosynthesis produces a 4-carbon molecule (Ehleringer & Cerling, 2002). These two pathways differ in their evolutionary emergence, as C_3 photosynthesis is the most primitive form of photosynthesis, and therefore the most common pathway (Ehleringer & Monson, 1993). C_4 photosynthesis is often considered a more advanced pathway, evolving much later than the C_3 pathway, and therefore is less common (Ehleringer & Cerling, 2002).

Before understanding the ecological advantages of each pathways, it may prove useful to review the mechanisms involved in C_3 and C_4 photosynthesis. In the C_3 pathway, RuBisCo (ribulose -1,5-biphospate carboxylase/oxygenase) catalyzes a reaction between RuBP (ribulose -1,5-biphospate) and atmospheric CO_2 in order to produce two 3-carbon PGA (phosphoglycerate) molecules (Sharkey, 1985). These PGA molecules are eventually broken down through respiration to create sugars as well as the building blocks for RuBP, in order to facilitate further photosynthetic production (Ehleringer & Monson, 1993). The inefficiency of this pathway occurs when atmospheric O_2 reacts with RuBisCo, rather than CO_2. This occurs due to natural affinity of RuBisCo to react with O_2 and CO_2. Despite a greater affinity for RuBisCo to react with CO_2, high atmospheric concentration of O_2 means that the C_3 pathway is not always perfect. When atmospheric O_2 reacts with RuBisCo, the by product is one PGA and one phosphoglycolate molecule (Sharkey, 1985). When this reaction takes place, the plant fails in producing sugars; the single PGA is reduced by respiration and RuBP is created along with the byproduct CO_2. This tendency for O_2 to bond with RuBisCo means that no beneficial product is created, underscoring the inefficiency of the C_3 pathway.

The first difference that must be understood is that C_3 photosynthesis takes place in the plant's mesophyll cells. Atmospheric gas enters through the stomata and reacts with RuBisCo inside the mesophyll cells where C_3 carbon fixation takes place. In C_4 plants, the C_3 portion of the photosynthetic reaction only takes place in bundle sheath cells in the interior of the cell, rather than in all mesophyll cells. The mesophyll cells of C_4 plants contain PEP (phosphoenolpyruvate) carboxylase, an enzyme that starts the initial reaction (Ehleringer & Monson, 1993). This enzyme reacts with atmospheric CO_2 and PEP in order to produce a 4-carbon molecule, oxaloacetate (Hatch, 1988). The important difference is that PEP carboxylase only reacts with CO_2 and not with O_2; leading to a higher efficiency. This oxaloacetate then moves from the mesophyll cells into the bundle sheath cells where it is decarboxylated into CO_2 and pyruvate (Ehleringer & Cerling, 2002). The pyruvate is then transferred back into the mesophyll cells to create more PEP to create the initial reaction, while the CO_2 remains inside the bundle sheath cells (Hatch, 1988). This creates an environment in which CO_2 concentrations are higher than atmospheric levels and C_3 carbon fixation takes place. Because this C_3 reaction occurs within the bundle sheath cells, where CO_2 concentrations are higher than in the mesophyll cells, the chances of RuBisCo reacting with O_2 is effectively removed. This reduces photorespiration, and increases the efficiency of photosynthetic production (Sharkey, 1985; Ehleringer & Monson, 1993).

Advantages of C_4 photosynthesis

C_4 photosynthesis is often considered a more advanced pathway when compared to the ancestral, C_3 pathway due to its more recent evolution (Hatch, 1988). There are multiple justifications behind this evolutionary advancement, the first of which has been underscored in the previous section with the alleviation of photorespiration. To further highlight this advantage, it is important to understand the energetic requirements for C_4 photosynthesis to take place. Because C_4 photosynthesis is a more complex form of carbon fixation, it does require addition adenosine triphosphate (ATP) in order to carry out, specifically two additional ATP (Ehleringer & Bjorkman, 1977). Despite this higher energetic requirement, the C_4 pathway continues to yield a higher light-use efficiency than the C_3 pathway due to higher rates of photorespiration with greater temperatures (Ehleringer & Pearcy, 1983). Because photorespiration does not occur in C_4 plants, light-use efficiency is consistent regardless of temperature (Edwards & Ku, 1987).

Perhaps the most relevant advantage of C_4 photosynthesis in dryland communities is drought-tolerance due to higher water-use efficiency. Despite the role that stomatal opening plays in water loss in both C_3 and C_4 plants, C_4 plants exhibit higher photosynthetic output that 3 Plants at equivalent rates of water loss (Osmond et al., 1982). This increased water-use efficiency occurs because in C_4 plants, photosynthetic rate remains constant regardless of CO_2 concentrations inside the leaf (Pearcy & Ehleringer, 1984). To emphasize this point, C_4 plants use 250-350 grams of transpired water to generate the equivalent biomass that a C_3 plant creates using 650-800 grams of water (Taylor et al., 1983). This is a profound advantage in arid ecosystems where precipitation is unreliable and high levels of evapotranspiration can lead to drought stress. This evolutionary advantage has led to higher concentrations of C_4 plants in arid ecosystems, especially in places with a summer monsoon precipitation pattern (Quade et al., 1989). It has been proposed that this adaptation to arid climate in conjunction with lower atmospheric CO_2 levels following the end of the Cretaceous (Ehleringer et al., 1991) would have promoted the evolution of C_4 photosynthesis. According to Ehleringer and Monson (1993), warmer temperatures would not have been enough on their own to select for the C_4 pathway. However, when temperature is considered together with atmospheric CO_2 reductions, the combination of pressures could have tipped the scales.

Coexistence of C_3 and C_4 species

Different environmental conditions have been shown to favor plant species of differing photosynthetic pathways. These abiotic filters (along with other site-specific characteristics) are responsible for the distribution of species that we see on the landscape (Ehleringer & Cerling, 2002). These filtering mechanisms do not only act upon spatial distribution patterns, but often we find that filtering creates a temporal distribution as well, with species occupying explicit growing seasons (Ehleringer & Monson, 1993). For example, in much of the Southwest, precipitation follows a bimodal pattern with the bulk of precipitation falling in the winter months and summer monsoon (Sheppard et al., 2002). This difference in seasonality leads to temporal differences in plant communities in which C_3 plants dominate the early spring and C_4 plants dominate the summer season (Shreve & Wiggins, 1964; Mulroy & Rundel, 1977). July minimum temperature was found to have a strong correlation with C_4 growth (Stowe & Teeri, 1978); because the summer monsoon typically begins during July (Sheppard, 2002), this marks the height of C_4 dominance in the Southwest. In areas with relatively consistent temperatures, C_3 and C_4 species also follow a topographic gradient in their distribution with C_4 plants occurring in drier areas and C_3 plants occupying cool, wet parts of the landscape (Archer, 1984). Another mechanism through which C_3 and C_4 plants can coexist on the landscape is through heterogeneity in overstory canopy structure. C_3 plants exhibit higher levels of shade tolerance (Ehleringer, 1978) when compared to C_4 plants. This variation in canopy closure can result in coexistence of C_3 and C_4 species, although it is likely that there will be temporal differences in growth as well. The following sections will focus on two perennial bunchgrass species that co-exist in the understory community of northern Arizona: *Festuca arizonica* (Arizona fescue, C_3), and *Muhlenbergia montana* (mountain muhly, C_4). Spread out across a temporal gradient, these two species dominate the community during their respective growing seasons.

F. arizonica: natural history

F. arizonica is a widespread, cool-season, C_3 perennial, native bunchgrass species (Fletcher et al., 2004; Allred, 2005) characteristic of late or climax communities (Hanks et al., 1983). Arizona fescue is considered amongst the most important species for forage throughout its range, for both wildlife and livestock (Humphrey, 1955; Ffolliott et al., 1999). It can be found in a variety of different regions including: the Lower Basin and Range, the Southern Rocky Mountains, the Colorado Plateau, and Rocky Mountain Piedmont (Bernard & Brown, 1977) and exists in Arizona, Colorado, New Mexico, Nevada, Texas, and Utah (Kearney et al., 1960). Arizona fescue is characteristic of ponderosa pine ecosystems, but can also inhabit fir-spruce, western hardwood, and pinyon-juniper forests as well as mountain meadows and grasslands (Garrison et al., 1977). Because Arizona fescue is a cool-season species, it primarily grows from April to July (Clary & Kruse, 1979), taking advantage of wet winter/spring conditions. Following vegetative growth in the spring, Arizona fescue flowers during the summer (June-August) (Kartesz, 1988), and seeds mature shortly after (September-October) (Van Dyne, 1958).

Although C_3 species are not typically thought of as drought-tolerant, Arizona fescue exhibits physiologic adaptations that allow it to persist in the arid Southwest in the form of deep and dense roots (Gay & Dwyer, 1965). These root adaptations, along with mycorrhizal associations averaging 3.5 species per individual (Molina et al., 1978), allow for nutrient acquisition in harsh environments. Arizona fescue is not a rhizomatous species (Cronquist et al., 1977), and sexual reproduction is facilitated by wind-pollinated, perfect flowers (Hitchcock, 1951). The number of flowering stalks produced each year have been found to decrease when exposed to extensive grazing (Smith, 1967), resulting in an overall reduction in abundance in heavily-grazed areas (Hanks et al., 1983). The sensitivity of Arizona fescue to intense grazing practices makes degradation of this species an effective indicator of poor grazing management (Gay & Dwyer, 1965). Arizona fescue, like many C_3 species, exhibits moderate shade tolerance (Van Dyne, 1958), although Naumburg et al. (2001) discovered that biomass production was reduced by 63% in densely shaded areas, when compared to unshaded areas. Many of the communities in which Arizona fescue persists are categorized by frequent, low intensity surface fires (Pyne, 1982; Moore et al., 1999). As a result, Arizona fescue has developed fire-resistant adaptations and has been found to survive most fires, recovering with the onset of monsoon precipitation (Servis & Boucher, 1999)

As mentioned above, Arizona fescue can be found in a variety of different habitats throughout the Southwest and can tolerate many extremes, highlighted by its low temperature tolerance of -40° C. It is generally found in areas that receive over 25.4 cm of annual precipitation but grows best in areas that receive more than 35.56 cm (Hassel et al., 1983). Dependent upon cool-season precipitation, Potter et al. (1998) report that Arizona fescue was found on high elevation sites that received 50% of the annual precipitation in the winter season, but was nonexistent on sites that only received 40% of annual precipitation in the winter. Commonly found on dry, shallow soils, Arizona fescue prefers clay loams as well as rocky soils containing gravel and sand (Dayton et al., 1937).

M. montana: natural history

M. montana is a warm-season, C_4, native perennial bunchgrass species that occurs in seral and climax communities (Arnold 1950; Currie, 1975; Dittberner & Olson, 1983). Mountain muhly comprises the characteristic Arizona fescue-mountain muhly bunchgrass community of the ponderosa pine forests that dominate northern Arizona (Currie, 1975). Similar to its C_3 counterpart, mountain muhly is an important forage for cattle and is the 3rd most foraged grass (behind *Poa pratensis* and *Festuca arizonica*) (Clary, 1975; Lowe, 1975). According to Humphrey (1970), mountain muhly plays an important role in livestock forage not because of its high palatability but rather for its abundance, although it does exhibit higher palatability in the growing season prior to maturation. Mountain muhly has a similar range to Arizona fescue, and can be found across the West (AZ, CA, CO, MT, NM, TX, UT, WY, Mexico) in the Sierra Mountains, throughout the Lower Basin and Range, the Rocky Mountains, through the Wyoming Basin, on the Colorado Plateau, in the Rocky Mountain Piedmont, and in the Upper Missouri Basin. Mountain muhly exists in many of the same ecosystems as Arizona fescue, such as Douglas-fir, ponderosa pine, fir-spruce, sagebrush, chaparral, and pinyon-juniper forests as well as in mountain, desert, and plains grasslands (Kearney et al., 1960; Harrington, 1964; Hitchcock et al., 1973; Dorn, 1988; Tapia et al., 1990; Jepson, 1993). Being a warm-season species, mountain muhly grows during late spring and summer months, with growth starting when high temperatures reach 50˚F (Pearson, 1965; Pearson, 1967; Herzman et al., 1988). Peak growth occurs during July and August following the beginning of monsoon precipitation, and can be interrupted by drought conditions in which mountain muhly enters into a semi-dormant state (Pearson, 1965; Pearson, 1967).

