Plant Responses to Environmental Heterogeneity in Great Basin Sagebrush Steppe

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Ecology, Evolution, and Conservation Biology

By
Sarah C. Barga

Dr. Elizabeth A. Leger/Dissertation Advisor

August, 2017
THE GRADUATE SCHOOL

We recommend that the dissertation prepared under our supervision by

SARAH C. BARGA

Entitled

Plant Responses To Environmental Heterogeneity In Great Basin Sagebrush Steppe

be accepted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Elizabeth Leger, Ph.D., Advisor

Marjorie Matocq, Ph.D., Committee Member

Guy Hoelzer, Ph.D., Committee Member

Lee Turner, Ph.D., Committee Member

Scott Mensing, Ph.D., Graduate School Representative

David W. Zeh, Ph. D., Dean, Graduate School

August, 2017
ABSTRACT

Plant populations experience both spatial and temporal environmental heterogeneity, and their strategies for coping with environmental heterogeneity are shaped by their inability to move in response to unfavorable conditions. In addition, human induced land-use change, including changes in grazing regimes and shorter fire-return intervals, has become increasingly common as a source of environmental heterogeneity experienced by plant populations. This research focuses on how native Great Basin plants respond to environmental heterogeneity, studying three stages of plant life-histories: seed germination, seed banks, and mature plants. My dissertation sought to: 1) identify relationships between climate variability and population-level variation in germination strategies of arid land forbs, 2) use occurrence records from herbaria to compare the climate niches for a group of arid land forbs, and 3) investigate the relationship between disturbance history and seed bank dynamics in sagebrush steppe communities.

The second chapter examines the similarities and differences between the climate niches and the geographic distributions of a set of co-occurring understory forbs found in sagebrush steppe systems. We used distribution models of the potential habitat for our species to estimate the range size, niche breadth, and geographic overlaps between our species. Next, we used model results to identify climate variables most predictive of the distributions of the individual species. Lastly, we compared the mean and variability for precipitation and temperature across known occurrence locations for each species to assess similarities and differences in climate characteristics where these species grow. We found that species varied in their predicted area of occupancy, niche breadth, and the climate characteristics most predictive of their suitable habitat. Only two of the ten species shared a comparable climate
niche. This work demonstrated that herbarium records can be used to estimate climate preferences and potential habitat for understudied species.

The third chapter investigates seed bank dynamics in a Great Basin sagebrush steppe system, comparing sites that differ in their disturbance history. We asked whether shrub cover, ground cover, climate, or disturbance history (fire and grazing) were predictive of the seed densities in the soil, the diversity of native and introduced species, the presence of rare species, and similarity between the above and below-ground species composition. We found that common measures of fire history and grazing use may be overly coarse for predicting the effects of disturbance on seed bank dynamics. We also found that shrub cover was highly predictive of the seed bank dynamics in this system. Shrub cover of early seral shrub species was predictive of patterns consistent with moderate disturbance or recovery from disturbance within the above and below-ground plant community, while increasing cover of later seral species, such as *Artemisia tridentata*, produced patterns indicating a longer time since disturbance.

The fourth chapter asks how mean climate and climate variation at individual sites and across a species’ range affects the specialist-generalist spectrum of germination strategies exhibited by ten arid land forbs. We investigated these relationships using climate data for the western United States, occurrence records from herbaria, and germination trials with field-collected seeds. We found that nine out of ten species exhibited population-level variation in germination, and that generalist strategies were associated with higher spatial variation in actual evapotranspiration at a local scale and higher variation in available water in the spring and annual precipitation at a range-wide scale.
ACKNOWLEDGEMENTS

I would like to thank my advisor, Beth Leger, for her dedication and advice. She made herself available to me when I needed her, provided constructive criticism that improved our work, and allowed me to branch our research into areas that were outside of my comfort zone. I am grateful for this friendship and partnership. I would like to thank Tom Dilts for his guidance and advice navigating the world of GIS. I truly benefited from the one-on-one help and direction when learning how to perform distribution modeling and GIS analyses; Tom was always there with ideas and relevant literature. I would like to thank my committee for their guidance, support, and dedication to mentorship. I would like to thank Jerry Tiehm for his excellent plant taxonomy classes, for helping me to identify many dead and flattened desert plants, and for our many games of lunchtime cribbage. I would like to thank the many undergraduates that helped me with my work, including: Travis Allen, Brittany Trimble, Lyndsey Boyer, Vicki Thill, Brianna Kooreman, and Marenna Disbro. They were an amazing help with all aspects of the lab and greenhouse work. I would like to thank Owen Baughman and Scot Ferguson for their help in the field. I am grateful for your off-road driving skills, attention to detail, and general knowledge and love of the Great Basin. I would like to thank my wonderful group of friends and researchers from the University of Nevada. I feel lucky to have received so much advice and feedback from so many different perspectives. I benefited from conversations, advice with data analysis, edits, moral support, and hands-on labor from many of you, and will be forever grateful, especially to the following individuals: Cynthia Scholl, Kevin Burls, Chris Moore, Dan Gibson, Angela Hornsby, Nick Pardikes, and Dash Hibbard.

Finally, I would like to thank my family for their unconditional love and support.
TABLE OF CONTENTS

Abstract ................................................................................................................................. i

Acknowledgements ............................................................................................................. iii

Table of Contents .............................................................................................................. iv

List of Tables ....................................................................................................................... v

List of Figures ..................................................................................................................... vi

Chapter I

Introduction ......................................................................................................................... 1

Chapter II

Using herbarium records to make climate niche comparisons among sub-dominant
forbs of the sagebrush steppe .......................................................................................... 13

Chapter III

Seed bank dynamics in the Great Basin: shrub cover and fire history predict
seed bank composition in an arid shrubland ...................................................................... 56

Chapter IV

Climate variability affects the germination strategies exhibited by arid land plants ............. 112

Chapter V

Conclusions .......................................................................................................................... 163
List of Tables

Chapter II

Table 1................................................................................................................................. 38
Table 2................................................................................................................................. 39
Table 3................................................................................................................................. 40
Supplementary Table 1 ...................................................................................................... 41
Supplementary Table 2 ...................................................................................................... 42
Supplementary Table 3 ...................................................................................................... 44

Chapter III

Table 1................................................................................................................................. 92
Table 2................................................................................................................................. 93
Supplementary Table 1 ...................................................................................................... 94
Supplementary Table 2 ...................................................................................................... 98
Supplementary Table 3 .................................................................................................... 99

Chapter IV

Table 1................................................................................................................................. 147
Table 2................................................................................................................................. 148
Table 3................................................................................................................................. 149
Table 4................................................................................................................................. 150
Table 5.................................................................................................................................. 151
Supplementary Table 1 ...................................................................................................... 152
Supplementary Table 2 ...................................................................................................... 154
Supplementary Table 3 .................................................................................................... 155
List of Figures

Chapter II

Figure Captions ........................................................................................................... 46

Figure 1 ......................................................................................................................... 48
Figure 2 ......................................................................................................................... 49
Figure 3 ......................................................................................................................... 50
Figure 4 ......................................................................................................................... 51
Figure 5 ......................................................................................................................... 52
Figure 6 ......................................................................................................................... 53
Figure 7 ......................................................................................................................... 54
Figure 8 ......................................................................................................................... 55

Chapter III

Figure Captions ........................................................................................................... 100

Figure 1 ......................................................................................................................... 102
Figure 2 ......................................................................................................................... 103
Figure 3 ......................................................................................................................... 104
Figure 4 ......................................................................................................................... 105
Figure 5 ......................................................................................................................... 106
Figure 6 ......................................................................................................................... 107
Figure 7 ......................................................................................................................... 108
Figure 8 ......................................................................................................................... 109
Figure 9 ................................................................................................................................. 110
Figure 10 ............................................................................................................................... 111

Chapter IV

Figure Captions .................................................................................................................. 156
Figure 1 .................................................................................................................................. 157
Figure 2 .................................................................................................................................. 159
Figure 3 .................................................................................................................................. 160
Figure 4 .................................................................................................................................. 161
CHAPTER I: Introduction

The responses of plants to environmental heterogeneity are strongly influenced by the fact that plants are immobile and must endure their local situation, unable to seek more favorable conditions (Bradshaw 1965). Plants experience environmental heterogeneity at both spatial and temporal scales, which can lead to variation in selection pressures that affect their growth and establishment (Lechowicz and Bell 1991; Levine and Rees 2004; Adler et al. 2006; Treurnicht et al. 2016). For example, arid environments tend to experience resource limitation, with high variability in the timing and quantity of precipitation, and this environmental variation is known to influence year-to-year differences in species composition (Venable et al. 1993) and reproductive success (Pake and Venable 1995). In addition, human induced land-use change, including the impacts of grazing and shorter fire-return intervals (Knick et al. 2011; Miller et al. 2011), has become increasingly common as a source of environmental heterogeneity experienced by natural plant populations.

Plant populations typically respond to heterogeneous environments by either increasing their level of specialization to a narrow range of conditions or by increasing their ability to exploit a broader range of conditions through a more generalist strategy. Specialization can be especially advantageous if the costs of being a generalist are high, e.g. if specialization allows for higher resource use efficiency than experienced by individuals with a more generalist strategy (Futuyma and Moreno 1988). Conversely, generalist strategies can enable a plant to change architectural, physiological, or phenological traits in response to environmental indicators of future resource availability (Sultan 2000). Specialist and generalist life-history strategies have been identified and studied in natural populations (Cook and Johnson 1968; Nagy and Rice 1997;
Kassen 2002; Heschel et al. 2004; Sambatti and Rice 2006), and it is highly likely that most populations of plant species achieve some balance of individuals representing strategies along the specialist-generalist spectrum (Bell et al. 2000).

Climate has a strong influence on the distribution of plant species (Hocker 1956; Gioia and Pigott 2000; Woodward et al. 2004). Geographic and inter-annual variation in precipitation and temperature can act as strong selective forces affecting the distribution of a species (Woodward and Williams 1987; Rehfeldt et al. 2006). Responses to mean climate are often used to estimate the climate niche of a species; however, species-level differences in tolerance to inter-annual climate variability may also be helpful for understanding the potential impacts future climate change on particular plant populations (Adler et al. 2006; Reyer et al. 2013). My second chapter explores how climate variability influences the distributions of sub-dominant arid land plants across shrublands within the western U.S., with the goal of improving our understanding of plant-climate interactions and whether there is evidence that climate may be influencing the temporal partitioning of resources among this co-occurring suite of plants.

Un-germinated seeds that persist in the soil, or seed banks, are important components of plant communities, and represents both a snapshot of the past vegetation in an area and the regenerative potential of a site (Koniak and Everett 1982; Simpson et al. 1989; Osem et al. 2006). This is especially true for annual plants, where the seed bank is the only source for population renewal. The species composition of the seed bank, including the relative proportion and diversity of native and introduced species, strongly influences the successional trajectory of an area after disturbance (Hassan and West 1986; Kemp 1989; Levassor et al. 1990). Deposited after maturation at the end of a growing season, some seeds in the seed bank germinate immediately when conditions become appropriate in the next growing season, forming a
transient seed bank (Thompson and Grime 1979). Other seeds possess dormancy mechanisms that prevent germination for one to many years, until appropriate conditions are met to stimulate germination (Thompson and Grime 1979; Baskin and Baskin 2014). Thus, seeds may persist in the soil for some time after plants have disappeared from the above-ground community, and there are many examples of plant communities where above-ground and below-ground diversity and composition are quite different (Hopfensperger 2007).

Desert seed banks are known to be spatially heterogeneous, with large site-to-site variation in seed bank composition despite similar above-ground vegetation (Kemp 1989). The relationship between the seed bank and the corresponding above-ground vegetation patterns remains poorly understood, especially for cold deserts (but see Pekas and Schupp, 2013). Because of the loss of seeds from the seed bank over time, extended periods without plant regeneration due to factors such as persistent drought, fire, high levels of herbivory, or strong competition with other species will limit the viable seed composition of the seed bank and may lead to an increased proportion of invasive exotic species (Bossuyt and Honnay 2008). In addition, the establishment of invasive grasses, such as cheatgrass (*Bromus tectorum*), following disturbance in sagebrush habitat has a dramatic effect on the herbaceous component of sagebrush communities, decreasing the abundance of native perennial grasses and native forbs and reducing habitat value of sagebrush systems (Miller et al. 2011). My third chapter explores the effect of disturbance on seed bank dynamics in Great Basin sagebrush steppe communities, with the goal of understanding how heterogeneity in disturbance may be affecting the presence of native and introduced species on the landscape.

Seed germination is a critical stage in the development of a plant, and is the first opportunity for interaction between a plant and its environment. Plants rely heavily on
environmental cues at this life-history stage, with dependence on environmental cues for germination acting as potential population bottlenecks (Menges 1991). Thus, climate influences the evolution of seed traits (Cochrane et al. 2015; Rosbakh and Poschlod 2015), and can shape the subsequent conditions and selection pressures experienced as the plant grows and establishes (Donohue et al. 2010; Poschlod et al. 2013; Fraaije et al. 2015; Mondoni et al. 2015; Jiménez-Alfaro et al. 2016). In addition, spatial and temporal variability in climate has the potential to differentially affect the life-history strategies of species, but also the strategies of populations across the geographic range of a species (Sher et al. 2004). Germination research involving desert forbs has identified both species-level differences in germination strategies (Forbis 2010; Baskin and Baskin 2014) and habitat-correlated germination timing within a species (Meyer et al. 1995). For example, Meyer et al. (1995) identified population-level variation within the same Penstemon species, where chilling induced both rapid germination of a fraction of the seeds and secondary dormancy in the remaining seeds. Despite growing evidence for population-level variation in plant traits (Sambatti and Rice 2006; Becker et al. 2008; Banta et al. 2012; Granado-Yela et al. 2013; Prendeville et al. 2013; Torres-Martinez et al. 2016), much less work has been done investigating these patterns using early life history traits and how they may relate to species responses to future climate variability (Cochrane et al. 2015; Jiménez-Alfaro et al. 2016). My fourth chapter examines species and population-level variation in germination strategies for a suite of co-occurring forbs and attempts to identify relationships between climate characteristics and breadth of cues that stimulate germination in these species.

Native forbs are increasingly of interest for use in Great Basin restoration, not only for their value to wildlife, but also for the ability of some annual forbs to suppress annual invaders, presumably due to similar phenology and growth requirements (i.e. Abella, Craig, Smith,
Newton, 2012; Leger, Goergen, & Forbis De Queiroz, 2014; Perry, Cronin, & Paschke, 2009; Uselman, Snyder, Leger, & Duke, 2014). Currently, there is great interest in the restoration of degraded sagebrush communities that lack a native, herbaceous understory component, and much ongoing work aims to increase the availability of native forbs for restoration (Shaw et al. 2005). Relative to native grasses, many of which are relatively easy to increase and harvest with conventional farming equipment, forb seeds can be difficult to produce in large numbers due to problems with insect pests, larger variation in growth form and seed harvestibility, and lower seed production (Shaw et al. 2005). Consequently, native forb seeds are typically more expensive than grass seeds, and the number of species available for purchase is far lower than the number of species that exist in intact sagebrush plant communities. When degradation has been relatively recent, some of this diversity may remain below-ground in soil seed banks, and this resource may represent an alternative method for increasing diversity and habitat value in areas with more recent disturbances.