There are many physiological adaptations that allow mountain muhly to persist in high abundance. Extreme drought tolerance can be attributed to C_4 carbon fixation as well as well-adapted root traits. The roots of mountain muhly have been known to compete with ponderosa pine seedlings because their roots are highly fibrous, and grow faster than their overstory counterparts (Berndt & Gibbons, 1958; Larson & Gilbert, 1969). According to Foxx and Tierney (1987), the deepest mountain muhly roots were found to be 9 feet deep, which allows penetration into the water table and increases drought tolerance. Along with its impressive root system, mountain muhly can reproduce vegetatively through tillering in which side shoots branch off from the main stem of the parent plant (Cronquist et al., 1977; Vose & White, 1987). Similar to Arizona fescue, mountain muhly has been shown to decrease in abundance following exposure to heavy grazing or trampling (Arnold, 1950; Johnson, 1956) and can be found more readily in areas without heavy disturbance. Like many C_4 species, mountain muhly grows best in full sun and lacks shade-tolerant adaptations (Arnold, 1950; Hickman, 1993). This preference for open growing condition means that mountain muhly decreases in abundance in dense stands of ponderosa pine (Arnold, 1950) as well as with higher litter abundance (Gary & Currie, 1977). This sensitivity to disturbance and over-grazing makes mountain muhly is a good indicator of range health and grazing management practices (Darrow, 1944). When growing conditions are optimal (open, park-like stands), Rietveld (1975) discovered that mountain muhly communities can be so dense that they resist invasion from ponderosa pine seedling. Given the historical, frequent, low-intensity surface fire regime of ponderosa pine stands (Pyne, 1982; Moore et al., 1999), it is no surprise that mountain muhly is a fire-adapted species. Capable of resprouting after fires, dense vegetative growth protects basal buds from experiencing catastrophic damage, however, overabundant litter presence can cause hot fires that may be detrimental to the plant (Munz, 1973; Vose & White, 1991; Hickman, 1993).

Due to its abundance in Arizona fescue-mountain muhly communities, it comes as no surprise that site-specific conditions for mountain muhly are similar to those of Arizona fescue. Although mountain muhly is found in both dry and moist locations, it requires well-drained soils (Hickman 1993). Like its C_3 counterpart, mountain muhly prefers coarse, clay loams, and can tolerate sandy, gravely growing conditions (Eyre, 1980; Andariese, 1982). Given its wide-ranging distribution, mountain muhly can persist through a variety of climate types throughout the western United States, and flowers from July to September, depending on location (Kearney et al. 1960; Cronquist et al., 1977).

Modeling of structured populations

Data-driven population models have become a highly-utilized tool in ecology and population biology due to their importance for examining species change over time due to land use change and climate change (Ozgul et al., 2010; Rees et al., 2014). Structured population models describe how population size and distribution changes over time by linking individual vital rates to population processes (Tuljapurkar & Caswell, 1997; Easterling et al., 2000). Caswell (1988; Taljapurkar & Caswell, 1997) explored environmental effects on vital rates (birth, reproduction, maturation, dispersal, death) in order to better understand how variation in individual rates can be used to infer population dynamics. This framework built upon matrix population modelling (Lefkovitch, 1965; Caswell, 1978) and eventually to "stage-based models." This approach takes into consideration that there are various life stages through which individuals pass in the course of their lives (Caswell, 2001). Rather than assuming vital rates to be consistent across life stages, "structured" population models assess individual differences in vital rates that occur throughout the population according to age, size, or developmental stage (Caswell, 1997). Variation in individual growth rates can lead to difficulty estimating the age of an individual; instead, size classes can be used in stage-based demographic analyses (Lefkovitch, 1965). The ease of use has led to widespread implementation of matrix modelling of structured populations. The simplicity of parameterizing a matrix from observational data allows for estimation of population growth rates based on changes in environmental conditions (Caswell, 2001; Ellner & Rees, 2006). Matrix models have proven to be useful tools in propelling forward ecological population modelling, however, when using continuous data, biological realism is sacrificed. When developing a matrix model, the study population is categorized into a finite number of stages or classes, even when considering a continuous variable (Easterling et al., 2000). This discretization can lead to sources of error when large numbers of bins are created because each discrete bin contains a low sample size (Ellner & Rees, 2006). The error associated with the utilization of continuous variables created a need to propel structured population modelling forward, building on the matrix framework and creating a new tool for population modelling: the integral projection model (IPM) (Easterling et al., 2000).

Integral projection models (IPM)

Working to minimize the effects of artificially placing continuous data into discrete bins, Easterling et al. (2000) created the Integral Projection Model (IPM) framework in order to preserve "biological realism" (Merow et al., 2014). Despite past attempts to determine optimal class boundaries for matrix models (Moloney, 1986), there was a need to eliminate error, rather than minimize it (Easterling et al., 2000). The IPM works on a matrix model framework by holding true to discrete time measures, without the need to place individuals into discrete stages (Easterling et al., 2000). The mathematical justification for the model has been described by Easterling (1998), and will not be discussed in detail in this review. The framework of the IPM allows for continuous size variation among individuals while using common demographic data (Childs et al., 2003). Demography is the link between individual and population-level processes, and is an essential tool in determining shifts in community composition under future climate scenarios (Merow et al., 2014). This framework accounts for temporal and spatial variation in demographic parameters based on environmental stochasticity (Moloney, 1986). Rather than using a projection matrix, a projection kernel is used in the IPM framework. This kernel (K) is composed of two sub-kernels (P & F), where (P) describes survival and growth and (F) is a measure of fecundity (Metcalf et al., 2013). As

$$n(y,t+1) = \int_{L}^{U} K(y,x)n(x,t)\mathrm{d}x \qquad \text{(Metcalf et al. 2013)}$$

eqn 1

$$= \int_{L}^{U} [P(y,x) + F(y,x)]n(x,t)\mathrm{d}x$$

described by Easterling et al. (2000) and Metcalf et al. (2013) in equation 1 (right), the state of a population is described by a distribution *n(y,t)*, which represents the number of size-y individuals at time (*t)* and *n(y, t + 1)* represents the distribution in time *(t+1)*.

Conclusion

Quantifying the effects of climate change on ecological communities is the first step in preparing land management and conservation strategies that promote healthy, resilient ecosystems. Data-driven structured population models have proven useful in attempts to understand the link between variation in individual vital rates and population-level processes. The integral projection model framework is appropriate for modelling structured populations when the study population is characterized by a continuous variable, such as size. This framework allows the user to link demographic data and environmental covariates to population dynamics in order to project future population growth or decline. In chapter 2, the creation of an integral projection model is used to examine the influence of seasonal weather patterns and size-class on two long-lived, perennial bunchgrasses.

In order to investigate the effect of differing photosynthetic pathways on population growth rates, we selected one C_3 and one C_4 graminoid species, *Festuca arizonica* (Arizona fescue) and *Muhlenbergia montana* (mountain muhly). Together, these two species represent the Arizona fescue-mountain muhly bunchgrass community that dominates northern Arizona. Given the different photosynthetic pathways of these two species, we expect differing responses to climate change, particularly variation in survival and growth to seasonal weather patterns. C_4 species such as mountain muhly are more drought-tolerant, and therefor may be better equipped to handle the projected drought conditions that will occur in upcoming decades throughout the Southwest. Should these climate model predictions hold true, it is possible that we may experience a C_3 to C_4 functional shift in response to severe and prolonged droughts. This can have implications on the understory community of northern Arizona, given the higher relative abundance of C_3 species (compared to C_4) in this community. A C_3 to C_4 shift could impact livestock and wildlife communities that rely on the high nutrient content and palatability of C_3 species such as Arizona fescue.

Chapter 2 will explore the ecological concepts introduced in this chapter, and serves as a self-contained manuscript. In chapter 3, a more extensive discussion of management implications is offered in order to bridge the gap between ecological theory and applied management and conservation.

CHAPTER 2:

DIRECT EFFECTS OF SEASONAL PRECIPITATION AND TEMPERATURE ON THE DEMOGRAPHY OF TWO DOMINANT BUNCHGRASSES IN NORTHERN ARIZONA

Abstract

Understanding plant population responses to climate and land-use change is fundamental to conservation and land management. Here, we focus on two dominant, perennial, bunchgrasses in northern Arizona: *Festuca arizonica* (Arizona fescue) and *Muhlenbergia montana* (mountain muhly). We used data from 68 annually remapped quadrats (2002-2018) to examine the effects of precipitation and temperature on the survival and growth of each species. We constructed life tables to examine their vital rates and then made population projections using an Integral Projection Model (IPM) framework to quantify the direct effects of seasonal precipitation and temperature on vital rates. We predicted that survival and growth of *F. arizonica* (a cool-season, C3 species) would be greater with increased spring precipitation and increased spring temperatures, and *M. montana* (a warm-season, C4 species) would be greater with increased summer precipitation and increased summer temperatures. First year survival probabilities were 0.17 and 0.07 and mean life expectancies were 1.19 and 1.07 years for *F. arizonica* and *M. montana*, respectively. Both species had lambda values less than 1 (0.90 for *F. arizonica*, and 0.88 for *M. montana*) indicating decreased population growth over the 17-year time period, however, neither plant recruitment nor fecundity were analyzed in this study. Plant size was the most important predictor for survival and growth of each species. Spring precipitation influenced survival and growth for *F. arizonica* while summer monsoon precipitation influenced survival and growth for *M. montana*. Growth of both species increased with warmer spring temperatures. Given their dominance, in this system, understanding the controls on demographic parameters of

these bunchgrass species is critical for predicting community response to changing environmental conditions.

Key words: structured population, integral projection model, demography, perennial graminoid

1. Introduction

It has become increasingly clear that changes in environmental conditions and land management practices have influenced both species distribution and ecosystem function (Woodward 1987; Pearson and Dawson 2003; Strahan et al., 2015, James et al. 2019). Although climate models continue to struggle with predicting changes in total precipitation amounts, models suggest that more precipitation will fall as rain and less as snow throughout much of the western United States (Harding et al., 2012; Wi et al., 2012). Along with this precipitation state change, climate models also predict a change in timing of precipitation, with more precipitation falling in cold months, and less in warm months (Eng et al., 2016). As plant communities are subjected to increasingly arid soil conditions, elevated evapotranspiration rates resulting from higher temperatures coupled with shifts in precipitation patterns and snowmelt result in soil moisture debts (Seager et al., 2007; Eng et al., 2016). These arid soil conditions threaten plant-available water, and can result in plants that are water-stressed (Hsiao, 1973). Climate models generally agree that a 2-6˚ C increase will occur over the next century (IPCC, 2014); although levels of warming are highly dependent upon climate mitigation strategies. Despite this variation, James et al. (2019) determined that a warming of just 2˚ C could result in a 30% reduction in graminoid seedling establishment in the arid Great Basin region. Together, these compounding climatic pressures can have profound effects on plant communities throughout the arid Southwest.

As climate effects on plant communities become more apparent, management decisions throughout the western United States have already led to changes in forest and rangeland community compositions when compared to reference conditions of the late 1800s (Moore et al., 1999; Laughlin et al., 2011; Clark et al., 2016) In the pine forests of northern Arizona, historical forest fire suppression has decreased fire return intervals (Cooper, 1960; Bataineh et al., 2006), elevated stand densities (Parsons & DeBenedetti, 1979; Swetnam & Baisan, 1996), and created community assemblages that are structurally and functionally different from reference conditions (Moore et al., 1999). This change in fire regime has also resulted in an increase in high-severity fires throughout the Southwest (Fulé et al., 2009; Singleton et al., 2019). Shifts in fire behavior have led to elevated stand densities, changing the structure of these systems (Moore et al., 2004; Fulé et al., 2009). In Colorado Plateau ponderosa pine (*Pinus ponderosa*) forests, a 7-fold increase in ponderosa pine basal area since the late 1800s has reduced herbaceous understory species richness by 21%, resulting in reduction of C_4 species and an increase in C_3 species (Laughlin et al., 2011). Strahan et al. (2015) quantified a shift in functional traits of overstory species as a result of these land-use changes in northern Arizona. The study determined that species are beginning to exhibit traits that are characteristic of fire-intolerant species. Along with fire suppression practices, extensive grazing throughout the region has also had effects on plant communities. Beginning with a study by Hill (1917), the USFS began monitoring the effects of livestock grazing on ponderosa pine seedling regeneration as well as on long-lived perennial bunchgrass species at Fort Valley Experimental Forest in northern Arizona. Hill (1917) determined that establishment of both ponderosa pine and perennial graminoids were being thwarted by intense livestock grazing. A more recent study by Souther et al. (2020) categorized the combined effects of grazing and climate on the same grassland community. Drought coupled with intense grazing led to persistence of non-native invaders, while moderate grazing practices showed a stabilizing effect on the community; these findings suggest that while excessive grazing practices should be avoided, moderate grazing can increase drought resilience (Souther et al., 2020).

In an attempt to quantify functional shifts in grassland communities in response to management practices and climate change, it is important to determine if species of differing photosynthetic pathways show varying levels of change. Munson et al. (2011) determined that C_3 perennial grasses have decreased in abundance in grassland communities on the Colorado Plateau as a result of increased aridity. C_3 species are on average less drought-adapted than their C_4 counterparts due to decreased water-use efficiency (Osmond et al., 1982; Taylor et al., 1983; Pearcy & Ehleringer, 1984). In addition to reduced drought-tolerance, C_3 species show higher shade-tolerance than C_4 species (Ehleringer, 1978). These differences mean that while C_4 species may be more likely to persist in a future characterized by more frequent drought periods, they occur in reduced abundance with higher levels of tree or shrub canopy closure (Laughlin et al., 2011). The opposing selective pressures of drought and canopy closure lead to uncertainty surrounding the fate of bunchgrass communities in the arid Southwest.