This research focuses on how native Great Basin plants respond to environmental heterogeneity, with an emphasis on Great Basin forbs. The three chapters of this dissertation examine the influence of environmental heterogeneity on the spatial distribution of species, the persistence of native plants in disturbed areas, and population-level variation in plant traits, using three aspects of plant life-history: mature plants, seed bank dynamics, and seed germination. The specific research questions for each topic are outlined in their respective chapters. Some of the broader contributions of this research include: 1) identifying the effects of climate on the geographic distributions for co-occurring herbaceous species, 2) determining the effects of disturbance on plant species persistence and community composition, and 3) identifying relationships between climate characteristics, both mean and variability, and the
specialist-generalist spectrum in germination strategies exhibited by herbaceous arid land species.

From a management perspective, this work furthers our understanding of which native forbs may be most effective for enhancing habitat value of moderately-degraded sagebrush steppe communities that maintain a shrub component but lack understory diversity. Specifically, I have: 1) identified the climatic niches and niche breadths for potential restoration species, 2) evaluated the effect of disturbance on the presence and persistence of native forb and grass species in the seed banks of Great Basin sagebrush steppe communities, and 3) determined seed germination strategies for some common forb species that have not yet been studied.

REFERENCES


Chapter II: Using herbarium records to make climate niche comparisons among sub-dominant forbs of the sagebrush steppe

ABSTRACT

Relatively little is known about the spatial distribution and associated environmental preferences of sub-dominant, herbaceous species that add diversity to many ecosystems. Herbarium records can be an important resource for estimating the climate-niche of under-studied or hard to detect species, and can lead to testable hypotheses about species coexistence and species-specific responses to climate. Here we use herbarium records and ecological niche models to estimate and compare the climate niche and area of occupancy of ten annual and perennial forb species common in sagebrush steppe systems, asking how climate niches differ among species with partially overlapping ranges. We obtained digital occurrence records from three herbaria for locations across the western United States. We used ecological niche modelling to estimate the area of occupancy, calculate niche breadth, and describe the climate characteristics of suitable habitat. We also used precipitation data for herbarium record locations from 1965-2014 to describe mean values and variability in precipitation. Species varied in the size and spatial distribution of their predicted area of occupancy and varied in niche breadth. Species also varied in climate variables that predicted suitable habitat, and differed in mean values, spatial variation, and inter-annual variation of annual and summer precipitation. Only two of ten species shared a comparable climate niche. Herbarium records helped identify contrasting niches for a suite of Great Basin understory forbs, and we observed only small overlaps in climatic niches. While ephemeral species can be difficult to detect with field surveys, our approach capitalized on years of collector and curator effort to estimate climate preferences for non-dominant species. These estimates can be used to guide species selection for
restoration, as well as help conservationists understand which species may be least tolerant of climate variability, and potentially most vulnerable to climate change.

INTRODUCTION

Identifying factors that influence differences in the geographic distribution and ecological niche among species is a core goal of ecology (MacArthur 1972; Gaston 1996), and one that is vital for predicting responses to global climate change (Parmesan and Yohe 2003). Although much research has explored the geographic distribution, and associated environmental preferences, of long-lived or dominant plant species (Sykes et al. 1996; Hamann and Wang 2006; Aguirre-Gutiérrez et al. 2015; Schlaepfer et al. 2015), far less work has focused on sub-dominant, herbaceous plants that contribute to the species diversity of many ecosystems (though see Hereford, Schmitt, and Ackerly 2017). Studying sub-dominant, herbaceous plants can be challenging due to their smaller size, patchy distribution, or ephemeral nature (Mulroy and Rundel 1977; Thompson and Grime 1979; Abella 2009). However, they are important for providing resources for wildlife and pollinators (Beale and Smith 1970; Petersen and Best 1987; Gathmann and Tscharntke 2002; Siegel Thines et al. 2004; Gregg and Crawford 2009; Connelly et al. 2011) and furnishing the understory diversity which is essential for ecosystem functioning (Anderson and Inouye 2001; Hooper et al. 2005). Thus, understanding factors shaping the distribution of these species will help ecologists anticipate possible causes of geographic shifts or contractions under future climate conditions, and help restoration practitioners select appropriate species when restoring degraded areas.

Climate is a primary force shaping the distribution of plant species (Hocker 1956; Gioia and Pigott 2000; Woodward et al. 2004), with geographic and inter-annual variation in precipitation and temperature acting as potential selective forces influencing the occurrence of individual
species (Woodward and Williams 1987; Rehfeldt et al. 2006). While differences in mean climate are often used to describe the climate preferences of plant species, such as mean annual precipitation or mean annual temperature, measuring species-level variation in tolerance for inter-annual and spatial climate variability may also be useful for understanding plant responses to climate change scenarios (Adler et al. 2006; Reyer et al. 2013). In addition, soil and topographic characteristics can also affect availability of water and other resources (Dyer 2009), and these variables are increasingly being used to create niche models that focus on plant ecophysiological processes using a water balance approach (Lutz et al. 2010; Dilts et al. 2015), producing models that are functionally more closely related to the physiological needs of plants.

Spatial and temporal variation in the availability of resources and species-level differences in tolerance for variability may facilitate the coexistence of sympatric plant species through the evolution of niche separation (Silvertown 2004), resulting in spatial and temporal partitioning of resource use among species. In arid environments, where precipitation is limited and the timing and quantity is highly variable, plant species can potentially partition their use of water resources as a way to avoid competition and maintain species coexistence (Chesson et al. 2004). For example, species can evolve differences in phenology (Beatley 1974; Aronson et al. 1992) or seed germination cues (Forbis 2010) that may enable them to differentiate the timing of their resource use from other overlapping species, such that species may overlap in areas they occupy, but might not overlap in resource use due to differences in timing. Year-to-year variation in environmental conditions can also mediate species diversity and coexistence within arid land plant communities, where different species are present (Venable et al. 1993) or achieve higher reproductive success (Pake and Venable 1995) in different years.
Here we explore the factors influencing sub-dominant plant distributions within western U.S. shrublands. The Great Basin desert of North America is an arid region within the western U.S. that contains large areas dominated by sagebrush steppe shrublands. Landscape-scale disturbances from the invasion of exotic species, such as cheatgrass (*Bromus tectorum* L.), the increase in frequency and size of wildfires, and other human activities in this region have caused degradation of native plant communities throughout the Great Basin, putting hundreds of species at risk (Billings 1994; Knapp 1996; Wisdom et al. 2003; Chambers et al. 2007).

Herbaceous plants are important forage and shelter resources for wildlife (Petersen and Best 1987; Siegel Thines et al. 2004; Gregg and Crawford 2009; Connelly et al. 2011) and pollinators (Cane and Love 2016) within this area (for further details, please see the Methods); consequently, there is increasing interest in understanding the ecology of herbaceous species and their current and potential distribution in this region (Shaw et al. 2005, 2012; Dumroese et al. 2015; Haidet and Olwell 2015). Currently, most range maps available for non-dominant plant species are at a coarse scale, indicating only county or state boundaries (Kartesz 2015; USDA NRCS 2017). These coarse boundaries can be misleading when investigating the ecology of specific plant species and their potential uses in restoration, as they almost certainly overestimate potential habitat. Using herbarium data to model the area of occupancy for under-studied plant species can provide a way to approximate appropriate habitat (Elith et al. 2006; Hernández and Navarro 2007; Doherty et al. 2017). Although museum records present some challenges, such as identification error and collection biases (Newbold 2010), they also provide a wealth of information describing the distribution of species over large areas (Newbold 2010). This is especially useful for ephemeral annual species, which may not be present during field surveys in a given year (Mulroy and Rundel 1977; Rathcke and Lacey 1985).
Our goal is to estimate suitable habitat for a suite of sub-dominant forbs commonly found in sagebrush dominated ecosystems and to examine similarities and differences between both the geographic distribution of suitable habitat and the climate niches of these species. Although our species occur in sympatry in some areas (Williams et al. 1992), their overall area of occupancy varies greatly (Kartesz 2015). First, we used maximum entropy (Maxent) models to estimate the potential habitat of each species, and calculated niche breadth and overlaps between the predicted areas of occupancy among species. Next, we assessed similarities and differences in the climate niches of our focal species; we used the Maxent results to identify the climate variables most predictive of habitat for each species and the species-specific relationships between abundance and the climate variables. We then calculated annual and seasonal values for precipitation variables across occurrence records, asking how species differed in mean precipitation, how much spatial variation in precipitation was observed, and how much inter-annual variability each species experienced. We expected that species would differ in niche breadth and the size and distribution of their predicted area of occupancy, as well as in the relative importance of specific climate variables and tolerance for climate variability.

We conclude by discussing how these predictions could be tested using field studies and how this information can be used in conservation and restoration efforts.

METHODS

SPECIES AND OCCURRENCES: We selected 4 perennial and 6 annual forbs that are commonly found in sagebrush steppe ecosystems in the western Great Basin. Understory forbs are important forage for imperiled sagebrush-obligate wildlife, such as the greater sage grouse (Centrocercus urophasianus) (Gregg and Crawford 2009; Connelly et al. 2011) and pygmy rabbits (Brachylagus
Idahoensis (Green and Flinders 1980), and some have been specifically documented among wildlife diets and as important pollinator plants (Drut et al. 1994; Gregg and Crawford 2009; Dumroese et al. 2015, 2016; Stiver et al. 2015). Perennials species included Agoseris grandiflora (Nutt.) Greene, Chaenactis douglasii (Hook.) Hook. and Arn., Crepis intermedia A. Gray, and Phacelia hastata Douglas ex Lehm.; annual species included Blepharipappus scaber Hook., Collinsia parviflora Lindl., Cryptantha pterocarya (Torr.) Greene, Gilia inconspicua (Sm.) Sweet, Mentzelia albicaulis (Hook.) Torr. and A. Gray, and Microsteris gracilis (Hook.) Greene. These species differ in phenology (see Supplemental Table 1), with annual species generally flowering earlier in the year and for a longer window (March-July), while these perennial species generally have a shorter bloom period (May-July). We obtained occurrence records from three herbaria with coverage spanning the western United States: The Intermountain Region Herbarium Network (http://intermountainbiota.org/portal/) (accessed: 01 December 2014), The Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/) (accessed: 30 April 2015), and the Burke Museum herbarium at the University of Washington (http://www.burkemuseum.org/research-and-collections/botany-and-herbarium/collections/database/) (accessed: 22 October 2015). We limited our points to collections from 1950 to the present, due to frequent uncertainty about location information provided for older specimens. We then identified spatial outliers, verified the accuracy of location information, and removed any questionable records from the dataset.

We focused our analysis on points within the Western U.S., as this represents the core of the range for our focal species. We performed geographic filtering of occurrence points for each species in order to reduce collection bias (Kramer-Schadt et al. 2013; Boria et al. 2014), using the SDM Toolbox for ArcGIS (Brown 2014) to remove duplicate points within a 20 km
buffer. This practice also attempts to reduce spatial auto-correlation when measuring environmental variables and improves model generalizability (Kramer-Schadt et al. 2013). We used the spatially-thinned set of occurrence points to perform the Maxent modeling, as removing spatially auto-correlated points has been shown to improve the performance of presence-only modeling methods (Veloz 2009; Hijmans 2012). We then randomly partitioned the thinned dataset for each species into a set used for model training (65%) and a set used for model validation (35%). Due to visible differences in sampling effort across states, we used the Target Group Sampling approach of Ponder et al. (2001) to create a bias file based on state boundaries. Bias was calculated by dividing the density of occurrences of all species in each state by the average density of occurrences across all states.

Environmental Variables: We chose 29 biologically relevant variables for inclusion in our modeling efforts (Table 1). These included measures of annual and seasonal precipitation and temperature, as well as a suite of bioclimatic variables (Booth et al. 1989) derived from 64-year averages of monthly temperature and precipitation values obtained from PRISM data for the western United States from 1950 to 2014, the period of herbarium record observations (Daly et al. 2008). We used a Thornthwaite water balance approach to calculate variables that take into consideration the simultaneous availability of water and energy for plants (Stephenson 1998; Lutz et al. 2010). Several of these variables were derived from climographs of actual evapo-transpiration (AET), potential evapo-transpiration (PET), water supply (WS), soil water balance (SWB), and climate water deficit (CWD), using methods outlined in Dilts et al. (2015).
Estimating area of occupancy, niche breadth, and overlap: Due to the lack of absence data for our focal species and the large number of presences available from herbarium records (Table 2), we used a presence-background modeling approach. Among presence-background modeling approaches, Maxent modeling is one of the best performing and most commonly used approaches for estimating potential habitat (Elith et al. 2006). We used Maxent (version 3.3.3k, Phillips et al. 2006) to identify the best model(s) of the potential habitat for our focal species across the western United States, relying on Maxent’s internal variable selection to identify which combination of variables had the most predictive power for each species (Elith et al. 2011). Model selection included species-specific optimization by varying the regularization parameter (1-5) and the feature types (linear, quadratic, product, threshold, and hinge) (Anderson and Gonzalez 2011; Warren and Seifert 2011). We selected the best model(s) for each species using Akaike’s information criterion (AIC) score, calculated using ENMTools (Warren et al. 2010). The model with the lowest AIC score was considered the best model, and models with AIC scores less than two points higher than the lowest AIC score were considered comparable. We created binary maps for all top models using the threshold value associated with maximum sensitivity plus specificity of the test data (Liu et al. 2013). For species with multiple top models, we considered an area to be part of a species’ estimated area of occupancy if it was predicted as potential habitat by two or more models, and created binary maps of these estimates (see Fig. 1, 2). We used ArcMap 10.1 (ESRI 2012) to calculate the relative percent overlap for each species pair by dividing area of overlap by total area occupied (see Supplemental Table 2). We also present the relative probability of suitable habitat for each species using the Maxent output probabilities. For species with more than one top model, we
averaged the predicted probabilities of occurrence from the Maxent results across all top models.

Niche breadth was calculated for each species using ENMTools and the output of the top Maxent models (Warren et al. 2010). The niche breadth function determines the amount of ecological niche space available by applying the Levins’ inverse concentration metric (Levins 1968). Niche breadth values range from 0 to 1 and are comparable among species, with lower values indicating a more narrow environmental tolerance and higher values indicating a broader environmental tolerance. Niche overlap between pairs of species (D) was calculated using the Schoener’s D statistic (Schoener 1968; Warren et al. 2008). D values range from 0 to 1, with 0 indicating no overlap in environmental space and 1 corresponding to complete overlap. Finally, we performed a pairwise niche equivalence test using ENMTools 1.4 (Warren et al. 2010), to determine whether niche spaces were interchangeable among species. D values were compared to a null distribution of 30 overlap values, and niches were determined to be non-equivalent if overlap was significantly lower than observed in the null distribution.