Determining the influence of historical climate variation on plant population dynamics can aid in forecasting future impacts of environmental change (Dalgleish et al., 2011). Demographic analyses can be used to infer population and life-history dynamics from individual vital rates such as survival, growth, and life expectancy (Harper, 1977; Franco & Silvertown, 2004; Lauenroth & Adler, 2008). One way to acquire demographic data is by long-term mapping of permanent quadrats (West et al., 1979; Lauenroth & Adler, 2008); these data can then be used in population modelling efforts (Easterling et al., 2001; Dalgleish et al., 2011). A common tool used for modeling biological populations is matrix populations modelling (Lefkovitch, 1965; Caswell, 1978; Caswell, 2001) due to ease of use and ability to use empirical data to predict population response (Ellner & Rees, 2006). Stage-based matrix population models take into consideration that individuals pass through various life stages during the course of their lives (Caswell 2001), and attempt to estimate differences in individual vital rates according to stages such as age, size, or developmental stage (Caswell, 1988; Tuljapurkar & Caswell, 1997). The integral projection model (IPM) structure utilizes much of the groundwork laid by matrix models, such as the generation of population growth rate (λ) and stable size distribution (Childs et al., 2003). The advantage of the IPM framework over traditional matrix models is the ability to incorporate continuous state variables (e.g., size, age) into analyses of population vital rates (Easterling et al., 2000; Merow et al., 2014). Population growth rate, or eigenvalue (λ), is affected by changes in the left (stable size distribution; *w*) and right (reproductive value; *v*) eigenvectors within the projection matrix (Ellner & Rees, 2006). These eigenvectors are used to determine responses in population size and distribution to environmental covariates (Caswell, 2001; Ellner & Rees, 2006).

Using demographic data collected between 2001 and 2018, we built IPMs for two perennial bunchgrass species: *Festuca arizonica* (Arizona fescue), and *Muhlenbergia montana* (mountain muhly). We chose these two species in order to determine the effects of size and weather on population dynamics of bunchgrass species with differing photosynthetic pathways. *F. arizonica* is a cool-season, C_3, perennial bunchgrass (Fletcher et al., 2004; Allred, 2005), while *M. montana* is a warm-season, C_4, perennial bunchgrass (Arnold, 1950; Dittberner & Olson, 1983). Together these species dominate the Arizona fescue-mountain muhly bunchgrass community of the ponderosa pine forests of northern Arizona (Currie, 1975), and are key sources of forage for wildlife and livestock (Humphrey, 1955; Lowe, 1975; Clary, 1975; Ffolliott et al., 1999). In addition to wildlife forage, bunchgrass species play an important role is controlling seedling establishment of ponderosa pine (Pearson, 1942; Arnold, 1950; Bakker & Moore, 2007), particularly in park-like settings (Rietveld, 1975).

Differing photosynthetic pathway leads to a separation in both growing season and spatial distribution between C_3 and C_4 species (Ehleringer & Monson, 1993) and thus these species are likely to respond to different environmental drivers. In much of the southwestern United States precipitation follows a bimodal pattern with the bulk of precipitation falling in winter and throughout the summer monsoon period (Sheppard et al., 2002). This difference in seasonality leads to a temporal divergence in species distribution in which C_3 plants dominate the cool-season, and C_4 plants dominate the warm-season (Shreve & Wiggins, 1964; Mulroy & Rundel, 1977). In areas with relatively consistent temperature across the landscape, C_3 and C_4 species also follow a topographic gradient with C_4 plants occurring in drier areas and C_3 plants occupying cool, mesic areas (Archer, 1984). Given the coexistence of these two species, our study set out to determine the seasonal temperature and precipitation effects, as well as the influence of size on population vital rates.

We modeled the effects of temperature and precipitation on vital rates of two native, perennial grasses to determine how: 1.) size affects survival and growth, 2.) temperature and precipitation affects survival and growth. In order to determine seasonal temperature and precipitation effects on vital rates we asked: 1.) How does size affect survival and growth of these two perennial grasses with C_3 versus C_4 photosynthetic pathways? 2.) How does temperature affect survival and growth of *F. arizonica* and *M. montana*? 3.) How does precipitation affect survival and growth of *F. arizonica* and *M. montana*? And 4.) How do these three factors affect population growth rates of *F. arizonica* and *M. montana*? We predicted that survival and growth of *F. arizonica* (C_3) would increase with higher spring precipitation and temperature, while *M. montana* (C_4) would increase with higher summer precipitation and temperature. We also predicted that larger individuals would have higher survival and growth rates for both *F. arizonica* and *M. montana.*

2. Material and Methods

2.1 Site description and data collection

This study took place in the ponderosa pine forests surrounding Flagstaff, Arizona (35.198˚N, 111.651˚W) within the Coconino National Forest. Utilizing long-term study plots established by Robert R. Hill in 1910, all plots fall within a 40 km radius of Flagstaff (Bakker et al., 2008). The topographical heterogeneity of the area is such that elevation of study sites ranges from 2050 to 2500 meters. Soils vary between sites, and are generally characterized as well-drained, rocky, sandy, clay loams; parent materials are predominantly limestone, sandstone, shale, cinders, and basalt (Laughlin et al., 2011). Ponderosa pine dominates the overstory while the understory is characteristic of an Arizona fescue-mountain muhly bunchgrass community. Classified as a semi-continental (Koppen Dsb/Csb) climate, precipitation is bimodal (winter and summer monsoon) with an average annual rainfall of 58 cm; roughly half of this precipitation falls during the winter (USClimateData.com, 2020). Suppression of frequent, low-intensity surface fires and historical domestic livestock overgrazing (Cooper, 1960; Mutch, 1970) has greatly increased forest densities from 72 trees ha^{-1} in 1870 to 1396 trees ha^{-1} in 1995 (Moore et al., 1999).

We collected data utilizing the chart quadrat method first used by Frederic Clements (1905; Weaver & Clements, 1929). This method uses fine-grain mapping of basal areas of every individual located within permanent 1-m^2 quadrats that were first established in 1910 (Hill, 1917; Hill 1920). These permanent quadrats are marked with angle iron and tagged with a unique identification number in order to ensure their location accuracy (Bakker et al., 2008). Data collection took place from August-September, following the summer monsoon, in order to capture peak plant growth. Adhering to historic protocol, the basal area of each individual was marked by hand. Graminoids were recorded as polygons, while shrubs and forbs were marked as points (Hill, 1920; Lauenroth &Adler, 2008). Each data sheet was then digitized using the ArcMap portion of Esri's ArcGIS and polygons for *F. arizonica* and *M. montana* were created.

2.2 Demographic analysis

We used a computer program developed by Lauenroth and Adler (2008) to generate demographic output data. The program tracks genets over time in order to produce vital rate and life-history information. Using shapefile data that was digitized in ArcMap, each unique polygon was assigned a tracking number and a 5 cm buffer is placed around it. The 5 cm buffer was used to account for field-mapping error and growth from year to year (Fair et al., 1999; Lauenroth & Adler, 2008). Overlapping polygons in year (*t*) were assumed to be the same genet from year (*t* - 1). New polygons falling outside of the 5cm buffer were designated as new recruits, and are assigned a unique tracking number; then, genets and new recruits were tracked from 2002 to 2018. Using this method, we were able to determine life expectancy, survival, growth, and number of new recruits per year. Both study species are known to be long-lived, and therefore maximum life span could not be determined in the 17-year course of this study. Over the course of the study period, we allowed for a "dormancy window" in order to account for a year of missing data, resulting from a quadrat not being sampled. The reason for this dormancy window was a break in sampling that occurred in 2008. This allowed us to infer survival and growth from 2007 to 2009, while assigning 2008 as a dormancy year.

2.3 Climate data

Monthly weather data were acquired from the Flagstaff Pulliam Airport via the National Oceanic & Atmospheric Administration (NOAA). Average monthly temperature and total monthly precipitation data were used to determine the influence of weather on species vital rates. We assigned the period of time from October of year (*t* - 1) to September of year (*t*) as a "water year" to capture influence on the growing season for year (*t*). After analyzing the effect of mean annual temperature and annual total precipitation, the water year was separated into four time periods based on seasonality: winter, early spring, late spring, and summer monsoon (Table 2.1). Precipitation and temperature were averaged over each season in order to capture year-to-year variation.

Table 2.1 | Seasonal weather data imported from Pulliam Airport, Flagstaff, AZ.

Weather Covariates	Data
Winter precipitation	Average total precipitation (Oct1 – Feb 28)
Early Spring precipitation	Average total precipitation (Mar 1 – Apr 30)
Late Spring precipitation	Average total precipitation (May 1 – Jun 30)
Monsoon precipitation	Average total precipitation (Jul 1 – Sep 30)
Winter temperature	Average monthly temperatures (Oct1 – Feb 28)
Early Spring temperature	Average monthly temperatures (Mar 1 – Apr 30)
Late Spring temperature	Average monthly temperatures (May 1 – Jun 30)
Monsoon temperature	Average monthly temperatures (Jul 1 – Sep 30)

2.4 Modeling Population Responses

We used the IPM framework and computing package *IPMpack* developed by Metcalf et al. for the statistical software *R* (2013), to construct two IPMs, one for *F. arizonica*, and one for *M. montana*. To build each IPM, we first generated demographic data with scripts created by Lauenroth and Adler (2008); this created information pertaining to the survival and growth of each genet and recruit for time (*t*) and (*t*+1). Survival from (*t*) to (*t*+1) was generated as binary (0/1) data while growth was calculated as size at *(t+1)* – size at *(t)*. Individual size was highly variable for both species (*F. arizonica* min: 0.002 cm, max: 1091 cm; *M. montana* min: 0.00003 cm, max: 699.8 cm), thus we log transformed the data for enhanced visualization.

The integral projection model framework allowed us to utilize continuous data on the size-structured population in order to infer population dynamics (Easterling et al., 2000). Survival and growth functions were created separately using *IPMpack* (Metcalf et al. 2013), this allowed us to determine unique combinations of environmental covariates that affected survival and growth, individually. Vital rate models were created using generalized linear regression models relating survival and growth to seasonal weather. Vital rate regression models include both linear and quadratic functions (e.g., spring precipitation and spring precipitaiton^2). We used Akaike Information Criterion (AIC) to select the most parsimonious model.

Model parameters were set using the slope and intercepts of the best-fit regression models for the survival function *s(x)* and the growth function *g(y,x)*; *s(x)* is the survival probability of an individual of size-*x*, and *g*(*x,y*) is the growth probability of a size-*x* individual reaching size-*y* (Ferrer-Cervantes et al., 2012). A P-matrix was created by applying the midpoint rule (Ellner & Rees, 2006; Metcalf et al., 2013). Because fecundity data was absent from the data set, the kernel (*k*) was estimated from the survival and growth kernel ($p(x,y) = s(x)g(x,y)$), exclusively. For further details on *IPMpack* and utilization of integral projection models see Easterling et al. (2000), Metcalf et al. (2013), Rees et al. (2014), and Merow et al. (2014).

3. Results

3.1 F. arizonica

The population (n=2959) of *F. arizonica* has declined over the 17-year study period; $\lambda = 0.90$. With a first-year survival probability of 0.17 and a mean life expectancy of 1.19 years (Table 2.2), our demographic data suggests that *F. arizonica* fits a type III survivorship curve. Species typical of type III survival exhibit a high probability of first year mortality which decreases over time (Pinder III et al., 1978). The distribution for the population is skewed towards a higher frequency of individuals in smaller size classes (Figure 2.1), underscoring the type III survivorship The best-fit model for survival of *F. arizonica* (C_3) (AIC = 2254.2) included a positive influence of size, early spring precipitation, and monsoon temperatures. The model that best predicted growth (AIC = 4554.3) included size, late spring precipitation, and early spring temperature (Table 2.3). Projection kernels built with the top survival and growth models as well as results from sensitivity and elasticity analyses can be found in figure 2.2.

Table 2.2 | Life table for FEAR & MUMO. *Max life span exceeds length of study.

Species	N	First Year Survival	Mean Life Expectancy	Max Life Span
F. arizonica	2959	0.1695	1.1915	16*
M. montana	3657	0.0707	1.0712	16*

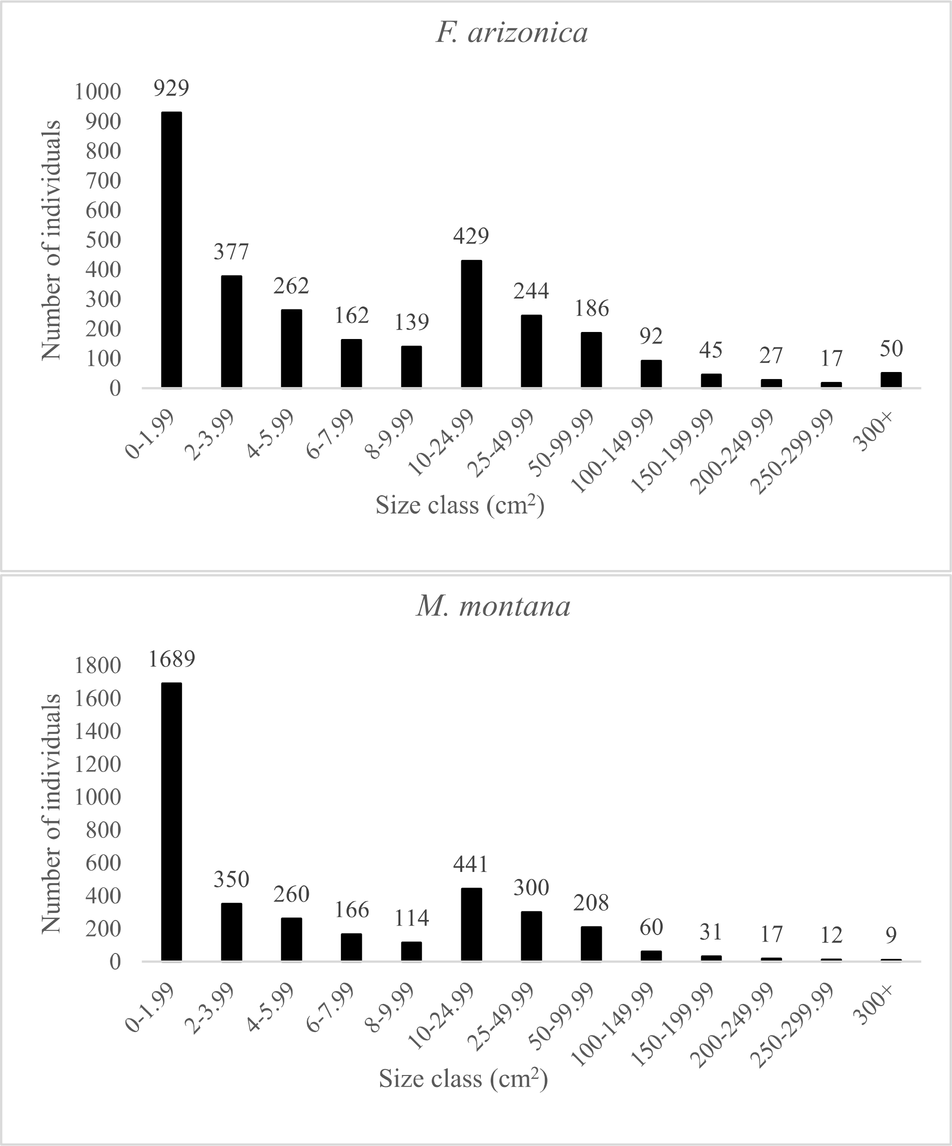


Figure 2.1 | Size distribution of *F. arizonica* & *M. montana*. Note change in x-axis for individuals <10 cm^2.

3.2 M. montana

The population (n=3657) of *M. montana* has declined throughout the course of this study; λ = 0.88. Exhibiting a type III survivorship curve, *M. montana* had a first-year survival probability of 0.07 and a mean life expectancy of 1.07 years (Table 2.2). The population distribution was heavily skewed towards individuals of smaller size classes (Figure 2.1). The model that best predicted (AIC = 2488.5) survival for *M. montana* (C_4) included logsize, monsoon precipitation, and winter temperature (Table 2.2). The best fit model (AIC=4508.1) for growth was comprised of logsize, monsoon precipitation, and late spring temperature (Table 2.3).

Table 2.3 | Model summary *for F. arizonica* & *M. montana*. *p <0.05

F. arizonica	***M. montana***
Lambda = 0.901	Lambda = 0.883
Survival: AIC = 2254.2	**Survival:** AIC = 2488.5
Survival ~ logsize + early spring precipitation + monsoon temperature	Survival ~ logsize + monsoon precipitation + winter temperature
Logsize, p-value = $2.0e^{-16}$*	Logsize, p-value = $2.0e^{-16}$*
Early spring precipitation, p-value = 0.8934	Monsoon precipitation, p-value = $9.58e^{-6}$*
Early spring precipitation^2, p-value = 0.0705	Monsoon precipitation^2, p-value = 0.005*
Monsoon temperature, p-value = $2.37e^{-7}$*	Winter temperature, p-value = 0.120
Monsoon temperature^2, p-value = $2.34e^{-7}$*	Winter temperature^2, p-value = 0.160
Growth: AIC = 4554.3	**Growth:** AIC = 4508.1
Growth ~ logsize + late spring precipitation + early spring temperature	Growth ~ logsize + monsoon precipitation + late spring temperature
Logsize, p-value = $2.0e^{-16}$*	Logsize, p-value = $2.0e^{-16}$*
Late spring precipitation, p-value = 0.659	Monsoon precipitation, p-value = $7e^{-5}$*
Late spring precipitation^2, p-value = 0.002*	Monsoon precipitation^2, p-value = $9.47e^{-8}$*
Early spring temperature, p-value = $2e^{-16}$*	Late spring temperature, p-value = $6.44e^{-6}$*
Early spring temperature^2, p-value = $2e^{-16}$*	Late spring temperature^2, p-value = $3.48e^{-6}$*

4. Discussion

4.1 Population growth

Understanding the interaction between abiotic conditions and plant population dynamics is key to predicting community response in a changing world. The integral projection model framework allows us to link plant demography to environmental conditions. In the case of *F. arizonica* and *M. montana*, we determined that plant populations are decreasing over time, as shown by lambda values less than one. It is likely that this decrease is in response to size-class distribution among *F. arizonica* and *M. montana* populations, as exhibited by lambda sensitivity to size. *F. arizonica* and *M. montana* populations demonstrated a greater number of individuals in the smaller size classes, in which survival probability was much lower. As individuals are recruited into higher size-classes, their probability of survival increases. This is expressed visually in the final output kernel as the “hot” (white) portion of the heatmap. While large individuals are likely to persist given their resilience to change, if smaller individuals fail to survive long enough to be recruited into larger class sizes, the population as a whole will suffer. It is likely that there exists a size threshold where individuals become large enough to buffer the effects that would lead to mortality in smaller individuals, however, determining this threshold did not fall within the scope of this study. This may be a useful direction for future analysis, and could aid in suggesting management practices to combat species loss. The consequence of this decrease in population growth could prove problematic for the herbaceous understory community in the ponderosa pine ecosystem, given the dominance and forage significance of these two graminoid species.

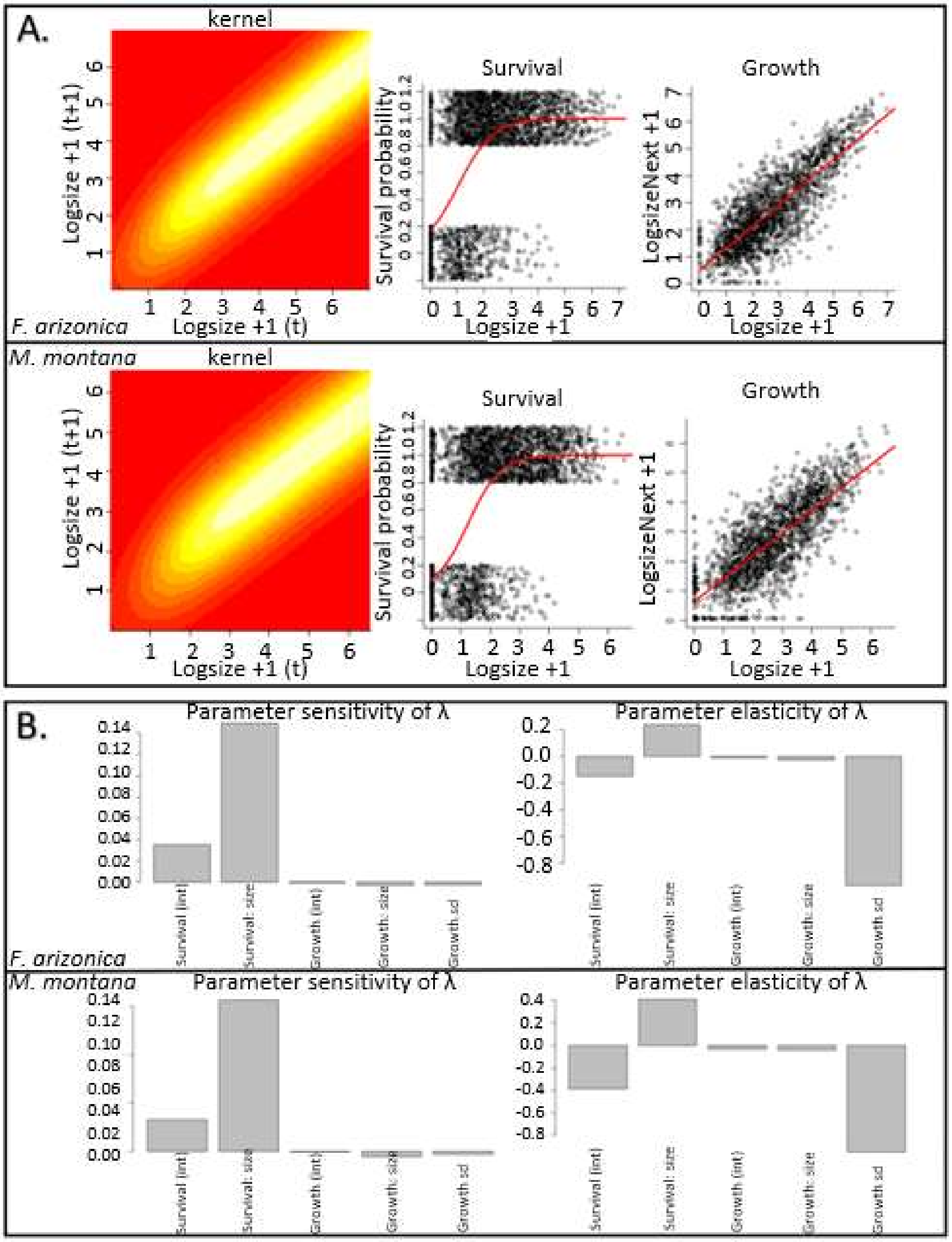


Figure 2.2| *F.arizonica* & *M. montana* output kernel and sensitivity

Panel A: Kernel (left) is displayed as a heatmap. Light colors in center associated with higher probability of survival and growth from *(t)* to (*t*+1). Fitted survival and growth curves (middle and right) for top-models using weather covariate data.

Panel B: Sensitivity (left) and elasticity (right) analyses determine sensitivity of lambda to survival and growth, independently.

4.2 C_3 vs. C_4 photosynthesis

Both species exhibited a decrease in population growth overtime. While population dynamics were similar between the two species, the environmental covariates that made up the best-fit models differed. The best-fit model for survival of *F. arizonica* included size, early spring precipitation, and monsoon temperature, while the best fit model for growth included size, late spring precipitation, and early spring temperature. The best-fit model for survival of *M. montana* included size, monsoon precipitation, and winter temperature, while the best fit model for growth included size, monsoon precipitation, and late spring temperature. The results supported our predictions that seasonal weather patterns had an effect on survival and growth for both *F. arizonica* and *M. montana* as indicated by a positive correlation between survival/growth and higher temperatures/precipitation within each species' respective growing season.

The growing season for *F. arizonica* starts around March/April with the onset of warm temperatures and snowmelt (Clary & Kruse, 1979). This vegetative growth continues until June or July when flowering begins to occur; flower development extends throughout August in response to the summer monsoon (Kearney et al., 1960; Kartesz, 1988). *F. arizonica* exhibited a positive correlation between survival and early spring precipitation and monsoon temperature. Positive growth was influenced by late spring precipitation and early spring temperatures. Early spring moisture is essential for survival of *F. arizonica*, while precipitation later in the spring encourages growth. The effect of monsoon temperature on survival is more difficult to interpret. It is possible that warm monsoon temperatures are correlated with monsoon precipitation, given the energy requirement necessary to generate monsoonal circulation. This temperature dependence may also be in response to *F. arizonica*'s long growing season, extending well into the summer months. The influence of early spring temperature on growth was expected, due to

F. arizonica's early onset growth that occurs in early spring. With the exception of survival based on monsoon temperature, all other weather covariate that influenced survival and growth of *F. arizonica* took place during the spring (both early and late). This spring dependence is expected in C_3 plants, given their initiation of cool-season growth in the Southwest.