COMPARING CLIMATE NICHES: We selected a suite of ten uncorrelated (Pearson’s correlation coefficient > ± 0.70) variables to include in Maxent models to describe the climate niche of each species and to allow for comparisons across species (see Supplemental Table 3). Variables included: mean maximum and minimum temperature, temperature range, annual and summer precipitation, precipitation seasonality, fraction of AET from precipitation, soil water balance, AET:CWD, and spring water availability. Modeling with these variables was performed as described above, and a top model was selected for each species. Although alternate top models existed for some species, all were very similar to the top model as indicated by the AIC values,
and for computational simplicity we picked only one top model per species. The permutation importance values and the ecological response curves were used to identify the climate variables most predictive of the distribution of each species (Phillips and Dudík 2008).

We focused our analysis of climate variation on two variables of interest: mean annual precipitation (mm) and mean summer precipitation (mm); temperature variables were not included in this analysis due to the very small amount of variation displayed in these variables, relative to precipitation. PRISM monthly precipitation rasters (mm) were downscaled from a 4 km² to a 500 m² grid size using the Climate Water Deficit Toolbox (Dilts 2015), and were used to extract monthly precipitation data for each occurrence point from 1950 to 2014. Downscaling was performed with the delta method using the difference in precipitation between the monthly PRISM precipitation raster and the 30 year PRISM precipitation normal at an 800 m² spatial resolution. We then calculated annual (January-December) and summer (June-August) precipitation totals for each year. We used these values to calculate the mean and standard deviation for each of the precipitation variables at each occurrence point through time (year-to-year variation) and for each year across each collection point (spatial variation).

We calculated the coefficient of variation (CV - standard deviation/mean) as a measure of climate variability for each variable across the occurrence points for each species. In order to account for unequal sample sizes for occurrence data among species, we calculated an unbiased CV using the methods of Abdi (2010), as follows:

$$CV_{\text{unbiased}} = \left( 1 + \frac{1}{4+N} \right) \times CV$$

Where N is the number of samples from the group being measured.

We used Program R (R Development Core Team 2016) to determine species-level differences in the mean values and climate variability for annual and summer precipitation.
First, we performed Type 2 ANOVAs to compare means and CVs using the `car` package (Fox and Weisberg 2011). If species differed, we performed Tukey’s Tests using the `agricolae` package (de Mendiburu 2016) to determine significant differences among species.

RESULTS

AREA OF OCCUPANCY, NICHE BREADTH, AND OVERLAP:

Species varied in the size of their potential area of occupancy (calculated from binary maps, see Fig. 1, 2) and niche breadth (Table 2). *Mentzelia albicaulis* possessed the largest area of occupancy (1,833,000 km$^2$) and *Blepharipappus scaber* possessed the smallest area of occupancy (490,000 km$^2$), with an average area of occupancy of 1,246,600 km$^2$ (Table 2). The predicted area of occupancy for our species overlapped in some areas, including parts of the Great Basin, but our estimates indicated that the extent, spatial distribution, and relative suitability of potential habitat differed greatly among most species (Fig. 3, 4). Niche breadth values varied from 0.76 (*Microsteris gracilis*) to 0.24 (*Agoseris grandiflora*), with higher numbers indicating a broader climatic range of suitability (Table 2). Pairwise niche comparisons suggested that only one pair of species occupied an equivalent niche (*Chaenactis douglasii* and *Crepis intermedia*- overlap of 0.91), despite the fact that some species overlap across a large portion of their predicted habitat (see Supplemental Table 2).

SIMILARITIES AND DIFFERENCES IN CLIMATE NICHES AMONG SPECIES:

Species varied in the climate variables that contributed most to predicting their distribution (Table 3, Fig. 5, 6). For perennials, maximum temperature, minimum temperature, and summer precipitation were most frequently important (Table 3). For annuals, summer
precipitation was highly influential (affecting 83% of species), followed by minimum
temperature and soil water balance (affecting 50% of species, Table 3). The direction of the
relationship and the degree of influence on predicted habitat suitability varied across species
(Fig. 5, 6). For example, increased summer precipitation had a slight positive effect on habitat
suitability for *Collinsia parviflora* and *Cryptantha pterocarya*, whereas increased summer
precipitation had a negative effect on potential habitat suitability for *Blepharipappus scaber*,
*Gilia inconspicua*, and *Mentzelia albicaulis*.

Our species occupied areas that differed in both their mean level of annual precipitation
\(F_{(9,3568)} = 84.91, p < 0.001\) and summer precipitation \(F_{(9,3568)} = 55.24, p < 0.001\). Species also
differed in the level of variation in precipitation across their range (annual: \(F_{(9,640)} = 189.67, p <
0.001\), summer: \(F_{(9,640)} = 86.55, p < 0.001\) and year-to-year variation at collection locations
(annual: \(F_{(9,3568)} = 212.09, p < 0.001\), \(p < 0.001\), summer: \(F_{(9,3568)} = 71.01, p < 0.001\) (Fig. 7, 8). For
example, among perennials, *Agoseris grandiflora* was collected from locations that experienced
higher levels of annual precipitation than other species, with moderate spatial variation and
very low year-to-year variation in precipitation across its range; however, the locations it
occupied also experienced much lower levels of summer precipitation than other species. In
contrast, the annual *Cryptantha pterocarya* occupied areas that experienced very low levels of
annual rainfall with moderate spatial variation and high year-to-year variation relative to other
species. In general, annual species grew in areas with lower quantities of mean annual and
summer precipitation as well as greater inter-annual variation in annual precipitation than
perennial species. The perennial *Agoseris grandiflora* grew in areas that were notably different
in precipitation characteristic than the other perennial species.
DISCUSSION

Predicting habitat for sub-dominant species can be challenging due to the ephemeral nature of some species and the lack of apparenty for others. Here, we used herbarium records to estimate the climate preferences of Great Basin forbs, identifying potentially contrasting niches for a suite of understory species. Although our study species displayed some overlap in the spatial distribution of their potential habitat (Fig. 3, 4), they appear to possess very different climate niches. In fact, our results indicate that only one pair of species, *Chaenactis douglasii* and *Crepis intermedia*, possesses overlapping climate niches. Other work using herbarium data to examine changes in size and reproduction over time for a subset of these species has also identified species-specific differences in response to climate (Leger 2013), supporting the result that these understory forbs vary in response to abiotic conditions.

Our models produce testable hypotheses about environmental conditions that should favor particular species and can serve as a foundation for understanding plant species coexistence, community diversity, and adaptation to climate. For example, while *Mentzelia albicaulus* and *Blepharipappus scaber* might occur at the same location, our data suggests that *M. albicaulus* would grow better in warmer, drier years (supported by Leger, 2013) while *B. scaber* would perform better in cooler years (Fig. 6). Identifying sympatric species with similar growth forms can be useful for examining how variation in climate niches among species may result from the temporal partitioning of resources through the storage effect (Angert et al. 2009; Chesson and Warner 1981), reflected in variation in species composition and performance on the landscape from year-to-year. Additionally, using habitat modeling to identify areas that vary in species diversity may be useful for examining diversity-stability relationships through mechanisms such as the portfolio effect (Tilman et al. 1998; Chalcraft 2013). This approach can
also help identify and explore strong abiotic predictors of species distributions. For example, it seems counter-intuitive that summer precipitation should be influential to species that do not typically survive long enough to be present during the summer season; the importance of summer precipitation has also been seen for the annual invader B. tectorum (Bradley 2009). Thus, summer precipitation may be an important indirect indicator of future resource availability or stronger competitive pressures from late season species (Bradley 2009).

Future work could involve testing the importance of genotype-environment relationships for producing patterns observed here, using field collections and reciprocal transplant studies across a range of environments. Such studies could indicate whether species with larger climate niches are persisting in disparate areas through phenotypic plasticity, i.e. responding to local conditions by adaptive changes in phenotypes, or show fixed differences in phenotypic traits, i.e. they persist via populations that are adapted to specific local conditions. Climate is not the only factor shaping the realized niches of these species (Silvertown 2004), and further experiments could ask to what degree competition, facilitation, and other interactions are affecting species distributions (Wisz et al. 2013).

Because of the conservation value of desert shrublands, our results are also relevant for conservation and restoration. From a land management perspective, this research establishes that herbarium records can be used to create estimated habitat maps for species that lack detailed habitat information, and also to identify species with high tolerance for climate variability and relatively large climate niches. Land managers could use these results to select appropriate restoration species based on the environmental conditions at the location being restored, or to prioritize planting of widely-adapted “generalist” species. This approach could be used in conjunction with recently developed tools built to help direct the effort of land
managers to efficiently and appropriately select climatically representative sites for specific restoration needs (Doherty et al. 2017). This type of information is especially important for species where seed availability is limited and can be expensive to procure (Shaw et al. 2012).

This work is also of value for conservation efforts, as it can identify species with narrow climate niches or low tolerance for environmental variation, which may be the most vulnerable to climate change (Thuiller, Lavoire, and Araújo 2005; Williams, Araujo, and Rasmont 2007).

Herbarium collections represent hours of fieldwork, preservation, and digitization efforts, and using these records to estimate potential habitat and isolate important variables is an excellent way to begin to understand relatively understudied elements of community diversity.

ACKNOWLEDGEMENTS

We would like to thank the Intermountain Region Herbarium Network, the Consortium of California Herbaria, and the Burke Museum herbarium at the University of Washington for digitizing their collections and making them available online.

REFERENCES


de Mendiburu F (2016) agricolae: statistical procedures for agricultural research. 


Dumroese RK, Luna T, Richardson BA, Kilkenny FF, Runyon JB (2015) Conserving and restoring


R Development Core Team (2016) R: A Language and Environment for Statistical Computing. R http://www.r-project.org/, Vienna, Austria


Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model


Table 1 Twenty-nine climate variables used in ecological niche models. All water-based variables are in units of millimeters and all temperature-based variables are in units of degrees Celcius.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Biological Relevance</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET - annual actual evapo-transpiration 1, 2</td>
<td>Proxy for productivity</td>
</tr>
<tr>
<td>CWD - annual climate water deficit 1, 2</td>
<td>Proxy for drought stress</td>
</tr>
<tr>
<td>PET - annual potential evapo-transpiration 1, 2</td>
<td>Climatic demand for water, excluding water availability</td>
</tr>
<tr>
<td>SWB - annual soil water balance 1, 2</td>
<td>Quantity of water stored in the soil from one month to the next</td>
</tr>
<tr>
<td>WS - annual water supply 1, 2</td>
<td>Total water supply for the year</td>
</tr>
<tr>
<td>Coefficient of variation of annual precipitation</td>
<td>Seasonality of precipitation</td>
</tr>
<tr>
<td>AET:CWD ratio</td>
<td>Relative CWD; values &gt; 1 are more mesic, values &lt; 1 are more xeric</td>
</tr>
<tr>
<td>PET:AET ratio</td>
<td>Relative drought indicator; values &gt; 1 indicate an unmet demand for water</td>
</tr>
<tr>
<td>SWB:AET ratio</td>
<td>Values &gt; 1 indicate more soil water storage than AET</td>
</tr>
<tr>
<td>WS:AET ratio</td>
<td>Values &gt; 1 indicate more water for soil water storage, runoff, or deep percolation</td>
</tr>
<tr>
<td>Positive difference between AET and SWB</td>
<td>Fraction of AET from month’s precipitation, not from soil</td>
</tr>
<tr>
<td>Positive difference between WS and the greater of AET or SWB</td>
<td>Cumulative water available for runoff or deep percolation</td>
</tr>
<tr>
<td>Spring ratio of WS and the greater of AET or SWB</td>
<td>Spring water available for runoff or deep percolation</td>
</tr>
<tr>
<td>Precipitation - total and seasonal 1, 4</td>
<td></td>
</tr>
<tr>
<td>Temperature range 3</td>
<td></td>
</tr>
<tr>
<td>Minimum temperature - total and seasonal 3, 4</td>
<td></td>
</tr>
<tr>
<td>Maximum temperature - total and seasonal 3, 4</td>
<td></td>
</tr>
</tbody>
</table>

1 See Dilts et al. 2015 for method of calculation
2 Summed for all months
3 Average for all months
4 Winter (Dec, Jan, Feb), Spring (Mar, Apr, May), Summer (Jun, Jul, Aug), Fall (Sep, Oct, Nov)
Table 2 Species specific evaluation of the top ecological niche model results for A) perennial and B) annual species. Values were obtained from Maxent models using environmental variables (Table 1) calculated for herbarium collection locations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Acronym</th>
<th>n</th>
<th>Training AUC</th>
<th>Test AUC</th>
<th>Niche Breadth</th>
<th>Predicted area of suitability (1000 km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agoseris grandiflora</td>
<td>AGGR</td>
<td>141</td>
<td>0.945</td>
<td>0.897</td>
<td>0.2421</td>
<td>650</td>
</tr>
<tr>
<td>Chaenactis douglasii</td>
<td>CHDO</td>
<td>456</td>
<td>0.770</td>
<td>0.737</td>
<td>0.7347</td>
<td>1400</td>
</tr>
<tr>
<td>Crepis intermedia</td>
<td>CRIN</td>
<td>173</td>
<td>0.779</td>
<td>0.768</td>
<td>0.6949</td>
<td>1581</td>
</tr>
<tr>
<td>Phacelia hastata</td>
<td>PHHA</td>
<td>468</td>
<td>0.797</td>
<td>0.831</td>
<td>0.6355</td>
<td>1388</td>
</tr>
<tr>
<td>B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blepharipappus scaber</td>
<td>BLSC</td>
<td>80</td>
<td>0.947</td>
<td>0.923</td>
<td>0.2864</td>
<td>490</td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>COPA</td>
<td>554</td>
<td>0.782</td>
<td>0.746</td>
<td>0.6946</td>
<td>1508</td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>CRPT</td>
<td>401</td>
<td>0.869</td>
<td>0.861</td>
<td>0.4236</td>
<td>844</td>
</tr>
<tr>
<td>Gilia inconspicua</td>
<td>GIIN</td>
<td>214</td>
<td>0.852</td>
<td>0.840</td>
<td>0.4539</td>
<td>1083</td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>MEAL</td>
<td>568</td>
<td>0.727</td>
<td>0.738</td>
<td>0.7589</td>
<td>1833</td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>MIGR</td>
<td>515</td>
<td>0.738</td>
<td>0.716</td>
<td>0.7631</td>
<td>1689</td>
</tr>
</tbody>
</table>