Peak growth for *M. montana* occurs much later than *F. arizonica*, and takes place primarily during July and August (Pearson, 1965). Flowering begins in September and inflorescence can stick around well into November and December (Kearney et al., 1960; Cronquist et al., 1977). Monsoon precipitation and winter temperature were positively correlated with survival of *M. montana*, while growth was influenced by monsoon precipitation and late spring temperature. The influence of monsoon precipitation on both survival and growth was expected; recall that *M. montana* is a C_4 species, and grows during the warm season when adequate moisture is available. Late spring temperature influence on growth does not come as a surprise because *M. montana* begins its growth cycle with the onset of warm spring temperatures. A warm spring is also necessary to generate the energy requirement for monsoonal circulation; high temperatures draw moisture from the Gulf of Mexico and the Gulf of California, sending precipitation across the Southwest and Mexico (Douglas, 1993; Adams & Comrie, 1997). Winter temperature's influence on survival of *M. montana* is difficult to tease apart, however an explanation may lie in the late emergence of inflorescence. Because C_4 plants rely heavily on monsoon moisture, their growing season extends into the autumn months, with seed maturation taking place in early winter. This energetic allocation to seed maturation could be why we see survival dependent upon winter temperatures. It is possible that rapid onset of cold temperatures in early winter could be consequential for *M. montana*.

4.4 Limitations and future direction of study

Long-term data sets like the one used for this study are rare and therefore immensely valuable for ecological analysis. A data limitation in the construction of integral projection models for *F. arizonica* and *M. montana* is a lack of data on fecundity or reproductive output (such as number of flowering stalks, number of and viability of seeds per individual) for these species at these sites. Without directly linking reproductive output to individuals, we have no way of quantifying flowering stalks, seed output to size and environmental covariates. The integral projection model framework typically uses a *Pmatrix* (survival and growth) and an *Fmatrix* (fecundity) to project population dynamics over time. While we were able to project survival and growth responses to seasonal weather data, a lack of fecundity data prohibited us from developing a complete story. Acquiring fecundity data can be complicated in studies such as this for a number of reasons. Although number of inflorescence can be used as a proxy for reproductive output (Gibson, 2015), using this proxy requires a number of assumptions. For example, a seed must fully develop in order to be considered viable. If environmental conditions are not met, seeds may not reach a viable state prior to shatter (Thurber et al., 2011). Another problematic assumption when using number of inflorescence as a proxy for fecundity is the fate of seeds. Even if average number of seeds per inflorescence could be determined and all seeds are assumed viable, there is no guarantee one seed equals one recruit the following year (Rabinowitz, 1981). Future modelling efforts could benefit from utilizing recruitment data as an estimation of reproductive output, similarly to the efforts of Dalgleish, Koons, & Adler (2010).

5. Conclusion

Deciphering the influence of seasonal weather patterns on plant population vital rates is critical for predicting community response to climate change. In this study we compared perennial bunchgrass species of differing photosynthetic pathways in order to determine seasonal influence on population dynamics. Each species showed a positive correlation between temperature and precipitation within their respective growing seasons and increased survival and growth. Recent literature suggests varying responses in C_3 and C_4 species depending upon changes in environmental conditions. For example, Munson et al. (2011) suggest that arid conditions in the southwest have led to a decrease in relative abundance in C_3 species. When quantifying the effects of tree canopy closure, Laughlin et al. (2011) found that C_3 species increased in relative abundance, while C_4 species decreased in relative abundance. These two studies underscore contrasting pressures understory communities are faced with elevated temperatures and forest stand densities, both in response to anthropogenic pressures. A study by Obermeier et al. (2018) analyzed the effects of changing environmental conditions on temperature, C_3 grass species, and found that lower precipitation totals and higher precipitation variability reduced above-ground biomass. Findings also suggest that drier conditions along with higher air temperatures decrease above-ground biomass (Obermeier et al., 2018). Although it has been suggested that CO_2 fertilization, which occurs under elevated atmospheric CO_2 levels (Ainsworth & Long, 2005) favors C_3 growth, Obermeier et al. (2018) also discovered that CO_2 fertilization reduced above-ground biomass as a result of diminished evaporative cooling and heat stress. Connor and Hawkes (2018) found that C_4 native grasses in Texas were 45% smaller as well as decreased photosynthetic production, reduced stomatal conductance, and decreased water-use efficiency after 3 years of extreme dry conditions when compared to controls. These findings suggest that both C_3 and C_4 species may suffer under future climate change. However, a modelling effort by Cotton et al. (2016) predicts up to a 50% expansion of C_4 grasses into the northern Great Plains through 2100, accompanied by a relative decrease in C_3 species, indicating the potential for a northern migration of C_4 grasses. Together, the combined effects could result in dramatic community composition shifts as well as changes in ecosystem function.

Despite the seasonal influence of weather, the strongest predictor of both survival and growth for each species was size. As individuals are recruited into larger size classes, their probability of survival greatly increases (Mithen et al., 1984). Populations in both species were skewed towards a higher frequency of small individuals and high first-year mortality probability was associated with decreasing population growth rates of both species over time. Although this study showed increased survival and growth for individuals of larger size-classes, it has been suggested that age structure is the most important determinant for survival and growth for populations such as long-lived perennial bunchgrasses that exhibit type III survivorship curves (Lauenroth & Adler, 2008; Chu & Adler, 2014**.** Despite the importance of modelling based on age-structured populations, determining age can be difficult for long-lived species, particularly when time of recruitment is unknown. Because age of individuals was not known in our study, we used size as a proxy for age. The use of size as a stand-in for age can have confounding effects as parental ramets have been shown to experience a reduction in size up to 50% in order to sustain growth of juveniles (Williams et al., 1991). This resource sharing amongst ramets underscores that individuals of smaller size-classes are potentially older than larger individuals in years in which they are sustaining growth of younger ramets. However, Moloney (1988) suggests that vital rates vary among size-classes in perennial bunchgrasses of North Carolina, and highlights the importance of recruitment into larger size classes to increase survival probability. While structuring a population model by age may prove the most useful for these bunchgrass, in cases where age data are unknown, size structuring may be the next best approach.

Although fecundity data were not available for this study, recruitment data may prove more useful at estimating population growth rates over time due to uncertainty surrounding the fate of seeds for bunchgrass species. In order for a recruit to enter into a population, seed production, dispersal, germination, establishment, and growth must all take place (Coffin & Lauenroth, 1992). In any of these steps, a seed can experience mortality, and recruitment will not occur. Therefore, measuring number of recruits may be a more useful tool in the IPM process, and was utilized by Dalgleish et al. (2010). Although recruits face a high mortality probability (Moloney, 1988; Lauenroth & Adler, 2008), and it has also been suggested that a density dependent relationship with recruitment exists with perennial bunchgrasses (Moloney, 1988; Briske & Butler, 1989), using recruitment data to help estimate population growth rates may prove to be the best available option.

Given the importance of *F. arizonica* and *M. montana* in the understory communities of the Southwest, decreasing population growth rates are cause for concern. Although populations are decreasing over time, it is unclear when this trend began to take hold. Intense grazing, changing climate, and elevated forest stand densities have placed immense pressures on the understory community of northern Arizona. Without a clear understanding of historical population dynamics for *F. arizonica* and *M. montana*, it is difficult to do more than speculate as to the timing and cause of population reductions. While *F. arizonica* and *M. montana* remain dominant in the Arizona fescue-mountain muhly bunchgrass community, further research is required into population dynamics of other species in this community. By utilizing this IPM framework on a community scale, it may be possible to predict the fate of northern Arizona's understory given future climate and management scenarios.

Literature cited

Adams, D. K., & Comrie A. C. (1997). The North American Monsoon. Bulletin of the American Meteorological Society, 78, 2197-2213.

Adler, P. B., Ellner, S. P., & Levine, J. M. (2010). Coexistence of perennial plants: An embarrassment of niches. Ecology Letters, 13(8), 1019–1029. https://doi.org/10.1111/j.1461-0248.2010.01496.x

Adler, P. B., HilleRisLambers, J., Kyriakidis, P. C., Guan, Q., & Levine, J. M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proceedings of the National Academy of Sciences of the United States of America, 103(34), 12793–12798. https://doi.org/10.1073/pnas.0600599103

Allred, K. W. (2005). Perennial Festuca (Gramineae) of New Mexico. Desert Plants, 21(2), 3-12.

Albertson, F. W., & Tomanek, G. W. (1965). Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. Ecology, 46(5), 714–720. https://doi.org/10.2307/1935011

Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytologist, 165(2), 351-372.

Archer, S. (1984). The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. American Midland Naturalist, 111, 138-42.

Arnold, J. F. (1950). Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Forestry, 48, 118-126.

Arnold, J. F. (1955). Plant life-form classification and its use in evaluating range conditions and trend. Journal of Range Management, 8(4), 176-181.

Bakker, J.D. (2005). Long-term vegetation dynamics of ponderosa pine forests PhD Dissertation. Northern Arizona University, Flagstaff

Bakker, J. D., & Moore, M. M. (2007). Controls on vegetation structure in southwestern ponderosa pine forests, 1941 and 2004. Ecology, 88(9), 2305-2319.

Bakker, J. D., Moore, M. M., & Laughlin, D. C. (2008). The Hill plots: A rare long-term vegetation study historical research. Rocky Mountain Research Station Proceedings, 55, 148–157.

Bakker, J. D., Rudebusch, F., & Moore, M. M. (2010). Effects of long-term livestock grazing and habitat on understory vegetation. Western North American Naturalist, 70(3), 334-344.

Bataineh, A. L., Oswald, B. P., Bataineh, M. M., Williams, H. M., & Coble, D. W. (2006). Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. Forest Ecology and Management, 235, 283–294.

Briske, D. D., & Butler, J. L. (1989). Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium*: interclonal versus intraclonal interference. The Journal of Ecology, 963-974.

Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology, 14, 215–230.

Caswell, H. (1988). Approaching size and age in matrix population models. Size-structured populations. London: Springer.

Caswell, H. (2001). Matrix population models: construction, analysis, and interpretation. Sunderland, MA: Sinauer Associates, Inc.

Childs, D. Z., Rees, M., Rose, K. E., Grubb, P. J., & Ellner, S. P. (2003). Evolution of complex flowering strategies: An age- and size-structured integral projection model. Proceedings of the Royal Society B: Biological Sciences, 270, 1829–1838.

Chu, C., & Adler, P. B. (2014). When should plant population models include age structure? Ecology, 102, 531–543.

Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., ... & Jackson, S. T. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global change biology, 22(7), 2329-2352.

Clary, W. P. (1975). Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge (RM-158). Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Clary, W. P., & Kruse, W. H. (1979). Phenology and rate of height growth of some forbs in the southwestern ponderosa pine type (RM-376). Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Clements, F. E. (1905). Research methods in ecology. Lincoln, NE: The University Publishing Company.

Clements, F. E., Weaver, J. E., & Hanson, H. C. (1929). Plant Competition: an analysis of community functions (No. QK901 C625).

Coffin, D. P., & Lauenroth, W. K. (1992). Spatial variability in seed production of the perennial bunchgrass Bouteloua gracilis (Gramineae). American Journal of Botany, 79(3), 347-353.

Connor, E. W., & Hawkes, C. V. (2018). Effects of extreme changes in precipitation on the physiology of C4 grasses. Oecologia, *188*(2), 355–365. https://doi.org/10.1007/s00442-018-4212-5

Cooper, C. F. (1960). Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Society of America, 30,129–164.

Cotton, J. M., Mosier, T. M., Cerling, T. E., Ehleringer, J. R., Hoppe, K. A., & Still, C. J. (2016, December). Climate change drives a northward expansion of C4 grasses in North America by the end of the century. In AGU Fall Meeting Abstracts.

Covington, W. W., Fulé, P. Z., Moore, M. M., Hart, S. C., Kolb, T. E., Mast, J. N., … Sackett, S. S. (1997). Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry, 95, 23–29. https://doi.org/10.1093/jof/95.4.23

Cronquist, A., Holmgren, A. H., Holmgren, N. H., Reveal, J. L., & Holmgren, P. K. (1977). Intermountain flora: Vascular plants of the Intermountain West, U.S.A. Vol. 6. The Monocotyledons. New York, NY: Columbia University Press.

Currie, P. O. (1975). Grazing management of ponderosa pine-bunchgrass ranges of the central Rocky Mountains (RM-159). Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Dalgleish, H. J., Koons, D. N., & Adler, P. B. (2010). Can life-history traits predict the response of forb populations to changes in climate variability? Journal of Ecology, 98(1), 209–217. https://doi.org/10.1111/j.1365-2745.2009.01585.x

Dalgleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., & Adler, P. B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. Ecology, 92, 75–85.

Dittberner, P. L., & Olson, M. R. (1983). The plant information network (PIN) data base: Colorado, Montana, North Dakota, Utah, and Wyoming. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service.

Douglas, M. W., Maddox, R. A., & Howard, K. (1993). The Mexican monsoon. Climatology, 6, 1665–1677.

Dowling, H.E. (2015). Mapped permanent quadrats: a window through time into herbaceous plant demography. MS Thesis. Northern Arizona University, Flagstaff.

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size specific sensitivity: applying a new structured population model. Ecology, 81, 694-708.

Ehleringer, J. R., & Monson, R. K. (1993). Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics, 24, 411-439.

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. American Naturalist, 167, 410–428.