n, number of herbarium record locations used for modeling the species distribution  
1 Test points for all models were better predicted than random prediction with the same fractional predicted area (P < 0.001)  
2 The area of suitable habitat was determined using the Maximum Test Sensitivity Plus Specificity threshold value produced by the ecological niche model for each species and converting to presence/absence binary maps
Table 3 Results of the permutation importance analysis for a set of 10 uncorrelated variables performed in MaxEnt. Values indicate the percentage of variable contribution to the ecological niche model for A) perennial and B) annual species. Variables with a contribution greater than 8, an arbitrary cut-off selected by assessing the values, are presented in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Agoseris grandiflora</th>
<th>Chaenactis douglasii</th>
<th>Crepis intermedia</th>
<th>Phacelia hastata</th>
<th>Percent of Species Affected</th>
</tr>
</thead>
<tbody>
<tr>
<td>A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>0</td>
<td>22.9</td>
<td>24.1</td>
<td>56.7</td>
<td>75</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>5.5</td>
<td>12.3</td>
<td>22.4</td>
<td>20.7</td>
<td>75</td>
</tr>
<tr>
<td>Temperature Range</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>3.6</td>
<td>0</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>2.3</td>
<td>1.3</td>
<td>5.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>37.7</td>
<td>32.4</td>
<td>46.1</td>
<td>6.5</td>
<td>75</td>
</tr>
<tr>
<td>Precipitation Seasonality</td>
<td>1.5</td>
<td>18.2</td>
<td>1.1</td>
<td>1.5</td>
<td>25</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>0</td>
<td>9.8</td>
<td>0</td>
<td>11</td>
<td>50</td>
</tr>
<tr>
<td>Soil Water Balance</td>
<td>52.5</td>
<td>0.7</td>
<td>0.9</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>AET:CWD</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Spring Water Availability</td>
<td>0.5</td>
<td>2.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable</th>
<th>Blepharipappus scaber</th>
<th>Collinsia parviflora</th>
<th>Cryptantha pterocarya</th>
<th>Gilia inconstictua</th>
<th>Mentzelia albicaulis</th>
<th>Microsteris gracilis</th>
<th>Percent of Species Affected</th>
</tr>
</thead>
<tbody>
<tr>
<td>B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>7.1</td>
<td>7.6</td>
<td>0.2</td>
<td>0</td>
<td>11.9</td>
<td>2.4</td>
<td>17</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>24.3</td>
<td>3.8</td>
<td>67</td>
<td>35.7</td>
<td>3.4</td>
<td>3.4</td>
<td>50</td>
</tr>
<tr>
<td>Temperature Range</td>
<td>0</td>
<td>0.2</td>
<td>4</td>
<td>2.6</td>
<td>0</td>
<td>11.3</td>
<td>17</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>2.8</td>
<td>7.4</td>
<td>11.4</td>
<td>0</td>
<td>14.1</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>47.7</td>
<td>11.5</td>
<td>8.6</td>
<td>28.2</td>
<td>45.3</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td>Precipitation Seasonality</td>
<td>0.8</td>
<td>26.1</td>
<td>2.3</td>
<td>19.7</td>
<td>3.5</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>10.8</td>
<td>14.4</td>
<td>3.4</td>
<td>4.6</td>
<td>0</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>Soil Water Balance</td>
<td>3.2</td>
<td>24.9</td>
<td>0</td>
<td>6.8</td>
<td>21.7</td>
<td>78.9</td>
<td>50</td>
</tr>
<tr>
<td>AET:CWD</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Spring Water Availability</td>
<td>3.2</td>
<td>3.9</td>
<td>3</td>
<td>2.3</td>
<td>0</td>
<td>3.9</td>
<td>0</td>
</tr>
</tbody>
</table>
**Supplemental Table 1** Flowering phenology of A) perennial and B) annual forbs included in our study. Information about the phenology of our focal species was obtained from the University of California’s Jepson Herbarium.

<table>
<thead>
<tr>
<th>Species</th>
<th>Acronym</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agoseris grandiflora</em></td>
<td>AGGR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chaenactis douglasii</em></td>
<td>CHDO</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crepis intermedia</em></td>
<td>CRIN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>PHHA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Blepharipappus scaber</em></td>
<td>BLSC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>COPA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cryptantha pterocarya</em></td>
<td>CRPT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gilia inconspicua</em></td>
<td>GIIN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mentzelia albicaulis</em></td>
<td>MEAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Microsteris gracilis</em></td>
<td>MIGR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Supplemental Table 2 Pairwise ecological niche comparisons for the focal species. Higher niche overlap values indicate a higher degree of similarity in habitat suitability for each pair. If the niche overlap value falls outside the range of niche equivalence values, then the niches are considered non-equivalent. The fraction of the range overlap indicates the proportion of overlapping area of suitable habitat for the two species relative to the total area of suitable habitat for each species (a or b). Perennial species are in bold and annual species are underlined. The one instance of niche equivalence is indicated by an *.

<table>
<thead>
<tr>
<th>Forb Species</th>
<th>Fraction of Range Overlap</th>
<th>Niche Overlap (D)</th>
<th>Niche Equivalence Distribution (D)</th>
<th>Relative to a</th>
<th>Relative to b</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Agoseris grandiflora</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chaenactis douglasii</td>
<td>0.441</td>
<td>0.872 - 0.931</td>
<td>0.494</td>
<td>0.229</td>
<td></td>
</tr>
<tr>
<td>Crepis intermedia</td>
<td>0.500</td>
<td>0.849 - 0.928</td>
<td>0.666</td>
<td>0.274</td>
<td></td>
</tr>
<tr>
<td>Phacelia hastata</td>
<td>0.504</td>
<td>0.864 - 0.927</td>
<td>0.668</td>
<td>0.313</td>
<td></td>
</tr>
<tr>
<td>Blepharipappus scaber</td>
<td>0.477</td>
<td>0.780 - 0.862</td>
<td>0.375</td>
<td>0.498</td>
<td></td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>0.505</td>
<td>0.857 - 0.923</td>
<td>0.774</td>
<td>0.334</td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.241</td>
<td>0.863 - 0.920</td>
<td>0.068</td>
<td>0.052</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.297</td>
<td>0.841 - 0.920</td>
<td>0.192</td>
<td>0.115</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.342</td>
<td>0.867 - 0.940</td>
<td>0.374</td>
<td>0.133</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.525</td>
<td>0.865 - 0.936</td>
<td>0.983</td>
<td>0.378</td>
<td></td>
</tr>
<tr>
<td><strong>Chaenactis douglasii</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crepis intermedia</td>
<td>0.910*</td>
<td>0.878 - 0.934*</td>
<td>0.963</td>
<td>0.853</td>
<td></td>
</tr>
<tr>
<td>Phacelia hastata</td>
<td>0.834</td>
<td>0.913 - 0.950</td>
<td>0.795</td>
<td>0.802</td>
<td></td>
</tr>
<tr>
<td>Blepharipappus scaber</td>
<td>0.521</td>
<td>0.849 - 0.934</td>
<td>0.306</td>
<td>0.876</td>
<td></td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>0.801</td>
<td>0.905 - 0.951</td>
<td>0.731</td>
<td>0.684</td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.393</td>
<td>0.899 - 0.955</td>
<td>0.138</td>
<td>0.229</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.544</td>
<td>0.897 - 0.941</td>
<td>0.467</td>
<td>0.605</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.649</td>
<td>0.920 - 0.962</td>
<td>0.610</td>
<td>0.466</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.777</td>
<td>0.914 - 0.959</td>
<td>0.734</td>
<td>0.608</td>
<td></td>
</tr>
<tr>
<td><strong>Crepis intermedia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phacelia hastata</td>
<td>0.851</td>
<td>0.860 - 0.935</td>
<td>0.770</td>
<td>0.877</td>
<td></td>
</tr>
<tr>
<td>Blepharipappus scaber</td>
<td>0.562</td>
<td>0.804 - 0.898</td>
<td>0.292</td>
<td>0.943</td>
<td></td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>0.819</td>
<td>0.877 - 0.930</td>
<td>0.731</td>
<td>0.767</td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.381</td>
<td>0.875 - 0.933</td>
<td>0.132</td>
<td>0.246</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.537</td>
<td>0.854 - 0.930</td>
<td>0.433</td>
<td>0.632</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.626</td>
<td>0.879 - 0.948</td>
<td>0.565</td>
<td>0.487</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.797</td>
<td>0.874 - 0.931</td>
<td>0.745</td>
<td>0.697</td>
<td></td>
</tr>
<tr>
<td><strong>Phacelia hastata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blepharipappus scaber</td>
<td>0.516</td>
<td>0.835 - 0.921</td>
<td>0.305</td>
<td>0.863</td>
<td></td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>0.842</td>
<td>0.903 - 0.949</td>
<td>0.844</td>
<td>0.777</td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.308</td>
<td>0.911 - 0.952</td>
<td>0.083</td>
<td>0.136</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.439</td>
<td>0.882 - 0.950</td>
<td>0.326</td>
<td>0.417</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.531</td>
<td>0.923 - 0.955</td>
<td>0.432</td>
<td>0.554</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.777</td>
<td>0.902 - 0.957</td>
<td>0.822</td>
<td>0.675</td>
<td></td>
</tr>
<tr>
<td><strong>Blepharipappus scaber</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>0.488</td>
<td>0.818 - 0.913</td>
<td>0.814</td>
<td>0.265</td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.365</td>
<td>0.827 - 0.910</td>
<td>0.212</td>
<td>0.123</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.531</td>
<td>0.818 - 0.904</td>
<td>0.708</td>
<td>0.320</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.445</td>
<td>0.846 - 0.936</td>
<td>0.778</td>
<td>0.208</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.496</td>
<td>0.839 - 0.913</td>
<td>0.967</td>
<td>0.281</td>
<td></td>
</tr>
<tr>
<td><strong>Collinsia parviflora</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.342</td>
<td>0.902 - 0.947</td>
<td>0.085</td>
<td>0.152</td>
<td></td>
</tr>
<tr>
<td>Gilia inconsipcua</td>
<td>0.463</td>
<td>0.889 - 0.932</td>
<td>0.334</td>
<td>0.464</td>
<td></td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.549</td>
<td>0.916 - 0.959</td>
<td>0.420</td>
<td>0.345</td>
<td></td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.872</td>
<td>0.913 - 0.945</td>
<td>0.902</td>
<td>0.805</td>
<td></td>
</tr>
</tbody>
</table>
Supplemental Table 2  
(continued)

<table>
<thead>
<tr>
<th>Forb Species</th>
<th>Niche Overlap (D)</th>
<th>Niche Equivalence Distribution (D)</th>
<th>Relative to a</th>
<th>Relative to b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptantha pterocarya</td>
<td>0.660</td>
<td>0.892 - 0.931</td>
<td>0.610</td>
<td>0.476</td>
</tr>
<tr>
<td>Gilia inconsipua</td>
<td>0.710</td>
<td>0.906 - 0.958</td>
<td>0.999</td>
<td>0.460</td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.424</td>
<td>0.896 - 0.950</td>
<td>0.315</td>
<td>0.157</td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>0.700</td>
<td>0.882 - 0.941</td>
<td>0.976</td>
<td>0.577</td>
</tr>
<tr>
<td>Gilia inconsipua</td>
<td>0.516</td>
<td>0.886 - 0.938</td>
<td>0.594</td>
<td>0.381</td>
</tr>
<tr>
<td>Mentzelia albicaulis</td>
<td>0.628</td>
<td>0.922 - 0.957</td>
<td>0.482</td>
<td>0.523</td>
</tr>
</tbody>
</table>
**Supplemental Table 3** Table of Pearson’s correlation values among the 29 climate variables based on the values extracted from the herbarium records for all species. The uncorrelated model variables are listed along the top of the table, and all possible model variables are listed along the left column of the table. The gray box appears around the portion of the correlation matrix that contains values for the uncorrelated variables used in the final distribution models. The focus was to maintain variables that were more easily interpretable, while limiting the correlation between variables to less than a 0.70 correlation value.

<table>
<thead>
<tr>
<th></th>
<th>Maximum Temperature</th>
<th>Cumulative Soil Water Balance</th>
<th>Precipitation Seasonality</th>
<th>Minimum Temperature</th>
<th>Temperature Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Temperature</td>
<td>1.000</td>
<td>-0.438</td>
<td>0.156</td>
<td>0.628</td>
<td>0.350</td>
</tr>
<tr>
<td>Cumulative SWB</td>
<td>-0.438</td>
<td>1.000</td>
<td>0.068</td>
<td>-0.051</td>
<td>-0.423</td>
</tr>
<tr>
<td>Precipitation Seasonality</td>
<td>0.156</td>
<td>0.068</td>
<td>1.000</td>
<td>0.602</td>
<td>-0.552</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>0.628</td>
<td>-0.051</td>
<td>0.602</td>
<td>1.000</td>
<td>-0.508</td>
</tr>
<tr>
<td>Temperature Range</td>
<td>0.350</td>
<td>-0.423</td>
<td>-0.552</td>
<td>-0.508</td>
<td>1.000</td>
</tr>
<tr>
<td>Spring Available Water</td>
<td>-0.446</td>
<td>-0.026</td>
<td>-0.292</td>
<td>-0.535</td>
<td>0.148</td>
</tr>
<tr>
<td>AET:CWD</td>
<td>-0.073</td>
<td>0.056</td>
<td>-0.028</td>
<td>-0.031</td>
<td>-0.043</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>-0.453</td>
<td>0.292</td>
<td>-0.323</td>
<td>-0.450</td>
<td>0.041</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>-0.498</td>
<td>0.570</td>
<td>0.277</td>
<td>0.025</td>
<td>-0.581</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>0.386</td>
<td>-0.469</td>
<td>0.122</td>
<td>0.166</td>
<td>0.227</td>
</tr>
<tr>
<td>Cumulative AET</td>
<td>0.896</td>
<td>-0.424</td>
<td>0.235</td>
<td>0.728</td>
<td>0.116</td>
</tr>
<tr>
<td>Cumulative Available Water</td>
<td>-0.195</td>
<td>0.243</td>
<td>0.324</td>
<td>0.179</td>
<td>-0.432</td>
</tr>
<tr>
<td>Cumulative CWD</td>
<td>0.886</td>
<td>-0.290</td>
<td>0.372</td>
<td>0.851</td>
<td>-0.044</td>
</tr>
<tr>
<td>Cumulative PET</td>
<td>0.886</td>
<td>-0.290</td>
<td>0.372</td>
<td>0.851</td>
<td>-0.044</td>
</tr>
<tr>
<td>Cumulative WS</td>
<td>-0.259</td>
<td>0.481</td>
<td>0.377</td>
<td>0.215</td>
<td>-0.546</td>
</tr>
<tr>
<td>Fall Precipitation</td>
<td>-0.492</td>
<td>0.586</td>
<td>0.140</td>
<td>-0.042</td>
<td>-0.494</td>
</tr>
<tr>
<td>Maximum Fall Temperature</td>
<td>0.923</td>
<td>-0.352</td>
<td>0.392</td>
<td>0.814</td>
<td>0.042</td>
</tr>
<tr>
<td>Maximum Spring Temperature</td>
<td>0.926</td>
<td>-0.337</td>
<td>0.348</td>
<td>0.804</td>
<td>0.058</td>
</tr>
<tr>
<td>Maximum Summer Temperature</td>
<td>0.997</td>
<td>-0.433</td>
<td>0.179</td>
<td>0.649</td>
<td>0.323</td>
</tr>
<tr>
<td>Maximum Winter Temperature</td>
<td>0.796</td>
<td>-0.250</td>
<td>0.503</td>
<td>0.888</td>
<td>-0.187</td>
</tr>
<tr>
<td>Minimum Fall Temperature</td>
<td>0.777</td>
<td>-0.180</td>
<td>0.487</td>
<td>0.947</td>
<td>-0.280</td>
</tr>
<tr>
<td>Minimum Spring Temperature</td>
<td>0.865</td>
<td>-0.235</td>
<td>0.408</td>
<td>0.900</td>
<td>-0.125</td>
</tr>
<tr>
<td>Minimum Summer Temperature</td>
<td>0.889</td>
<td>-0.323</td>
<td>0.267</td>
<td>0.779</td>
<td>0.047</td>
</tr>
<tr>
<td>Minimum Winter Temperature</td>
<td>0.657</td>
<td>-0.072</td>
<td>0.593</td>
<td>0.998</td>
<td>-0.473</td>
</tr>
<tr>
<td>PET:AET</td>
<td>0.757</td>
<td>-0.363</td>
<td>0.059</td>
<td>0.528</td>
<td>0.203</td>
</tr>
<tr>
<td>Spring Precipitation</td>
<td>-0.574</td>
<td>0.571</td>
<td>0.198</td>
<td>-0.088</td>
<td>-0.530</td>
</tr>
<tr>
<td>SWB:AET</td>
<td>-0.569</td>
<td>0.951</td>
<td>-0.011</td>
<td>-0.177</td>
<td>-0.417</td>
</tr>
<tr>
<td>Winter Precipitation</td>
<td>-0.341</td>
<td>0.481</td>
<td>0.455</td>
<td>0.224</td>
<td>-0.647</td>
</tr>
<tr>
<td>WS:AET</td>
<td>-0.390</td>
<td>0.447</td>
<td>0.335</td>
<td>0.101</td>
<td>-0.554</td>
</tr>
</tbody>
</table>
## Supplemental Table 3 (continued)