Eng, k., Wolock, D. M., & Dettinger, M. D. (2016). Sensitivity of intermittent streams to climate variations in the USA. River Research and Applications, 32, 885-895.

Fair, J., Lauenroth, W. K., & Coffin, D. P. (1999). Demography of Bouteloua gracilis in a mixed prairie: analysis of genets and individuals. Ecology, 87, 233–243.

Ffolliott, P. F., & Baker, M. B. Jr. (1999). Montane forests in the southwestern United States. Ecology and management of forests, woodlands, and shrublands in the dryland regions of the United States and Mexico: perspectives for the 21st century. Tucson, AZ: The University of Arizona.

Fletcher, R., & Robbie, W. A. (2004). Historic and current conditions of southwestern grasslands. Assessment of grassland ecosystem conditions in the southwestern United States (RMRS-GTR-135). Fort Collins, CO: General Technical Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Franco, M., & Silvertown, J. (2004). Comparative demography of plants based upon elasticities of vital rates. Ecology, 85, 531–538.

Gibson, D. J. (2015). Methods in comparative plant population ecology. Oxford University Press.

Harding, B. L., Wood, A. W., & Prairie, J. R. (2012). The implications of climate change scenario selection for future streamflow projection in the Upper Colorado River Basin. Hydrology and Earth System Sciences Discussions, 9, 847–894.

Harper, J. L. (1977). Population Biology of Plants. London: Academic Press.

Hill, R. R. (1920). Charting quadrats with a pantograph. Ecology, 1, 270–273.

Hill, R. R. (1917). Effects of grazing upon western yellow-pine reproduction in the national forests of Arizona and New Mexico (No. 580). US Department of Agriculture.

Hsiao, T. C. (1973). Plant responses to water stress. Annual review of plant physiology, 24(1), 519-570.

Humphrey, R. R. (1955). Forage production on Arizona ranges: IV. Coconino, Navajo, Apache counties: A study in range condition. Tucson, AZ: University of Arizona.

James, J. J., Sheley, R. L., Leger, E. A., Adler, P. B., Hardegree, S. P., Gornish, E. S., & Rinella, M. J. (2019). Increased soil temperature and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration. Applied Ecology, 56(12), 2609–2619. https://doi.org/10.1111/1365-2664.13508

Kartesz. J. T. (1988). A flora of Nevada. (Doctoral dissertation). University of Nevada, Reno.

Kearney, T. H., Peebles, R. H., Howell, J. T., & McClintock, E. (1960). Arizona flora. 2nd ed. Berkeley, CA: University of California Press.

Lauenroth, W. K., & Adler, P. B. (2008). Demography of perennial grassland plants: Survival, life expectancy and life span. Ecology, 96, 1023–1032.

Laughlin, D.C. (2009). Functional consequences of long-term vegetation dynamics. PhD Dissertation. Northern Arizona University, Flagstaff

Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Functional Ecology, 24(3), 493-501.

Laughlin, D. C., Moore, M. M., & Fulé, P. Z. (2011). A century of increasing pine density and associated shifts in understory plant strategies. Ecology, 92, 556–561.

Lefkovitch, L. P. (1965). The study of population growth in organisms grouped by stages. Biometrics, 21, 1-18.

Lowe, P. O. (1975). Potential wildlife benefits of fire in ponderosa pine forests. (Master Thesis) University of Arizona, Tucson, AZ.

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., … Mcmahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. Methods in Ecology and Evolution, 5, 99–110.

Metcalf, C. J. E., McMahon, S. M., Salguero-Gómez, R., & Jongejans, E. (2013). IPMpack: An R package for integral projection models. Methods in Ecology and Evolution, 4, 195–200.

Mithen, R., Harper, J. L., & Weiner, J. (1984). Growth and mortality of individual plants as a function of "available area." Oecologia, 62(1), 57-60.

Moloney, K. A. (1988). Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. Ecology, 69(5), 1588-1598.

Moore, M. M., Covington, W. W., and P. Z. Fule. (1999) Reference Conditions and Ecological Restoration : A Southwestern Ponderosa Pine Perspective. Ecological Society of America, 9, 1266–1277.

Moore, M. M., Huffman, D. W., Fulé, P. Z., Covington, W. W., & Crouse, J. E. (2004). Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science, 50(2), 162-176.

Mote, P. W., Li, S., Lettenmaier, D. P., Xiao, M., & Engel, R. (2018). Dramatic declines in snowpack in the western US. Npj Climate and Atmospheric Science, 1(1). https://doi.org/10.1038/s41612-018-0012-1

Mulroy, T. W., Rundel, P. W. (1977) Annual plants: adaptations to desert environments. BioScience, 27, 109-14.

Mutch, R. W. (1970). Wildland fires and ecosystems a hypothesis. Ecology, 51, 046-1051.

Munson, S. M., Belnap, J., & Okin, G. S. (2011). Responses of wind erosion to climate-induced vegetation changes on the Colorado Plateau. Proceedings of the National Academy of Sciences of the United States of America, 108, 3854–3859.

Obermeier, W. A., Lehnert, L. W., Ivanov, M. A., Luterbacher, J., & Bendix, J. (2018). Reduced Summer Aboveground Productivity in Temperate C3 Grasslands Under Future Climate Regimes. Earth's Future, 6(5), 716–729. https://doi.org/10.1029/2018EF000833

Parsons, D.J., & DeBenedetti S. H. (1979). Impact of fire suppression on a mixed-conifer forest. Forest Ecology & Management, 2, 21–33.

Pearson, G. A. (1942). Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the southwest. Ecological Monographs 12, 315-338.

Pearson, H. A. (1965). Studies of forage digestibility under ponderosa pine stands. Proceedings: Society of American Foresters meeting, 1964 September 27 - October 1, Denver, CO. Washington, DC: Society of American Foresters.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global ecology and biogeography, 12, 361-371.

Peltier, D. M. P., Fell, M., & Ogle, K. (2016). Legacy effects of drought in the southwestern United States: A multi-species synthesis. Ecological Monographs, 86(3), 312–326. https://doi.org/10.1002/ecm.1219

Pinder III, J.E., Wiener J. G., & Smith, M. H. (1978). The Weibull Distribution: A new method of summarizing survivorship data. The Ecological Society of America, 59, 175-179.

Rabinowitz, D. (1981). Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. Oikos, 191-195.

Rees, M., Childs, D. Z., & Ellner, S. P. (2014). Building integral projection models: A user's guide. Animal Ecology, 83, 528–545.

Rietveld, W. J. (1975). Phytotoxic grass residues reduce germination and initial root growth of ponderosa pine (Vol. 153). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., … Naik, N. (2007). Model Projections of an Imminent Transition to a more Arid climate in Southernwestern North America. Science, 316, 1181–1184.

Sheppard, P. R., Comrie, A. C., Packin, G. D., Angersbach, K., & Hughes, M. K. (2002). Climate Research 21, 219–238.

Shreve. F., & Wiggins, I.L. (1964). Vegetation and Flora of the Sonoran Desert. Palo Alto, CA: Stanford University Press.

Singleton, M. P., Thode, A. E., Sánchez Meador, A. J., & Iniguez, J. M. (2019). Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. Forest Ecology and Management, 433(September 2018), 709–719. https://doi.org/10.1016/j.foreco.2018.11.039

Souther, S., Loeser, M., Crews, T. E., & Sisk, T. (2020). Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland. Ecological Applications, 30(3), 1–14. https://doi.org/10.1002/eap.2048

Strahan, R.T. (2013). A functional trait perspective on demography, community assembly, and response to long-term grazing. PhD Dissertation. Northern Arizona University, Flagstaff.

Strahan, R. T., Laughlin, D. C., Bakker, J. D., & Moore, M. M. (2015). Long-term protection from heavy livestock grazing affects ponderosa pine understory composition and functional traits. Rangeland Ecology & Management, 68(3), 257-265.

Strahan, R. T., Sánchez Meador, A. J., Huffman, D. W., & Laughlin, D. C. (2016). Shifts in community-level traits and functional diversity in a mixed conifer forest: a legacy of land-use change. Journal of Applied Ecology, 53(6), 1755–1765. https://doi.org/10.1111/1365-2664.12737

Swetnam, T. W., & Baisan, C. H. (1996). Historical fire regime patterns in the southwestern United States since AD 1700. Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium, Los Alamos, New Mexico.

Thurber, C. S., Hepler, P. K., & Caicedo, A. L. (2011). Timing is everything: early degradation of abscission layer is associated with increased seed shattering in US weedy rice. BMC Plant Biology, 11(1), 14.

Tuljapurkar, S., and Caswell, H. (1997). Structured-Population Models in Marine, Terrestrial, and Fresh- water Systems, New York: Chapman & Hall.

US Climate Data (2020). Retrieved from https://www.usclimatedata.com/climate/flagstaff/arizona/united-states/usaz0068

West, N. E., Rea, K. H. & Harniss, R. O. (1979). Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology, 60, 376–388.

Wi, S., Dominguez, F., Durcik, M., Valdes, J., Diaz, H. F., & Castro, C. L. (2012). Climate change projection of snowfall in the Colorado River Basin using dynamical downscaling. Water Resources Research, 48(5) 1-17.

Williams, D. G., & Briske, D. D. (1991). Size and ecological significance of the physiological individual in the bunchgrass Schizachyrium scoparium. Oikos, 41-47.

Williams, A. P., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., … Livneh, B. (2020). Large contribution from anthropogenic warming to an emerging North American megadrought. Science, 368(6488), 314–318. https://doi.org/10.1126/science.aaz9600

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

CHAPTER 3:

CONCLUSION AND MANAGEMENT IMPLICATIONS

Anthropogenic pressures have had tremendous effects on ecological communities around the globe, and can no-longer go unacknowledged. Our ability to shape the environment has been recognized as a defining force of nature, delineating our current geologic era as the Anthropocene (Crutzen, 2006). In the coming decades, the development of climate mitigation and adaptation strategies will be pertinent to the survival of our species as well as countless others. In no discipline does the need for adaptive capacity carry more weight than in the management of our natural resources. A collaborative effort between empirical researchers and management agencies is necessary for promoting ecosystems that are resilient to environmental change. This includes the implementation of current literature in the development of management strategies as well as the contextualization of research in a way that can be applied in conservation, restoration, or management. The motivation behind this research is to serve as a foundation for understanding population dynamics of the understory community in the ponderosa pine forests of northern Arizona. This study applies advancements in ecological population modelling in order to predict the fate of the Arizona fescue-mountain muhly bunchgrass community. Because Arizona fescue and mountain muhly are dominant species of differing photosynthetic pathways, there are important management implications that can be drawn from this research.

The outcome that is perhaps the most pertinent from a management and conservation perspective is that both species are showing decreasing population growth rates over time. The importance of size on both survival and growth of Arizona fescue and mountain muhly may also have important management implications. Both species demonstrated a mean life expectancy of

~ 1 year, indicating a high first year mortality probability. This suggests that even if recruitment is high in a particular year, there still exists a low probability that recruits will survive until the following year. High first year mortality is contrasted by exceedingly long lifespans of large individuals. In many cases, this 17-year study failed to capture the longevity of these large graminoids. The ability of these species to survive for decades is strongly dependent upon their recruitment to larger size-classes. With a first-year survival probability of 0.17 and 0.07 for *F. arizonica* and *M. montana*, respectively, it is likely that high seed output is important for population persistence. Although fecundity data was not available for this study, ongoing research is attempting to determine reproductive output potential of these species.

In our study, we determined a seasonal precipitation effect on recruitment of *F. arizonica* and *M. montana* (figure 3.1). *F. arizonica* appears to respond with higher recruitment in years with higher early spring precipitation. *M. montana* seems to respond with higher recruitment one year following high monsoon precipitation, suggesting that a one-year lag relationship may exist.

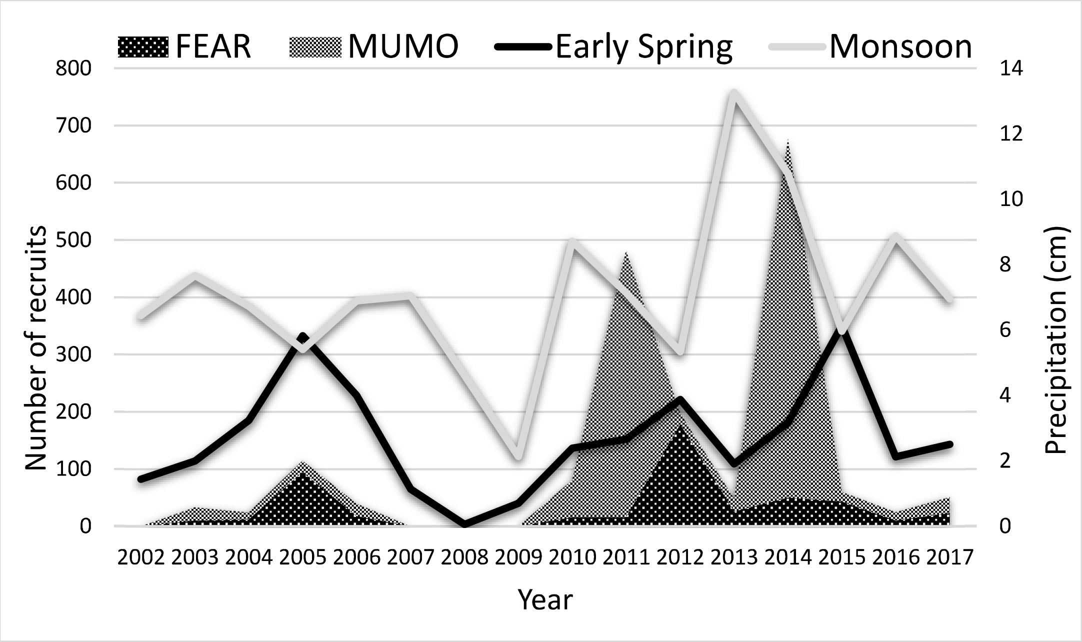


Figure 3.1| *F. arizonica* (FEAR) & *M. montana* (MUMO) recruitment and precipitation

The discovery of size-dependent survival and high first-year mortality probabilities are important for management of these foundational species. For example, given the decrease in population growth rates of both species, it would be prudent to execute a monitoring protocol that evaluates the growth of small individuals as they enter into higher size-classes. Because large individuals are likely to persist for extended periods of time (Moloney, 1988), it is unlikely that the short-term structure of these communities is changing at an alarming rate. However, the fate of the understory remains unknown, given the lack of data pertaining to max life expectancy of these species. If populations continue to shrink, there will eventually be a time in which large individuals die off, and are not replaced due to low survival probability of small individuals. Although future research is being carried out on the reproductive output of these species, a low first-year survival probability points to the importance of high seed output. This population parameter must be considered from a management perspective in order to facilitate the persistent of these dominant graminoids. While it is unreasonable to advocate for the seeding of these individuals on a landscape scale, post-disturbance seeding in restoration initiatives may help improve long-term population resilience.

The differing effects of season weather patterns on population dynamics of each species is an important discovery; however, determining a way to apply this knowledge is difficult. To review, the influence of seasonal precipitation and temperature differed according to growing season. That is, Arizona fescue (C_3) grows in the cool-season, from early spring to early summer, and mountain muhly (C_4) grows in the warm-season, from late spring to fall. The importance of spring precipitation for Arizona fescue and monsoon precipitation for mountain muhly may be an important management consideration under future climate scenarios. For example, if seeding and monitoring efforts were to take place, understanding the temporal effect of precipitation on species of different growing seasons (resulting from different photosynthetic pathways) would be essential. Although there remain many unknowns surrounding future climate scenarios, understanding how a population responds to temporal shifts in precipitation could help develop management strategies.

Although this study focused deeply on ecological theory to build data-driven, structured population models, the motivation was thoroughly rooted in application. Expanding our knowledge of plant population dynamics will better inform our decisions about how to manage ecological communities. Although the future is clouded in uncertainty, collaborative research and monitoring efforts can drive forward empirical and applied fields. It is through these joint efforts that scientific advancements emerge, and now more than ever, progress must be made.

LITERATURE CITED

Adams, D. K., & Comrie A. C. (1997). The North American Monsoon. Bulletin of the American Meteorological Society, 78, 2197-2213.

Allred, K. W. (2005). Perennial Festuca (Gramineae) of New Mexico. Desert Plants, 21(2), 3-12.

Andariese, S. W. (1982). Time-response graphs for understory production following fall prescribed burning in Arizona ponderosa pine on basalt soils (Doctoral dissertation). Northern Arizona University, Flagstaff, AZ.

Archer, S. (1984). The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. American Midland Naturalist, 111, 138-42.

Arnold, J. F. (1950). Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Forestry, 48, 118-126.

Bakker, J. D., & Moore, M. M. (2007). Controls on vegetation structure in Southwestern ponderosa pine forests, 1941 and 2004. Ecology, 88(9), 2305–2319.

Bakker, J. D., Moore, M. M., & Laughlin, D. C. (2008). The Hill plots: A rare long-term vegetation study historical research. Rocky Mountain Research Station Proceedings, 55, 148–157.

Bataineh, A. L., Oswald, B. P., Bataineh, M. M., Williams, H. M., & Coble, D. W. (2006). Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire. Forest Ecology and Management, 235, 283–294.

Bernard, S. R., Brown, S. R., & Brown, K. F. (1977). Distribution of Mammals, Reptiles, and Amphibians by BLM-physiographic Regions and AW Kuchler's Associations for the Eleven Western States (Vol. 301). Department of the Interior, Bureau of Land Management.

Berndt, H. W., & Gibbons, R. D. (1958). Root distribution of some native trees and understory plants growing on three sites within ponderosa pine watersheds in Colorado. Rocky Mountain Forest and Range Experiment Station.

Bond, W. J., & Keeley, J. E. (2005). Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in ecology & evolution, 20(7), 387-394.

Brown, J. H., Valone, T. J., & Curtin, C. G. (1997). Reorganization of an arid ecosystem in response to recent. PNAS, 94, 9729–9733.

Burkle, L. A., Myers, J. A., & Belote, R. T. (2015). Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere, 6(10), 1-14.

Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology, 14, 215–230.

Caswell, H. (1988). Approaching size and age in matrix population models. Size-structured populations. London: Springer.

Caswell, H. (2001). Matrix population models: construction, analysis, and interpretation. Sunderland, MA: Sinauer Associates, Inc.

Cavender-Bares, J., & Reich, P. B. (2012). Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. Ecology, 93(sp8), S52-S69.

Cayan, D. R., Das, T., Pierce, D. W., Barnett, T. P., Tyree, M., & Gershunova, A. (2010). Future dryness in the Southwest US and the hydrology of the early 21st century drought. Proceedings of the National Academy of Sciences of the United States of America, 107(50), 21271–21276.

Childs, D. Z., Rees, M., Rose, K. E., Grubb, P. J., & Ellner, S. P. (2003). Evolution of complex flowering strategies: An age- and size-structured integral projection model. Proceedings of the Royal Society B: Biological Sciences, 270, 1829–1838.

Chu, C., & Adler, P. B. (2014). When should plant population models include age structure? Ecology, 102, 531–543.

Clary, W. P. (1975). Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge (RM-158). Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Clary, W. P., & Kruse, W. H. (1979). Phenology and rate of height growth of some forbs in the southwestern ponderosa pine type (RM-376). Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Clements, F. E. (1905). Research methods in ecology. Lincoln, NE: The University Publishing Company.

Clements, F. E. (1936). Nature and structure of the climax. Ecology, 24, 255-284.

Cook, B. I., Ault, T. R., & Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advancements, 1, 1–8.

Cooper, C. F. (1960). Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Society of America, 30,129–164.

Covington, W. W., Fulé, P. Z., Moore, M. M., Hart, S. C., Kolb, T. E., Mast, J. N., … Sackett, S. S. (1997). Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry, 95, 23–29. https://doi.org/10.1093/jof/95.4.23

Cronquist, A., Holmgren, A. H., Holmgren, N. H., Reveal, J. L., & Holmgren, P. K. (1977). Intermountain flora: Vascular plants of the Intermountain West, U.S.A. Vol. 6. The Monocotyledons. New York, NY: Columbia University Press.

Crutzen, P. J. (2006). The “anthropocene”. In Earth system science in the anthropocene (pp. 13-18). Springer, Berlin, Heidelberg.

Currie, P. O. (1975). Grazing management of ponderosa pine-bunchgrass ranges of the central Rocky Mountains (RM-159). Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Dalgleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., & Adler, P. B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. Ecology, 92, 75–85.

Darrow, R. A. (1944). Arizona Range Resources and Their Utilization I. Cochise County. College of Agriculture, University of Arizona, Tucson, AZ.

Dayton, W. A., Lommasson, T., & Park, B. C. (1937). Range plant handbook. US Government Printing Office.

Dessler, A. E. (2010). A determination of the cloud feedback from climate variations over the past decade. New Series, 330, 1523-1527.

Dittberner, P. L., & Olson, M. R. (1983). The plant information network (PIN) data base: Colorado, Montana, North Dakota, Utah, and Wyoming. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service.

Dorn, R. D. (1988). Vascular plants of Wyoming. Mountain West Publishing: Cheyenne, WY.

Douglas, M. W., Maddox, R. A., & Howard, K. (1993). The Mexican monsoon. Climatology, 6, 1665–1677.

Dufresne, J. L., Foujols, M. A., Denvil, S., Caubel, A., Marti, O., Aumont, O., … Vuichard, N. (2013). Climate change projections using the IPSL-CM5 Earth System Model: From CMIP3 to CMIP5. In Climate Dynamics, 40, 2123-2165.

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size specific sensitivity: applying a new structured population model. Ecology, 81, 694-708.

Edwards, G. E., & Ku, M. S. B. (1987). Biochemistry of C3–C4 intermediates. Stumpf PK. The biochemistry of plants, Vol. 10 (pp. 275-325). Academic Press: New York, NY.

Ehleringer, J., & Björkman, O. (1977). Quantum Yields for CO(2) Uptake in C(3) and C(4) Plants: Dependence on Temperature, CO(2), and O(2) Concentration. Plant Physiology, 59(1), 86–90.

Ehleringer, J. R. (1978). Implications of quantum yield differences on the distributions of C 3 and C 4 grasses. Oecologia, 31(3), 255-267.

Ehleringer, J., & Pearcy R. W. (1983). Variation in quantum yield for CO_2 uptake among C_3 and C_4 plants. Plant Phisiology, 73, 555-559.

Ehleringer, J. R., Sage, R. F., Flanagan, L. B., & Pearcy, R. W. (1991). Climate change and the evolution of C4 photosynthesis. Trends in ecology & evolution, 6(3), 95-99.

Ehleringer, J. R., & Monson, R. K. (1993). Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics, 24, 411-439.

Ehleringer, J. R., & Cerling, T. E. (2002). C3 and C4 photosynthesis. Encyclopedia of Global Environmental Change. The Earth System: Biological and Ecological Dimensions of Global Environmental Change, 2, 186–190.

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. American Naturalist, 167, 410–428.

Eng, k., Wolock, D. M., & Dettinger, M. D. (2016). Sensitivity of intermittent streams to climate variations in the USA. River Research and Applications, 32, 885-895.

Eyre, F. H. (1980). Forest cover types. Society of American Foresters: Washington, DC.

Fair, J., Lauenroth, W. K., & Coffin, D. P. (1999). Demography of Bouteloua gracilis in a mixed prairie: analysis of genets and individuals. Ecology, 87, 233–243.

Ffolliott, P. F., & Baker, M. B. Jr. (1999). Montane forests in the southwestern United States. Ecology and management of forests, woodlands, and shrublands in the dryland regions of the United States and Mexico: perspectives for the 21st century. Tucson, AZ: The University of Arizona.

Fletcher, R., & Robbie, W. A. (2004). Historic and current conditions of southwestern grasslands. Assessment of grassland ecosystem conditions in the southwestern United States (RMRS-GTR-135). Fort Collins, CO: General Technical Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Franco, M., & Silvertown, J. (2004). Comparative demography of plants based upon elasticities of vital rates. Ecology, 85, 531–538.

Fulé, P. Z., W. W. Covington, and M. M. Moore. (1997). Determining reference conditions for ecosystem management of southwestern pondersosa pine forests. Ecological Applications, 7, 895-908.

Garrison, G. A., Bjugstad, A. J., Duncan, D. A., Lewis, M. E. & Smith, D. R. (1977). Vegetation and environmental features of forest and range ecosystems (No. 475). Department of Agriculture, Forest Service.

Gary, H. L., & Currie, P. O. (1977). The Front Range pine type: a 40-year photographic record of plant recovery on an abused watershed (Vol. 46). Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Gay, C. W., & Dwyer, D. D. (1965). New Mexico range plants.

Grinnell, J. (1917). The niche-relationships of the California Thrasher. The Auk, 34, 427-433.

Grinnell, J. (1924). Geography and evolution. Ecology, 5, 225-229.

Hanks, J. P. (1983). A habitat type classification system for ponderosa pine forests of northern Arizona (Vol. 97). Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.

Harding, B. L., Wood, A. W., & Prairie, J. R. (2012). The implications of climate change scenario selection for future streamflow projection in the Upper Colorado River Basin. Hydrology and Earth System Sciences Discussions, 9, 847–894.

Harper, J. L. (1977). Population Biology of Plants. London: Academic Press.

Harper, J. L. (1980). Plant demography and ecological theory. Oikos, 34, 244-253.

Harrington, H. D. (1964). Manual of the Plants of Colorado: For the Identification of the Ferns and Flowering Plants of the State. Sage Books.