<table>
<thead>
<tr>
<th></th>
<th>Spring Available Water</th>
<th>AET:CWD</th>
<th>Summer Precipitation</th>
<th>Annual Precipitation</th>
<th>Fraction of AET from Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Temperature</td>
<td>-0.446</td>
<td>-0.073</td>
<td>-0.453</td>
<td>-0.498</td>
<td>0.386</td>
</tr>
<tr>
<td>Cumulative SWB</td>
<td>-0.026</td>
<td>0.056</td>
<td>0.292</td>
<td>0.570</td>
<td>0.469</td>
</tr>
<tr>
<td>Precipitation Seasonality</td>
<td>-0.292</td>
<td>-0.028</td>
<td>-0.323</td>
<td>0.277</td>
<td>0.122</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>-0.535</td>
<td>-0.031</td>
<td>-0.450</td>
<td>0.025</td>
<td>0.166</td>
</tr>
<tr>
<td>Temperature Range</td>
<td>0.148</td>
<td>-0.043</td>
<td>0.041</td>
<td>-0.581</td>
<td>0.227</td>
</tr>
<tr>
<td>Spring Available Water</td>
<td>1.000</td>
<td>0.038</td>
<td>1.000</td>
<td>0.092</td>
<td>-0.060</td>
</tr>
<tr>
<td>AET:CWD</td>
<td>0.270</td>
<td>0.092</td>
<td>1.000</td>
<td>0.273</td>
<td>0.219</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>0.039</td>
<td>0.087</td>
<td>0.273</td>
<td>1.000</td>
<td>-0.210</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>-0.060</td>
<td>-0.048</td>
<td>0.219</td>
<td>-0.210</td>
<td>1.000</td>
</tr>
<tr>
<td>Cumulative AET</td>
<td>-0.412</td>
<td>-0.045</td>
<td>-0.498</td>
<td>-0.454</td>
<td>0.226</td>
</tr>
<tr>
<td>Cumulative Available Water</td>
<td>-0.006</td>
<td>0.052</td>
<td>0.042</td>
<td>0.845</td>
<td>-0.011</td>
</tr>
<tr>
<td>Cumulative CWD</td>
<td>-0.503</td>
<td>-0.046</td>
<td>-0.398</td>
<td>-0.281</td>
<td>0.341</td>
</tr>
<tr>
<td>Cumulative PET</td>
<td>-0.503</td>
<td>-0.046</td>
<td>-0.398</td>
<td>-0.281</td>
<td>0.341</td>
</tr>
<tr>
<td>Cumulative WS</td>
<td>-0.085</td>
<td>0.056</td>
<td>0.177</td>
<td>0.921</td>
<td>-0.020</td>
</tr>
<tr>
<td>Fall Precipitation</td>
<td>0.030</td>
<td>0.111</td>
<td>0.346</td>
<td>0.964</td>
<td>-0.217</td>
</tr>
<tr>
<td>Maximum Fall Temperature</td>
<td>-0.506</td>
<td>-0.065</td>
<td>-0.465</td>
<td>-0.337</td>
<td>0.395</td>
</tr>
<tr>
<td>Maximum Spring Temperature</td>
<td>-0.522</td>
<td>-0.058</td>
<td>-0.404</td>
<td>-0.354</td>
<td>0.399</td>
</tr>
<tr>
<td>Maximum Summer Temperature</td>
<td>-0.459</td>
<td>-0.072</td>
<td>-0.437</td>
<td>-0.488</td>
<td>0.402</td>
</tr>
<tr>
<td>Maximum Winter Temperature</td>
<td>-0.498</td>
<td>-0.049</td>
<td>-0.407</td>
<td>-0.199</td>
<td>0.357</td>
</tr>
<tr>
<td>Minimum Fall Temperature</td>
<td>-0.526</td>
<td>-0.042</td>
<td>-0.415</td>
<td>-0.121</td>
<td>0.298</td>
</tr>
<tr>
<td>Minimum Spring Temperature</td>
<td>-0.550</td>
<td>-0.051</td>
<td>-0.436</td>
<td>-0.237</td>
<td>0.317</td>
</tr>
<tr>
<td>Minimum Summer Temperature</td>
<td>-0.460</td>
<td>-0.050</td>
<td>-0.338</td>
<td>-0.325</td>
<td>0.397</td>
</tr>
<tr>
<td>Minimum Winter Temperature</td>
<td>-0.544</td>
<td>-0.035</td>
<td>-0.464</td>
<td>0.004</td>
<td>0.182</td>
</tr>
<tr>
<td>PET:AET</td>
<td>-0.300</td>
<td>-0.032</td>
<td>-0.478</td>
<td>-0.443</td>
<td>-0.026</td>
</tr>
<tr>
<td>Spring Precipitation</td>
<td>0.136</td>
<td>0.088</td>
<td>0.288</td>
<td>0.969</td>
<td>-0.279</td>
</tr>
<tr>
<td>SWB:AET</td>
<td>0.057</td>
<td>0.074</td>
<td>0.348</td>
<td>0.548</td>
<td>-0.580</td>
</tr>
<tr>
<td>Winter Precipitation</td>
<td>-0.074</td>
<td>0.051</td>
<td>-0.014</td>
<td>0.948</td>
<td>-0.218</td>
</tr>
<tr>
<td>WS:AET</td>
<td>0.039</td>
<td>0.096</td>
<td>0.114</td>
<td>0.955</td>
<td>-0.224</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

Fig. 1 Maps of potential range for perennial species, including: A) *Agoseris grandiflora*, B) *Chaenactis douglasii*, C) *Crepis intermedia*, and D) *Phacelia hastata*. These maps represent areas with high environmental suitability and were created using Maxent modeling with the herbarium records and our collection of 29 environmental variables.

Fig. 2 Maps of potential range for annual species, including: A) *Blepharipappus scaber*, B) *Collinsia parviflora*, C) *Cryptantha pterocarya*, D) *Gilia inconspicua*, E) *Mentzelia albicaulis*, and F) *Microsteris gracilis*. These maps represent areas with high environmental suitability and were created using Maxent modeling with the herbarium records and our collection 29 environmental variables.

Fig. 3 Estimated potential habitat for perennial species. Maps depict environmental suitability using a red-yellow-blue color ramp, with red indicating a high probability and blue indicating a low probability of suitable habitat relative to a minimum-maximum stretch type based on the Maxent output probabilities for each species. These maps were created using Maxent modeling based on herbarium records and the full suite of 29 environmental variables.

Fig. 4 Estimated potential habitat for annual species. Maps depict environmental suitability using a red-yellow-blue color ramp, with red indicating a high probability and blue indicating a low probability of suitable habitat relative to a minimum-maximum stretch type based on the Maxent output probabilities for each species. These maps were created using Maxent modeling based on herbarium records and the full suite of 29 environmental variables.

Fig. 5 Ecological response curves demonstrating relationships between environmental variables and predicted habitat suitability for each perennial species. Response curves are based on the results of ecological niche models using ten uncorrelated variables. The x-axis for each variable represents the range of that variable across the study area (western U.S.), with all water-based variables in units of millimeters and all temperature-based variables in units of degrees Celsius, and the y-axis represents the predicted habitat suitability ranging from 0 (unsuitable) to 1 (suitable). Gray boxes indicate variables that were important for describing suitable habitat for a particular species (permutation importance > 8).

Fig. 6 Ecological response curves demonstrating relationships between environmental variables and predicted habitat suitability for each annual species. Response curves are based on the results of ecological niche models using ten uncorrelated variables. The x-axis for each variable represents the range of that variable across the study area (western U.S.), with all water-based variables in units of millimeters and all temperature-based variables in units of degrees Celsius, and the y-axis represents the predicted habitat suitability ranging from 0 (unsuitable) to 1 (suitable). Gray boxes indicate variables that were important for describing suitable habitat for a particular species (permutation importance > 8).
**Fig. 7** Boxplots of mean (A), spatial variation (B), and temporal variation (C) of annual precipitation at herbarium collection locations. Variation is measured using the coefficient of variation (CV) for total annual precipitation for each year. Spatial variation is measured across the collection locations for each species from 1950-2014 and temporal variation is measured across all years from 1950-2014 at each location. See Table 2 for species acronyms. Letters that appear above each boxplot indicate the results of Tukey’s tests that differentiate significant differences in means between species by assigning them a different letter.

**Fig. 8** Boxplots of mean (A), spatial variation (B), and temporal variation (C) of summer precipitation at herbarium collection locations. Variation is measured using the coefficient of variation (CV) for total summer precipitation for each year. Spatial variation is measured across the collection locations for each species from 1950-2014 and temporal variation is measured across all years from 1950-2014 at each location. See Table 2 for species acronyms. Letters that appear above each boxplot indicate the results of Tukey’s tests that differentiate significant differences in means between species by assigning them a different letter.
Fig. 1

A) *Agoseris grandiflora*  
B) *Chaenactis douglasii*  
C) *Crepis intermedia*  
D) *Phacelia hastata*
A) Blepharipappus scaber  
B) Collinsia parviflora  
C) Cryptantha pterocarya  
D) Gilia inconspicua  
E) Mentzelia albicaulis  
F) Microsteris gracilis

Fig. 2
Fig. 3

A) Agoseris grandiflora
B) Chaenactis douglasii
C) Crepis intermedia
D) Phacelia hastata
A) Blepharipappus scaber
B) Collinsia parviflora
C) Cryptantha pterocarya
D) Gilia inconspicua
E) Mentzelia albicaulis
F) Microsteris gracilis

Fig. 4
Range of values across the western United States

Fig. 5
Fig. 6

Range of values across the western United States
Fig. 7
Fig. 8
ABSTRACT

Un-germinated seeds that remain dormant in the soil are an important contribution to the regenerative potential of an area. Understanding factors that affect seed bank dynamics in arid regions may provide insight into how deserts respond to environmental change, and provide an opportunity to increase native diversity in degraded areas. Our goal was to characterize seed banks in a Great Basin sagebrush steppe system, using field surveys and seed bank studies to compare 17 sites in Northern Nevada that differed in above-ground vegetation, fire history, and grazing use. We tested whether shrub cover, ground cover, climate, or disturbance history were predictive of seed densities, diversity, the presence of rare species, and similarity between above and below-ground communities. We found that fire frequency and a course measure of grazing use were not highly predictive of seed bank dynamics, with the exception that fire on a plot <10 years ago increased similarity between the above and below-ground community composition, and that climate variables affected above-, but not below-ground, measures. In contrast, shrub cover was highly predictive of multiple below-ground responses. Cover of two early seral species (*Chrysothamnus viscidiflorus* and *Ericameria nauseosa*) was predictive of patterns consistent with moderate disturbance or recovery from disturbance, including increased densities of annual and introduced species and increased richness of introduced species. Increased
cover of *Artemisia tridentata* was associated with increased below-ground richness of rare native species. Ground cover also predicted seed bank composition: introduced species richness was lower with greater cover of standing dead shrubs and rock, and below-ground native evenness increased with increasing bare ground and rock. Relative to coarse measures of fire history, climate, and grazing use, on-the-ground cover estimates were more reliable predictors of seed bank composition, and suggest that management activities in areas dominated by *A. tridentata* would have the most desirable restoration outcomes.

INTRODUCTION

Un-germinated seeds that persist in the soil are important components of plant communities that affect long-term species composition (Hopfensperger 2007). While the seeds of some species exist in the seed bank for less than one year, forming the transient seed bank, seeds of other species may endure in the seedbank for greater than a year, sometimes much longer, forming a persistent seed bank (Thompson and Grime 1979). Persistent seed banks arise from dormancy mechanisms that prevent germination until appropriate dormancy-breaking conditions are met (Baskin and Baskin 2014). Viable seeds may remain in the soil for some time after plants have disappeared from the above-ground community, and there are many examples of plant communities where above-ground and below-ground diversity and composition are quite different (Kemp 1989; Hopfensperger 2007). The species composition of the seed bank, including the relative proportion and diversity of native and introduced species, strongly
influences the successional trajectory of an area after disturbance (Hassan and West 1986; Kemp 1989; Levassor et al. 1990). Given this, the soil seed bank can be viewed as both a snapshot of the past vegetation in an area and the regenerative potential of a site (Koniak and Everett 1982; Simpson et al. 1989; Osem et al. 2006a).

Plants growing in arid systems and in areas with high environmental variability, such as the cold deserts of the Great Basin, often evolve high levels of seed dormancy, as this strategy can allow species persistence during extended periods of reproductive failure during drought or unfavorable precipitation regimes (Facelli et al. 2005; Kinloch and Friedel 2005). Thus, persistent seed banks are especially common in harsh and variable environments (Freas and Kemp 1983; Jurado and Flores 2005). Additionally, desert seed banks are known to be spatially heterogeneous, with large site-to-site variation in seed bank composition despite similarities in above-ground vegetation (Young and Evans 1975; Kemp 1989; Guo et al. 1998), and predicting the composition of desert seed banks remains challenging. Seed banks of Great Basin annuals, in particular, fluctuate as a result of temporal variability in productivity (Young and Evans 1975), and differences in dispersal ability and seed longevity also impact seed bank composition (Guo et al. 1998). While dormant seeds can sometimes persist for long periods of time in the soil, granivory and hostile environmental conditions can have significant detrimental impacts on seed longevity within desert seed banks (Kemp 1989; Chambers and MacMahon 1994). The loss of seeds from the seed bank over time due to germination and extended periods without plant regeneration will limit the viable seed
composition of the seed bank and, in disturbed sites, may lead to an increased proportion of introduced species (Bossuyt and Honnay 2008).