Hassell, W., Carlson, J., & Doughty, J. (1983, November). Grasses for revegetation of mountain sites. In in Managing intermountain rangelands–improvement of range and wildlife habitats:

proceedings of symposia; 1981 September 15–17; Twin Falls, Idaho; 1982 June 22–24; Elko, Nevada (pp. 95-101). Ogden, Utah, General Technical Report INT-157: United States Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Hatch, M. D., Agostino, A., & Burnell, J. N. (1988). Photosynthesis in phosphoenolpyruvate carboxykinase-type C 4 plants: Activity and role of mitochondria in bundle sheath cells. Archives of Biochemistry and Biophysics, 261(2), 357–367.

Herzman, C. W., Hyde, R. M., & Fonte, C. S. (1988). Handbook of Colorado native grasses. Bulletin (Colorado State University. Cooperative Extension Service); 450A.

Hill, R. R. (1920). Charting quadrats with a pantograph. Ecology, 1, 270–273.

Hitchcock, A. S., & Chase, A. (1951). Manual of the grasses of the United States (Vol. 2). US Department of Agriculture.

Hitchcock, C. L., & Cronquist, A. (1973). Flora of the Pacific Northwest. University of Washington Press: Seattle, WA.

Humphrey, R. R. (1955). Forage production on Arizona ranges: IV. Coconino, Navajo, Apache counties: A study in range condition. Tucson, AZ: University of Arizona.

Humphrey, R. R. (1970). Arizona range grasses: Their description, forage value and management. The University of Arizona Press: Tucson, AZ.

IPCC, 2014: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Jepson, W. L., & Hickman, J. C. (1993). The Jepson manual: higher plants of California. University of California Press: Berkeley, CA.

Jongejans, E., de Kroon, H., Tuljapurkar, S., & Shea, K. (2010). Plant populations track rather than buffer climate fluctuations. Ecology Letters, 13(6), 736–743.

Kartesz. J. T. (1988). A flora of Nevada. (Doctoral dissertation). University of Nevada, Reno.

Kearney, T. H., Peebles, R. H., Howell, J. T., & McClintock, E. (1960). Arizona flora. 2nd ed. Berkeley, CA: University of California Press.

Larson, M. M., & Schubert, G. H. (1969). Root competition between ponderosa pine seedlings and grass (Vol. 54). Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.

Lauenroth, W. K., & Adler, P. B. (2008). Demography of perennial grassland plants: Survival, life expectancy and life span. Ecology, 96, 1023–1032.

Laughlin, D. C., & Moore, M. M. (2008). Forest and range research on the "Wild Bill Plots" (1927-2007) (RMRS-P-53CD). Fort Collins, CO: USDA, Forest Service, Rocky Mountain Research Station.

Laughlin, D. C., Moore, M. M., & Fulé, P. Z. (2011). A century of increasing pine density and associated shifts in understory plant strategies. Ecology, 92, 556–561.

Lefkovitch, L. P. (1965). The study of population growth in organisms grouped by stages. Biometrics, 21, 1-18.

Lowe, P. O. (1975). Potential wildlife benefits of fire in ponderosa pine forests. (Master Thesis) University of Arizona, Tucson, AZ.

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. Evolution, 17, 373-387.

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., … Mcmahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. Methods in Ecology and Evolution, 5, 99–110.

Metcalf, C. J. E., McMahon, S. M., Salguero-Gómez, R., & Jongejans, E. (2013). IPMpack: An R package for integral projection models. Methods in Ecology and Evolution, 4, 195–200.

Molina, R. J., Trappe, J. M., & Strickler, G. S. (1978). Mycorrhizal fungi associated with Festuca in the western United States and Canada. Canadian Journal of Botany, 56(14), 1691-1695.

Moloney, K. A. (1986). A generalized algorithm for determining category size. Oecologia, 69, 176-180.

Moore, M. M., Covington, W. W., and P. Z. Fule. (1999) Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Society of America, 9, 1266–1277.

Mulroy, T. W., Rundel, P. W. (1977) Annual plants: adaptations to desert environments. BioScience, 27, 109-14.

Mutch, R. W. (1970). Wildland fires and ecosystems a hypothesis. Ecology, 51, 046-1051.

Munson, S. M., Belnap, J., & Okin, G. S. (2011). Responses of wind erosion to climate-induced vegetation changes on the Colorado Plateau. Proceedings of the National Academy of Sciences of the United States of America, 108, 3854–3859.

Münz, P. A., & Keck, D. D. (1973). A California flora and supplement. University of California Press: Berkeley, CA.

Myers, J. A., Chase, J. M., Crandall, R. M., & Jiménez, I. (2015). Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. Journal of Ecology, 103(5), 1291-1299.

Naumburg, E., DeWald, L. E., & Kolb, T. E. (2001). Shade responses of five grasses native to southwestern US Pinus ponderosa forests. Canadian Journal of Botany, 79(9), 1001-1009.

Odum, E. P. (1969). The strategy of ecosystem development. Science, 164, 262-270.

Osmond, C. B., Winter, K., & Ziegler, H. (1982). Functional significance of different pathways of CO 2 fixation in photosynthesis. In Physiological plant ecology II (pp. 479-547). Springer, Berlin, Heidelberg.

Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., … Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. Nature, 466(7305), 482–485. https://doi.org/10.1038/nature09210

Parsons, D.J., & DeBenedetti S. H. (1979). Impact of fire suppression on a mixed-conifer forest. Forest Ecology & Management, 2, 21–33.

Pearcy, R. W., & Ehleringer, J. (1984). Comparative ecophysiology of C3 and C4 plants. Plant, Cell & Environment, 7(1), 1-13.

Pearson, H. A. (1965). Studies of forage digestibility under ponderosa pine stands. Proceedings: Society of American Foresters meeting, 1964 September 27 - October 1, Denver, CO. Washington, DC: Society of American Foresters.

Pearson, H. A. (1967). Phenology of Arizona fescue and mountain muhly in the northern Arizona ponderosa pine type (Vol. 89). Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global ecology and biogeography, 12, 361-371.

Pinder III, J.E., Wiener J. G., & Smith, M. H. (1978). The Weibull Distribution: A new method of summarizing survivorship data. The Ecological Society of America, 59, 175-179.

Potter, D. U., Gosz, J. R., Molles, M. C., & Scuderi, L. A. (1998). Lightning, precipitation and vegetation at landscape scale. Landscape Ecology, 13(4), 203-214.

Quade, J., Cerling, T. E., & Bowman, J. R. (1989). Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature, 342(6246), 163-166.

Rees, M., Childs, D. Z., & Ellner, S. P. (2014). Building integral projection models: A user's guide. Animal Ecology, 83, 528–545.

Reichler, T., & Kim, J. (2008). How well do coupled models simulate today's climate? American Meteorological Society, 819, 303-311.

Rietveld, W. J. (1975). Phytotoxic grass residues reduce germination and initial root growth of ponderosa pine (Vol. 153). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., … Naik, N. (2007). Model Projections of an Imminent Transition to a more Arid climate in Southernwestern North America. Science, 316, 1181–1184.

Shackley, S., & Wynne, B. (1996). Representing uncertainty in global climate change science and policy: boundary-ordering. Science, Technology, & Human Values, 21, 275-302.

Sharkey, T. D. (1985). O2-insensitive photosynthesis in C3 plants. Its occurrence and a possible explanation. Plant Physiology, 78, 71-75.

Sheppard, P. R., Comrie, A. C., Packin, G. D., Angersbach, K., & Hughes, M. K. (2002). Climate Research 21, 219–238.

Shreve. F., & Wiggins, I.L. (1964). Vegetation and Flora of the Sonoran Desert. Palo Alto, CA: Stanford University Press.

Smith, D. R. (1967). Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado (No. 1371). US Department of Agriculture, Forest Service.

Stowe, L. G., & Teeri, J. A. (1978). The geographic distribution of C4 species of the Dicotyledonae in relation to climate. The American Naturalist, 112(985), 609-623.

Swetnam, T. W., & Baisan, C. H. (1996). Historical fire regime patterns in the southwestern United States since AD 1700. Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium, Los Alamos, New Mexico.

Tapia, L. B., Ffolliott, P. F., & Guertin, D. P. (1990). Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. Rangeland Ecology & Management/Journal of Range Management Archives, 43(1), 25-28.

Taylor, C. (1983). Village and farmstead: a history of rural settlement in England. G. Philip.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America, 101(30), 10854–10861.

Tuljapurkar, S., and Caswell, H. (1997). Structured-Population Models in Marine, Terrestrial, and Fresh- water Systems, New York: Chapman & Hall.

Van Dyne, G. M. (1958). Ranges and range plants. Montana State College.

Vandermeer. J. H. (1972). Niche theory. Annual Review of Ecology and Systematics, 3, 107-132.

Vose, J. M., & White, A. S. (1987). Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. Canadian Journal of Botany, 65(11), 2280-2290.

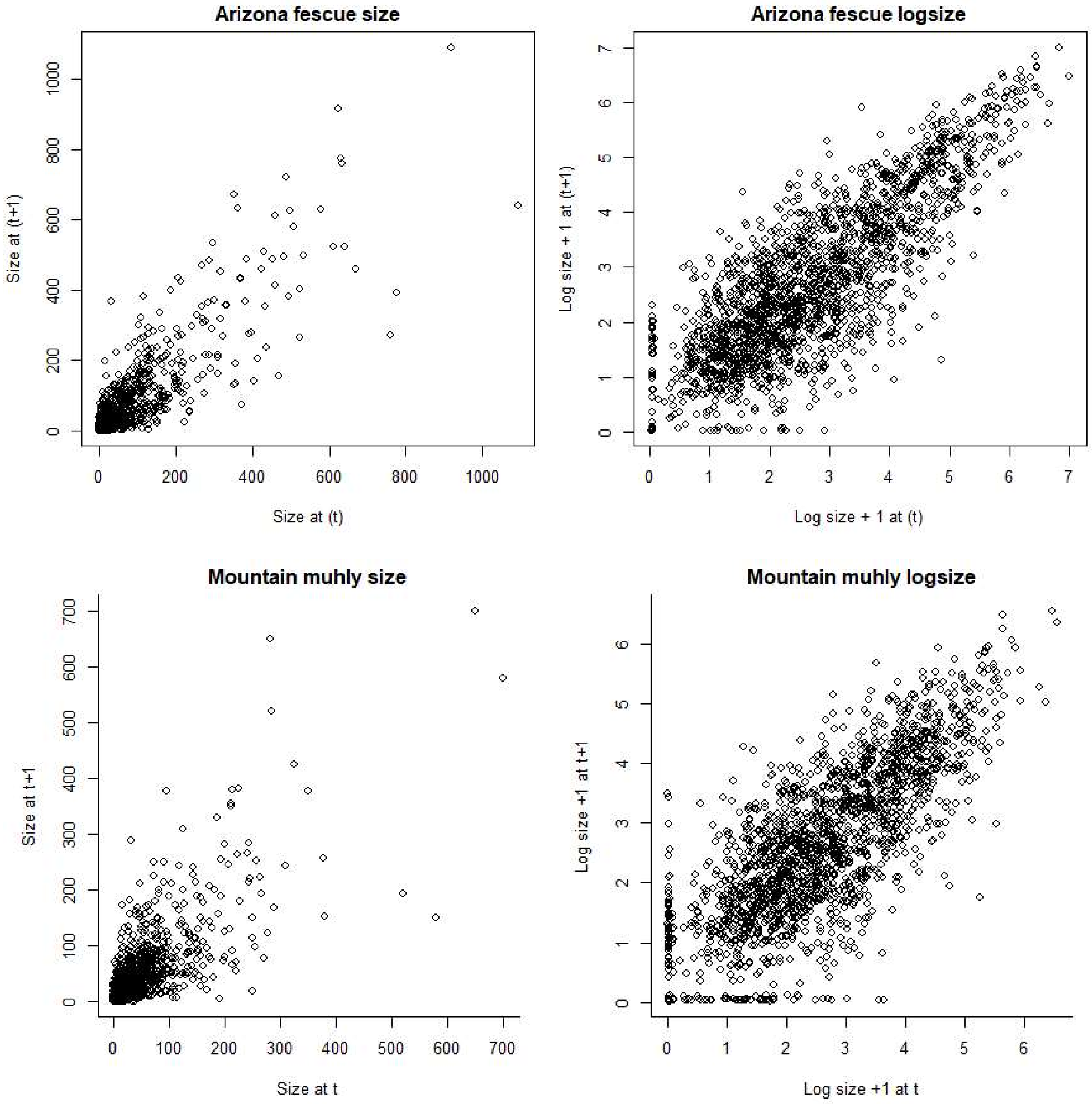
West, N. E., Rea, K. H. & Harniss, R. O. (1979). Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology, 60, 376–388.

Wi, S., Dominguez, F., Durcik, M., Valdes, J., Diaz, H. F., & Castro, C. L. (2012). Climate change projection of snowfall in the Colorado River Basin using dynamical downscaling. Water Resources Research, 48(5) 1-17.

Williams, A. P., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., … Livneh, B. (2020). Large contribution from anthropogenic warming to an emerging North American megadrought. Science, 368(6488), 314–318. https://doi.org/10.1126/science.aaz9600

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

APPENDICES



Appendix A | *F. arizonica* & *M. montana* log-transformations