While recent research has explored the effects of climate change (Gutierrez et al. 2000) and disturbance (Humphrey and Schupp 2001; Osem et al. 2006a, b; Wright and Clarke 2009) on seed banks in desert plant communities, seed bank dynamics in arid and semi-arid systems, and in cold deserts in particular, remain poorly understood (Facelli et al., 2005; Kemp, 1989; but see Pekas and Schupp, 2013). Seed banks in arid regions are highly transient (Gul and Weber 2001), and climate factors can influence seed bank composition. For example, heavy precipitation events allow replenishment of ephemeral forbs in the seed bank (Gutierrez et al. 2000). Biotic factors, such as shrubs (Li 2008), can contribute to the distribution of seeds within the seed bank, and plant litter can trap seeds during dispersal (Chambers and MacMahon 1994) and can constrain the germination of seeds (Facelli and Pickett 1991; Xiong and Nilsson 1999). Fire and grazing use can also change seed bank characteristics in an area. In some areas, invasive annuals can dominate the seed bank and prevent establishment of native perennials after fire (Humphrey and Schupp (2001), and grazing can have highly variable effects on similarity between the above-ground and below-ground community composition, depending on site history and grazing timing and intensity (Bakker and de Vries 1992; Peco et al. 1998; Kinloch and Friedel 2005; Osem et al. 2006a). Here, we contrast the predictive power of easily-obtained but potentially coarse site characteristics (estimated local climate, fire history, permitted grazing animals) with on-site measurements of ground and vegetation cover, asking which factors are most
predictive of seed bank composition. Identifying easy-to-measure factors that are predictive of seed bank dynamics in an area are important for land management, as the success of actions to increase diversity in degraded systems, such as chaining, herbicides, or prescribed fire, depends largely on the existence of seed banks of desirable species that can increase after management (Meyer 1994; Bakker and Berendse 1999; Pywell et al. 2002; Smith et al. 2002).

The Great Basin desert of North America is an arid region that contains broad expanses of sagebrush steppe vegetation. Degradation of sagebrush shrublands affects the ability of these communities to provide ecosystem services such as biodiversity and habitat for obligate sagebrush species. For example, degradation of sage-grouse brooding habitat has resulted in population reductions and range shifts, evidenced by abandonment of sites by sage-grouse that were once active leks and nesting grounds (Aldridge and Boyce 2007; Knick et al. 2011). Within the Great Basin, plant communities vary greatly in composition, from relatively intact systems (often at higher elevations) to highly degraded sites (Young et al. 1972; West 1999). Some of the most degraded sites have lost a majority of their native plant communities, likely due to the combined effects of multiple disturbance factors such as inappropriate grazing, invasion by introduced annual grasses, and repeated fire (Knick et al. 2011; Miller et al. 2011). Other sites may have experienced fewer disturbance factors (i.e. heavy grazing pressure and some invasion, but no fire) or less frequent or intense disturbances, and thus may retain some elements of their native structure, such as an intact shrub community but a degraded native understory community (West 1999). Restoration opportunities vary on
these different types of sites, and responses to treatments can vary greatly depending on the abundance of introduced and native seeds in the soil.

Here, our goal was to characterize the seed bank and above-ground vegetation for a series of sagebrush steppe sites that currently or historically serve as appropriate sage-grouse nesting habitat, but vary in their fire history, grazing use, and current vegetation composition. We present the results of above-ground vegetation and seed bank characteristics for 17 sites located within two ecoregions in Northern Nevada, and address the following questions:

1) What is the relationship between site characteristics (including shrub cover, ground cover, climate, fire history, and grazing use) and the density of introduced and native seeds in the seed bank?

2) Can site characteristics predict seed bank and above-ground diversity (measured by richness and evenness) and the presence of rare native species?

3) Can site characteristics predict how well the seed bank and above-ground vegetation mirror one another in species composition?

We predicted that, overall, site disturbance history would have the strongest influence on seed bank composition, and expected that the density of introduced species would increase and that species richness would decrease in areas with more recent fires and higher grazing allocation. Given that water is a limiting resource in many sagebrush dominated sites, we expected to see a positive relationship between precipitation and native seed density and richness in the seedbank. We also expected that shrub cover would be associated with seed bank composition, given the known
relationships between shrub composition and disturbance history (Young and Evans 1974; Morris and Leger 2016). Specifically, we predicted that there would be a positive relationship between shrub cover of sagebrush (Artemisia tridentata Nutt.) and native richness, and that we would find more rare species in areas with greater sagebrush cover. We expected the opposite relationships to occur in areas with higher cover of rabbitbrush species (Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird and Chrysothamnus viscidiflorus (Hook.) Nutt.), as these species are more abundant after disturbance (Miller et al. 2013). Finally, we predicted that below-ground species composition would be more similar to the above-ground composition in areas with higher levels of disturbance and lower precipitation.

MATERIALS AND METHODS

STUDY SITE

Sites were selected within two sagebrush-dominated ecoregions located in north-eastern Nevada (Fig. 1), as designated by the Environmental Protection Agency (Level IV Ecoregions: Central Basin and Range - 13m and Northern Basin and Range - 80a) (Omernik and Griffith 2014). These ecoregions were selected based on their importance for sensitive wildlife habitat, and specific study sites were selected using a nesting habitat model for the greater sage-grouse (Gibson et al. 2016), a species of concern in the Great Basin. Study sites were selected randomly in areas of high nesting habitat quality within 6km buffer around 17 current or historic sage-grouse lek. Sites were rejected if they were inaccessible, and a new site was generated. We used historic
fire maps (1910-2013) and historic grazing animal use information from the United States Bureau of Land Management to estimate disturbance history at each site. On federal lands, grazing is measured in animal unit months (AUMs). We tabulated the number of AUMs for the allotment surrounding each research site by subtracting the suspended AUMs from the permitted AUMs for each location (https://www.blm.gov/ - last accessed: 04March15). We quantified the fire history on our sites using both distance and temporal metrics. In order to quantify fire frequency for sites experiencing multiple fires at different spatial and temporal scales, we created four distinct fire categories. We noted whether fires occurred either on the site (hereafter, “on-site”) or within 1 km of a site (“nearby”), and further noted whether the fire(s) were within 10 years (“recent”) or greater than 10 years from the sampling date (“past”). We based our definition for “recent” and “past” fire on the estimates of long-term vegetation recovery in sagebrush, which can begin to occur >10 years after a fire (Miller et al. 2013). We established our measure of fire “on” or “nearby” to account for potential seed dispersal of introduced species from neighboring sites that have burned.

Vegetation and Seed Bank Sampling

Plant surveys and seedbank sampling took place in June 2014, with the goal of sampling the seed bank at the point where most seeds had germinated for the season but before seeds of most species had fallen to the ground from that year’s seed production. Each site was represented by one 4-hectare plot, which was sampled using
twenty randomly-placed 1m² quadrats in a stratified random design, with five quadrats placed in each of the four quadrants of the plot. Within each quadrat, we assessed the percent cover of each species and collected four 128cm³ soil samples from the top 5cm of soil in each quadrat, including the litter layer. These samples were bulked to represent the seed bank in that 1 m² location. We also assessed shrub cover across the plot using a point-intercept sampling method at 1m intervals along five 25m transects randomly located within each plot. We noted all living shrub species encountered along a transect, as well as dead shrubs that were still providing woody structure on the landscape, and we referred to the latter as standing dead.
QUANTIFYING THE SEED BANK

We assessed the seedbank using our standard lab method (Espeland et al. 2010). Seed bank samples were processed in the greenhouse at the University of Nevada, Reno starting in October 2014. Samples were sieved through a $\frac{1}{2}$ cm screen to remove large rocks. Tables and trays (Garland - Mini Seed Tray 6.5”L X 4”W X 2”H) were prepared such that they allowed for wicking of moisture in and out of the soil samples. This procedure included covering the tables with tarps and placing a layer of quilt batting between the tarp and the trays. Trays were filled with 1 cm of vermiculite and topped with landscaping cloth. Once the trays were prepared, we evenly spread a $118.3 \text{ cm}^3$ portion of each soil sample over the top of the landscaping cloth. In order to promote an even distribution of the samples from each plot across the greenhouse area, trays were arranged in four blocks using a stratified random design, with each block having an equal number of samples from each plot and all blocks placed along the same greenhouse table in an east-west orientation. The location assignment on the table for blocks, and trays within blocks, were randomized every two weeks throughout the experiment.

The experimental design consisted of eight treatments, with each treatment period lasting until seedling emergence tapered to nearly zero for at least two weeks (Table 1), with samples checked for emergence once or more per week. Timing of water application was initiated in fall, corresponding to the typical growing season phenology in our region, and the greenhouse temperature was constrained to highs and lows consistent with ambient weather, with high temperatures ranging between 16-21°C and
low temperatures allowed to fluctuate with ambient conditions, but held to a minimum of 2 Cº to prevent freezing pipes in the greenhouse. All watering occurred three times each week for 10 minutes using a watering system with overhead misters, and watering for the first treatment period began in October 2014. At the beginning of the second treatment period, soil samples were stirred and then watered normally thereafter. The third treatment was a dry period at ambient temperature; followed by a fourth treatment period that again involved normal watering during warmer summer temperatures. The fifth treatment period was a dry, summer period. The sixth treatment was a wet treatment, which began the following fall. At the beginning of the fifth treatment period, we applied 3ml of a 5% liquid smoke solution (pH 3, Lazy Kettle Brand Hickory Liquid Smoke) prepared using methods outlined in Doherty and Cohn (2000) followed by normal watering, to trigger germination by any species that break dormancy in response to fire cues. The final treatment included the application of gibberellic acid (GA), a plant hormone that can trigger emergence in dormant seeds. We applied 3ml of GA solution (10mg/L - Super-Grow SG-GA3 20) to each tray and provided normal watering thereafter. The smoke and GA treatments did not reveal any new species, but did stimulate the germination of additional seeds of previously germinated species. As seedlings emerged from the trays, we cataloged each distinct morphotype. A subset of the seedlings of each morphotype was photographed and raised to maturity for identification purposes. We were unable to identify a small portion of both the above and below-ground plants, equivalent to less than 1% of individuals, and these plants were excluded from our analyses. Nineteen morphotypes were identified to
genus, and were analyzed as a single species at each site. We also identified two species within the seedbank that were riparian obligate species (*Veronica anagallis-aquatica* L. and *Myosurus apetalus* C. Gay). Because these species were only represented by a few seeds and would not normally grow in our focal habitats, we excluded them from our analyses.

**DATA ANALYSIS**

We analyzed our data using generalized linear models (GLMs) in program R (R Development Core Team 2016) in a two-step process. First, we asked how well different types of environmental characteristics predicted above and below-ground characteristics, running separate models for each set of characters. Second, if multiple top models were identified for a particular response variable, we used an iterative model averaging process that included all environmental characteristics to determine which were the most predictive. Categories of environmental characteristics were: shrub cover, ground cover, climate, and disturbance. The predictor variables for the shrub cover model included the fraction of shrub cover of the three most dominant shrubs on our sites: *A. tridentata*, *C. viscidiflorus*, and *E. nauseosa*. The predictor variables for the ground cover model included the fraction of different types of ground cover at our sites based on our quadrat sampling, as predictor variables, including: standing dead, bare ground, litter, and rock. The predictor variables for the climate model included annual measures of precipitation (mm), minimum temperature (°C), and maximum temperature (°C) at the sites based on 64 year averages derived using PRISM data from 1950-2014 (Daly et al. 2008). Lastly, the predictor variables for the
disturbance model included AUMs, number of recent fires nearby, number of past fires nearby, number of recent fires on site, and number of past fires on site. We performed a Pearson’s correlation analysis among all predictor variables to confirm that they were not highly correlated (R < ±0.7). We also used plots of residual versus fitted values to check for trends within the residuals for each of the models. We ran preliminary analyses to determine whether the block factor in our greenhouse experimental design was predictive of seed bank composition, and found that it did not have a significant effect. This factor was not included in final models.

When analyzing our GLMs, we selected the best model using Akaike’s information criterion (AIC) scores, with better models possessing lower AIC scores and models <2 from the best model considered to be comparable to the best model. When we identified multiple top models for a particular response variable, the second step was to analyze the GLMs using multi-model inference using the MuMIn package for program R (Barton 2016). For this step, we generated a set of candidate models using the dredge function, each containing no more than three terms from the global set of predictor variables from all of the aforementioned models. We then performed model averaging across all candidate models in order to obtain estimates of the regression coefficients for each variable averaged across all models and weighted by the corrected AIC scores for those models. We report both the zero average results (ZA; includes parameter estimates of zero for predictor variables that are excluded from a particular model when performing model averaging) and the natural average results (NA; only averages the parameter estimates for models containing that particular variable). The
ZA approach is best for comparing the relative importance of different parameters, while the NA approach is best for determining the importance of an individual parameter (Burnham and Anderson 2002; Grueber et al. 2011). We also report estimates of parameter importance (IMP) for each of the predictor variables, calculated based on the proportion of highly predictive models containing the focal parameter: higher IMP values can result when a parameter is included in more models and/or is included in highly predictive models. For model selection, we present the groups of environmental characteristics that produced top models, as well as the individual significance of factors in those models. We also present results of model averaging for response variables with multiple top models. When there were significant relationships, we present the results of linear regressions for a select group of factors and responses.

We tabulated seed bank densities for each site by species status, noting whether each species was annual, perennial, native or introduced (USDA NRCS 2017). We averaged seed densities across all 20 samples taken from a site for use as a response variable in our GLMs. We also calculated above-ground and below-ground diversity metrics. We calculated species richness by counting the number of species observed within the seed bank samples from each site, and species evenness for both native and introduced species from the average values for either seed density or percent cover for species across all samples for a site. Evenness was calculated as follows:

$$\left(\frac{\left(\sum_{i=1}^{S} (P(i) \times \ln P(i))\right) \times -1}{\ln(S)}\right)$$
Here, $S$ is the total number of species and $P(i)$ is the proportion of species $i$ within the sample.

To determine the presence of rare species, we summed the number of unique native species found at each of our seventeen sites, calculating this number separately for above and below-ground species composition. We designated a species as “rare” if it only occurred at one of our sites; forty-five species in the above-ground community and fifteen species in the below-ground community received this distinction. Species richness, species evenness, and the number of rare plants on a site were used as response variables in our GLMs, for both above and below-ground communities. Finally, we calculated two measures of similarity between the above and below-ground species composition at our sites for use as response variables in our GLMs. First, we calculated the Bray-Curtis (Sorensen) similarity index (Gardener 2014) for the presence/absence of species, with higher values indicating that the above and below-ground communities are more similar. Next, we calculated the Bray-Curtis dissimilarity index (Gardener 2014) for the density of species, with higher values indicating that the above and below-ground communities are more different from each other. Standardized effect sizes for our models were obtained using the QuantPsyc package in program R (Fletcher 2012).

RESULTS

ABOVE-GROUND AND SEED BANK COMPOSITION

In total, we identified 126 species in the above-ground community and 62 species in the seed bank (Supplemental Table 1). Overall, 27 species were found in both
the above-ground and below-ground communities across all sites. These included 19 native species (10 annuals and 9 perennials) and 8 introduced species (6 annuals and 2 perennials) (Fig. 2); note that these species were not necessarily found in both the above and below-ground communities at all sites (Supplemental Table 1). Species found in both the above and below-ground communities made up 12.7-41.7% of the cover in the above-ground community and 54.2-99% of the contents of the seed bank.

Across sites, the above-ground vegetation was composed of 50-95% cover of native species and 0.7-62.2% cover of introduced species (Fig. 3A). The most common invasive species were annuals, including *Alyssum desertorum* Stapf, *Ceratocephala testiculata* (Crantz) Roth, and *Bromus tectorum* L. Some sites also possessed high above-ground densities of the perennial grass *Agropyron cristatum* (L.) Gaertn., probably as a result of past seeding efforts due to disturbance. Native species composition varied greatly from site-to-site, with many sites possessing unique assemblages of native species. However, some species were present at a large proportion of sites, including: the annual forbs *Collinsia parviflora* Lindl. and *Microsteris gracilis* (Hook.) Greene (> 64% of sites), perennial forbs of the *Phlox* L. genus (> 82% of sites), the perennial grasses *Elymus elymoides* (Raf.) Swezey and *Poa secunda* J. Presl (> 82% of sites), and the perennial shrubs *A. tridentata* and *C. viscidiflorus* (> 94% of sites).

Below-ground, 53.3-85.7% of the 62 species identified in the seed bank were native, and invasive species made up between 20-96.7% of the density of seeds in the seedbank across all sites (Fig. 3B). Every site contained seeds of the introduced annuals *A. desertorum* and *C. testiculatum* in the seed bank, whereas 82% of sites contained *B.*
tectorum and 65% contained Draba verna L. (Supplemental Table 1). Other invasive species formed only a very small portion of the seed bank across sites (Fig. 3B). The most common native annual forbs in the seed bank included C. parviflora, Gayophytum ramosissimum Torr. & A. Gray, and M. gracilis, all of which were present at greater than 82% of sites. The most common native grasses included annual grasses of the genus Vulpia C.C. Gmel., which were present at greater than 94% of sites, and the perennial grass P. secunda, present at all sites. The only seeds of woody plants found in the seed bank were of the shrub genus Artemisia L., found at 82% of sites.

What is the relationship between site characteristics (including shrub cover, ground cover, climate, fire history, and grazing use) and the density of introduced and native seeds in the seed bank?

Contrary to our prediction, disturbance history was not the best predictor of seed bank density. Rather, shrub cover was the best predictor of the seed density of both native and introduced species (Table 2A). Introduced species density was higher when there was increased cover of E. nauseosa ($P = 0.008$), and seed bank densities of native annual species were higher in areas with more cover of C. viscidiflorus ($P = 0.004$) (Fig. 4). Density of native perennial species in the seed bank tended to increase with increasing cover of E. nauseosa ($P = 0.087$), but though this was the best predictor identified with model selection, this factor was not significant (Fig. 4).
CAN SITE CHARACTERISTICS PREDICT SEED BANK AND ABOVE-GROUND DIVERSITY (RICHNESS AND EVENNESS) AND THE PRESENCE OF RARE NATIVE SPECIES?

**ABOVE-GROUND RICHNESS:** Shrub cover was one of the two best predictors of above-ground native species richness (Table 2B), with the richness of native species increasing with increasing shrub cover of *A. tridentata* (*P* = 0.041) and *C. viscidiflorus* (*P* = 0.047) (Fig. 5A, 6A, 6B). The predictive ability of the climate model was comparable to that of the shrub model, but none of the climate variables were significantly associated with above-ground native species richness. Model averaging found that above-ground native species richness increased when there was fire nearby > 10 years ago (NA: *P* = 0.009, ZA: *P* = 0.190), and decreased as maximum temperatures increased (NA: *P* = 0.003, ZA: *P* = 0.116) (Supplemental Table 2). The above-ground richness of introduced species was best predicted by ground cover (Table 2B), increasing with decreasing amounts of standing dead (*P* = 0.0097) and rock (*P* = 0.005) on a site (Fig. 5B, 6C, 6D).

**BELOW-GROUND RICHNESS:** Below-ground native species richness was best predicted by disturbance history and shrub cover (Table 2B). Native species richness in the seed bank increased when there was fire nearby < 10 years ago (*P* = 0.070). Shrub cover was a comparable predictor of below-ground richness of native species, with increased below-ground richness in communities with greater cover of *E. nauseosa*, but this variable was not individually significant (*P* = 0.076). Model averaging identified that the following characteristics were most predictive of seed bank richness: the richness of native species in the seedbank increased with increasing cover of *A. tridentata* (NA: *P* = 0.085, ZA: *P* = 0.515), increased when there was fire nearby < 10 years ago (NA: *P* =
0.053, ZA: \( P = 0.421 \), and decreased when there was fire on a site > 10 years ago (NA: \( P = 0.090 \), ZA: \( P = 0.540 \)) (Supplemental Table 3A). Again, shrub cover and disturbance history were comparable in their ability to predict the richness of introduced species in the seed bank (Table 2B). Model averaging found that below-ground richness of introduced species increased with increasing shrub cover of \( E. nauseosa \) (NA: \( P = 0.0004 \), ZA: \( P = 0.007 \)) and decreased when there was fire nearby > 10 years ago (NA: \( P = 0.0003 \), ZA: \( P = 0.004 \)) (Supplemental Table 3B).

**Above-ground evenness:** Shrub cover best predicted above-ground native species evenness (Table 2B), with species evenness decreasing with increasing cover of \( A. tridentata \) (\( P = 0.063 \)) (Fig. 7A, 8A). In areas with lower native species evenness, the species composition and abundances varied from site-to-site, however, \( P. secunda \), a common native perennial grass, and two perennial Phlox species (\( P. hoodii \) and \( P. longifolia \)) were dominant species at several of the sites. These plots also contained high densities of other perennial forb species, including \( Leptodactylon pungens \) (Torr.) Torr. ex Nutt., \( Viola beckwithii \) Torr. & A. Gray, and the grasses \( E. elymoides \) and \( Hesperostipa comata \) (Trin. & Rupr.) Barkworth. Climate best predicted above-ground introduced species evenness (Table 2B), with evenness increasing with increasing precipitation (\( P = 0.001 \)) and maximum temperature (\( P = 0.009 \)) (Fig. 7B, 8B).

**Below-ground evenness:** Ground cover best predicted below-ground native species evenness (Table 2B), with evenness increasing with increasing rocky ground cover (\( P = 0.022 \)) (Fig. 7C). Shrub cover and disturbance history were comparable predictors of below-ground evenness of introduced species (Table 2B), and evenness
was found to decrease with increasing cover of *E. nauseosa* (NA: $P = 0.041$, ZA: $P = 0.334$) and when fire was on a site > 10 years ago (NA: $P = 0.021$, ZA: $P = 0.266$) (Supplemental Table 3C).

**Rare plants above- and below-ground:** Shrub cover was the best predictor of both the above- and below-ground presence of rare plants (Table 2C). Above-ground, the presence of rare species increased with increasing cover of *C. viscidiflorus* ($P = 0.031$) (Fig. 9A, 9B). Below-ground, the presence of rare species increased with increasing shrub cover of *A. tridentata* ($P = 0.007$) (Fig. 9A, 9C).

**Can site characteristics predict how well the seed bank and above-ground vegetation mirror one another in species composition?**

Ground cover was the best predictor of the similarity between the presence of above and below-ground plant species (Table 2D). Sites possessing a higher degree of similarity were those with higher cover of bare ground ($P = 0.043$) and more litter cover ($P = 0.018$) (Fig. 10A). This similarity was mostly due to the presence of introduced species, such as *A. desertorum, C. testiculata, B. tectorum,* and *A. spicatum*; however, native species, such as *C. parviflora* and *P. secunda*, also contributed to the observed similarities. Disturbance history was the best predictor of the dissimilarity between the density of species above and below-ground (Table 2D). Sites experiencing fire <10 years ago possessed a higher degree of similarity ($P = 0.017$) (Fig. 10B). These similarities were predominantly due to their low above and below-ground species richness. The most similar communities were characterized by the presence of the introduced species *B.*
tectorum, A. desertorum, and C. testiculata, although P. secunda also contributed to the similarity in these communities, and C. parviflora, M. gracilis, and A. tridentata were also partially responsible for these results.

DISCUSSION

Research exploring the seedbank dynamics within a community can provide insight into the environmental factors that shape the community and, ultimately, how it may respond to disturbance and environmental change (Simpson et al. 1989). In deserts, where environmental conditions can vary greatly from year-to-year, seed banks can be important part of bet-hedging strategies that ultimately shape above-ground species composition (Venable 2007; Gremer et al. 2016). This research aimed to identify environmental characteristics that are predictive of the seed bank composition within areas of high wildlife habitat value in the Great Basin, assisting our predictions of how particular types of habitat may respond to environmental change and restoration efforts. We found that shrub cover was the most predictive of seed bank composition. Of ten responses related to below-ground factors, shrub cover was predictive of seven factors, including seed densities and richness of native and introduced species, evenness of introduced species, and the presence of rare species. Fire history was the next most predictive factor, sharing top-model status with shrub composition for three below-ground responses (native and introduced richness, introduced evenness), and was the main predictor of dissimilarity above- and below-ground. Climate factors were
associated with several above-ground, but no below-ground responses, and AUMs were not predictive of any of our response variables.

Shrubs are indicators of past disturbance and keystone species that can affect the successional trajectory of a community. In our study, native annual seed densities were higher in areas with greater cover of *C. viscidiflorus*, introduced seed densities and richness were higher and introduced evenness was lower when there was greater of *E. nauseosa*, and there were more rare species in seed banks of sites with greater *A. tridentata* cover. Both *C. viscidiflorus* and *E. nauseosa* are found in areas that have experienced disturbance in the past (Scheinost et al. 2010; Tilley and St. John 2012; Miller et al. 2013), and both annual and introduced species are also known to perform well in disturbed areas in this region (Beatley 1969; Young et al. 1972). Differences in seed bank densities between areas containing different early-seral shrubs (*C. viscidiflora* and *E. nauseosa*) indicate potential differences in the ecology of these shrub species. One possibility is that these shrubs may have different preferences for soil type, differ in response to past disturbance, or other environmental conditions that also result in different understory communities. Another possibility is that the environmental requirements and disturbance for these shrubs are the same, but that the shrub species differ in the types of microsite conditions they provide for understory species (Donovan and Ehleringer 1994). Future work could differentiate the role that these two species play, as either indicators of past change or engineers of understory and seed bank dynamics.
Foundation species, such as *A. tridentata*, reduce invasion by introduced species and help to maintain communities of native plants (Prevéy et al. 2010). *A. tridentata* is a later-seral species in this system, indicating that an area has experienced little to no disturbance for between 10-70 years (West 1999; Morris and Leger 2016). Although the cover of *A. tridentata* and *C. viscidiflorus* was not highly correlated ($R^2 = 0.029$), sites with higher native species richness typically contained some proportion of both of these shrub types. This may indicate that the site has either experienced patchy disturbance in the past or may be recovering from disturbance. Moderate levels of disturbance are thought to create more niches for supporting a higher diversity of species (Connell 1978; Hobbs and Huenneke 1992). Sites with higher cover of *A. tridentata* typically contained more above-ground native perennial species, likely indicating that they have not experienced recent disturbance and have reached a later successional stage, one which might not possess as many micro-site types for supporting diverse communities (Hobbs and Huenneke 1992). The relationships we found between shrub cover and the richness of rare species also support the idea that areas experiencing a moderate level of disturbance would have more niches to support a broader range of above-ground species; whereas areas dominated by late seral species, like *A. tridentata*, may have supported a broader range of species over time and contain a multitude of species within their seed banks in a state of dormancy.

In addition to our on-the-ground measurements, we incorporated coarse measures of fire history, climate, and grazing use into our modeling, as this information is broadly available for researchers as well as land managers for use in decision-making.
Our research indicated that while some of these measures were predictive of seed bank dynamics, AUM permits, in particular, were not predictive of above- or below-ground responses. Grazing pressure by livestock is notoriously difficult to quantify (Landsberg and Crowley 2004), and estimating the effects of grazing using AUMs is challenging, because it does not take into consideration many important factors, such as: the dietary preferences of the animals (West 1999), their movements through space, their densities across the allotment, and the amount of time they spend in an area (Pringle and Landsberg 2004). These important factors likely explain the wide variation in results of studies on grazing and seed banks in arid systems (Bakker and de Vries 1992; Peco et al. 1998; Kinloch and Friedel 2005; Osem et al. 2006a).

Similarly, estimating site fire history is challenging, considering that fire frequency from mapped perimeters does not account for other important aspects of fire, such as: fire intensity and the rate of spread (Brooks et al. 2004; Miller et al. 2013). Despite the coarseness of our fire estimate, this factor was associated with some response variables, including above-ground richness of native species and below-ground richness and evenness of introduced species. Fire frequency was also the best predictor of the similarity between the relative densities of species contained in the above and below-ground communities. This pattern was primarily due to high densities of introduced species, probably as a result of recent fires on these sites, as indicated by our model. As previously mentioned, introduced plant species tend to dominate the seed bank after fires, at the expense of native species (Knapp 1996; Humphrey and Schupp 2001). Finally, while climate means were predictive of some above-ground
characteristics (including richness of native species and evenness of introduced species), they were not associated with any below-ground characters. Above-ground evenness of introduced species was associated with sites dominated by *B. tectorum* and/or *C. testiculata*. Sites with low evenness also possessed low species richness of introduced species, and may experience high temperatures that are unsuitable for the success of native species, but with water resources that can be exploited by the opportunistic introduced species they contain (Davis et al. 2000). While abiotic factors clearly affect seed production, more fine-scaled information (like previous year’s precipitation) may be more predictive than averages across years.

Ground cover is known to vary across sagebrush communities, with this factor influencing seedling recruitment. For example, sagebrush communities possessing low levels of introduced species are typically characterized by bare interspaces between shrubs, with shrubs acting as nurse plants for native herbaceous species (Callaway 1995). Litter can have a positive effect on plant establishment in desert systems (Xiong and Nilsson 1999), due to its capacity to retain moisture and provide suitable conditions for seedlings (Facelli and Pickett 1991). In our study, we also found that bare ground and litter were strong predictors of the similarity in species present in the above and below-ground communities, with sites with less bare ground and more litter showing high similarities and low richness.

The loss of woody species and increased cover by water-impermeable surfaces may create an opportunity for highly opportunistic introduced species to dominate in an area, as a result of higher availability of water in particular microsites (Prevéy et al.
Other research has shown that rocks may act as obstacles to seeds landing or dispersing through an area, accumulating seeds along their edges and/or facilitating burial in the crevices between rocks, but that they may not provide suitable sites for seedling survival (Chambers 2000). In our study, we found that ground cover predicted below-ground evenness of native species, above-ground richness of introduced species, and similarity in the presence of species in the above and below-ground communities. Sites with higher amounts of rocky ground cover typically contained low to moderate densities of native species within their seed banks; these seeds may have remained dormant due to sub-optimal conditions for germination. Areas with high amounts of rock and standing dead were typically dominated by one or two aggressive introduced species, B. tectorum and/or C. testiculata. Because increases in resource availability, even over short periods, can increase invasion success (Davis and Pelsor 2001), these competitive introduced species may have benefited from water resources made available as a result of both shrub death and a more concentrated delivery of moisture by run-off from rocky ground cover.

Overall, our results indicate that field surveys of shrub and ground cover may be useful tools for predicting seed bank dynamics in areas of sagebrush steppe. Acquiring these data is fairly straightforward, and can potentially provide insight regarding the long term disturbance history of an area and the relative presence of native and introduced species. These findings support other research showing that plants may act as strong indicators of the effects of land use on rangeland biodiversity (Landsberg and Crowley 2004). Further work should be done to explore these patterns and to
distinguish what differences in the ecology between *C. viscidiflorus* and *E. nauseosa* are affecting seed bank composition, with the hope of being able to disentangle their contrasting relationships to the seed bank dynamics of native and introduced species.

**ACKNOWLEDGEMENTS**

I am thankful for the dedication of Owen Baughman and Scott Ferguson when collecting vegetation data and seed bank samples, and for their help navigating the rough and winding roads through Nevada. I would like to thank Vicki Thill, Brianna Kooreman, and Marenna Disbro for their help with data entry, seedling identification, and work in the greenhouse. I would also like to thank Jerry Tiehm for his expert help identifying plants from both the field surveys and the seed bank study.
REFERENCES


257–282


Peco B, Ortega M, Levassor C (1998) Similarity between seed bank and vegetation in...


R Development Core Team (2016) R: a language and environment for statistical computing.


USDA NRCS (2017) The PLANTS Database - National Plant Data Team, Greensboro, NC.

U.S. Department of Agriculture, Natural Resources Conservation Service,


West NE (1999) Synecology and disturbance regimes of sagebrush steppe ecosystems.


Young JA, Evans RA (1975) Germinability of seed reserves in a Big Sagebrush community.


Table 1 Schedule of seed bank treatments. Each treatment period lasted until seedling emergence tapered to nearly zero for at least two weeks. All watering occurred three times each week for 10 minutes using a watering system with overhead misters.

<table>
<thead>
<tr>
<th>Date of Onset</th>
<th>Treatment Phase</th>
<th>Duration (weeks)</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 October 2014</td>
<td>First</td>
<td>20</td>
<td>Watering</td>
</tr>
<tr>
<td>4 March 2015</td>
<td>Second</td>
<td>8</td>
<td>Stir Soil, Watering</td>
</tr>
<tr>
<td>27 April 2015</td>
<td>Third</td>
<td>8</td>
<td>Dry</td>
</tr>
<tr>
<td>1 July 2015</td>
<td>Fourth</td>
<td>5</td>
<td>Watering</td>
</tr>
<tr>
<td>4 August 2015</td>
<td>Fifth</td>
<td>11</td>
<td>Dry</td>
</tr>
<tr>
<td>20 October 2015</td>
<td>Sixth</td>
<td>3</td>
<td>Watering</td>
</tr>
<tr>
<td>10 November 2015</td>
<td>Seventh</td>
<td>10</td>
<td>Smoke Water</td>
</tr>
<tr>
<td>22 January 2016</td>
<td>Eighth</td>
<td>6</td>
<td>Gibberellic Acid</td>
</tr>
</tbody>
</table>
Table 2 Model results for generalized linear models and model averaging assessing the relationships between (A) seed density, (B) diversity, (C) rarity, and (D) above vs. below-ground similarity and environmental characteristics. The relationship column shows the specific relationships between the response and the model variables. For response variables with multiple best models, the AIC values and model averaging results for the natural average (NA) are provided in their own column.

A. Seed Density (m⁻²)

<table>
<thead>
<tr>
<th>Best Model</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native Annual Shrub Cover</td>
<td>↑ CHVI**</td>
</tr>
<tr>
<td>Native Perennial Shrub Cover</td>
<td>↑ ERNA¹</td>
</tr>
<tr>
<td>Introduced Shrub Cover</td>
<td>↑ ERNA**</td>
</tr>
</tbody>
</table>

B. Diversity

<table>
<thead>
<tr>
<th>Community</th>
<th>Native/Introduced</th>
<th>Model Selection</th>
<th>AIC</th>
<th>Relationship</th>
<th>Model Averaging (NA)</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Richness</td>
<td>Above-Ground</td>
<td>Native Shrub Cover</td>
<td>121.17</td>
<td>↑ ARTR¹, ↑ CHVI*</td>
<td>↑ Fire Near &gt;10 Years**, ↓ Maximum Temp.***</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Climate</td>
<td>121.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduced Ground Cover</td>
<td>↓ Standing Dead**, ↓ Rock**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Below-Ground</td>
<td>Native Disturbance</td>
<td>85.56</td>
<td>↑ Fire Near &lt;10 years¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shrub Cover</td>
<td>86.18</td>
<td>↑ ERNA¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduced Shrub Cover</td>
<td>63.34</td>
<td>↑ ERNA***, ↓ Fire Near &gt;10 Years***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Disturbance</td>
<td>64.99</td>
<td>↓ Fire Near &gt;10 Years¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evenness</td>
<td>Above-Ground</td>
<td>Native Shrub Cover</td>
<td>9.44</td>
<td>↓ ERNA*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduced Climate</td>
<td>↑ Precipitation**, ↑ Maximum Temp.**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Below-Ground</td>
<td>Native Ground Cover</td>
<td>↑ Rock*, ↑ Bare Ground*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduced Shrub Cover</td>
<td>9.44</td>
<td>↓ ERNA*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Disturbance</td>
<td>10.67</td>
<td>↓ Fire On &gt;10 Years¹</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

C. Rarity

<table>
<thead>
<tr>
<th>Best Model</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above-Ground Shrub Cover</td>
<td>↑ CHVI*</td>
</tr>
<tr>
<td>Below-Ground Shrub Cover</td>
<td>↑ ARTR**</td>
</tr>
</tbody>
</table>

D. Above vs. Below-Ground

<table>
<thead>
<tr>
<th>Best Model</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Similarity - Presence Ground Cover</td>
<td>↑ Litter*, ↑ Bare Ground*</td>
</tr>
<tr>
<td>Dissimilarity - Density Disturbance</td>
<td>↓ Fire On &lt;10 Years¹</td>
</tr>
</tbody>
</table>

ARTR = A. tridentata, CHVI = C. viscidiflorus, ERNA = E. nauseosa

$\text{t} = P < 0.10, * = P < 0.05, ** = P < 0.01, *** = P < 0.001$
### Supplemental Table 1.

List of all species in the above and below-ground communities, listing life history information and the number of plots where the species occurred. I = introduced, N = native, W = riparian oblicate, AF = annual forb, PF = perennial forb, AG = annual grass, PG = perennial grass, PW = perennial woody

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Plant Code</th>
<th>Native/Introduced</th>
<th>Growth Form</th>
<th>Below-Ground</th>
<th>Above-Ground</th>
<th>Both</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achillea</td>
<td>millefolium</td>
<td>ACMI</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Achnatherum</td>
<td>hymenoides</td>
<td>ACHY</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Achnatherum</td>
<td>thurberianum</td>
<td>ACTH</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Agropyron</td>
<td>cristatum</td>
<td>AGCR</td>
<td>I</td>
<td>PG</td>
<td>3</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Agropyron</td>
<td>spicatum</td>
<td>AGSP</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Agrostis</td>
<td>gigantea</td>
<td>AGGI</td>
<td>I</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Allium</td>
<td>acuminatum</td>
<td>ALAC</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Allium</td>
<td>nevadense</td>
<td>ALNE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Alyssum</td>
<td>desertorum</td>
<td>ALDE</td>
<td>I</td>
<td>AF</td>
<td>17</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Amelanchier</td>
<td>alnifolia</td>
<td>AMAL</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Antennaria</td>
<td>dimorpha</td>
<td>ANDI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Antennaria</td>
<td>stenophylla</td>
<td>ANST</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Arabis</td>
<td>holboellii</td>
<td>ARHO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Arabis</td>
<td>puberula</td>
<td>ARPU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Arnica</td>
<td>sororia</td>
<td>ARSO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Artemisia</td>
<td>arbuscula</td>
<td>ARAR</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Artemisia</td>
<td>nova</td>
<td>ARNO</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Artemisia</td>
<td>tridentata</td>
<td>ARTR</td>
<td>N</td>
<td>PW</td>
<td>14</td>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td>Artemisia</td>
<td>vaseyana</td>
<td>ARVA</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>beckwithii</td>
<td>ASBE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>calycosus</td>
<td>ASCA</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Astragalus</td>
<td>cibarius</td>
<td>ASCI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>filipes</td>
<td>ASFI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>lentiginosus</td>
<td>ASLE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>megacarpus</td>
<td>ASME</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>newberryi</td>
<td>ASNE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>purshii</td>
<td>ASPU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>salmonis</td>
<td>ASSA</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Astragalus</td>
<td>sp</td>
<td>ASSP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Balsamorhiza</td>
<td>hookeri</td>
<td>BAHO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Bassia</td>
<td>prostrata</td>
<td>BAPR</td>
<td>I</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Boechera</td>
<td>holboellii</td>
<td>BOHO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Bromus</td>
<td>tectorum</td>
<td>BRTE</td>
<td>I</td>
<td>AG</td>
<td>14</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>Calochortus</td>
<td>nuttallii</td>
<td>CANU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Carex</td>
<td>douglasii</td>
<td>CADO</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Carex</td>
<td>praegracilis</td>
<td>CAPR</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Carex</td>
<td>sp</td>
<td>CASP</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Cerastium</td>
<td>dubium</td>
<td>CEDU</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ceratocephala</td>
<td>testiculata</td>
<td>CETE</td>
<td>I</td>
<td>AF</td>
<td>17</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Chaenactis</td>
<td>douglasii</td>
<td>CHDO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Code</td>
<td>Native/Introduced</td>
<td>Growth Form</td>
<td>Below-Ground</td>
<td>Above-Ground</td>
<td>Both</td>
</tr>
<tr>
<td>--------------------</td>
<td>---------------</td>
<td>------</td>
<td>-------------------</td>
<td>-------------</td>
<td>--------------</td>
<td>--------------</td>
<td>------</td>
</tr>
<tr>
<td>Chenopodium</td>
<td>rubrum</td>
<td>CHRU</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chenopodium</td>
<td>sp</td>
<td>CHSP</td>
<td>I</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Chorispora</td>
<td>tenella</td>
<td>CHTE</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chorizanthe</td>
<td>watsonii</td>
<td>CHWA</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Chrysanthemum</td>
<td>viscidiflorus</td>
<td>CHVI</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>Cirsiium</td>
<td>subniveum</td>
<td>CISU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Collinsia</td>
<td>parviflora</td>
<td>COPA</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td>Comandra</td>
<td>umbellata</td>
<td>COUM</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Cordylanthus</td>
<td>kingii</td>
<td>COKI</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Cordylanthus</td>
<td>ramosus</td>
<td>CORA</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Crepis</td>
<td>acuminata</td>
<td>CRAC</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Crepis</td>
<td>modocensis</td>
<td>CRM0</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Crepis</td>
<td>occidentalis</td>
<td>CROC</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Crepis</td>
<td>sp</td>
<td>CRSP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>cinerea</td>
<td>CRCI1</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>circumscissa</td>
<td>CRCI2</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>flavoculata</td>
<td>CRFL</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>humilis</td>
<td>CRHU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>scoparia</td>
<td>CRSC</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>torreyana</td>
<td>CRTO</td>
<td>N</td>
<td>AF</td>
<td>8</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cryptantha</td>
<td>watsonii</td>
<td>CRWA</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cymopterus</td>
<td>ibapensis</td>
<td>CYIB</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Danthonia</td>
<td>unispicata</td>
<td>DAUN</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Delphinium</td>
<td>andersonii</td>
<td>DEAN</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Descurainia</td>
<td>pinnata</td>
<td>DEPI</td>
<td>N</td>
<td>AF</td>
<td>11</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Descurainia</td>
<td>sophia</td>
<td>DESO</td>
<td>I</td>
<td>AF</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Draba</td>
<td>verna</td>
<td>DRVE</td>
<td>I</td>
<td>AF</td>
<td>11</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Elymus</td>
<td>elymoides</td>
<td>ELEL</td>
<td>N</td>
<td>PG</td>
<td>3</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>Elymus</td>
<td>lanceolatus</td>
<td>ELLA</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Epilobium</td>
<td>brachycarpum</td>
<td>EPBR</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Epilobium</td>
<td>ciliatum</td>
<td>EPCI</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Eriastrum</td>
<td>signatum</td>
<td>ERSI</td>
<td>N</td>
<td>AF</td>
<td>9</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Ericameria</td>
<td>nauseosa</td>
<td>ERNA</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Erigeron</td>
<td>argentatus</td>
<td>ERAR</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Erigeron</td>
<td>bloomeri</td>
<td>ERBL</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Erigeron</td>
<td>chrysopsidis</td>
<td>ERCH</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Erigeron</td>
<td>divergens</td>
<td>ERDI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Erigeron</td>
<td>jonesii</td>
<td>ERJO</td>
<td>I</td>
<td>PF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Eriogonum</td>
<td>microthecum</td>
<td>ERMI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Eriogonum</td>
<td>ovalifolium</td>
<td>EROV</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Eriogonum</td>
<td>sphaerocephalum</td>
<td>ERSP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Eriogonum</td>
<td>strictum</td>
<td>ERST</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Eriophyllum</td>
<td>lanatum</td>
<td>ERLA</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Erodium</td>
<td>cicutarium</td>
<td>ERCI</td>
<td>I</td>
<td>AF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
### Supplemental Table 1. (Continued)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Plant Code</th>
<th>Native/ Introduced</th>
<th>Growth Form</th>
<th>Below-Ground</th>
<th>Above-Ground</th>
<th>Both</th>
</tr>
</thead>
<tbody>
<tr>
<td>Festuca</td>
<td>idahoensis</td>
<td>FEID</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Gayophytum</td>
<td>diffusum</td>
<td>GADI</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Gayophytum</td>
<td>ramosissimum</td>
<td>GARA</td>
<td>N</td>
<td>AF</td>
<td>16</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Gilia</td>
<td>inconspicua</td>
<td>GIIN</td>
<td>N</td>
<td>AF</td>
<td>12</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Gilia</td>
<td>sinuata</td>
<td>GISI</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gnaphalium</td>
<td>palustre</td>
<td>GNPA</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Haplopappus</td>
<td>acaulis</td>
<td>HAAC</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Haplopappus</td>
<td>stenophyllus</td>
<td>HAST</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Hesperostipa</td>
<td>comata</td>
<td>HECO</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Holosteum</td>
<td>umbellatum</td>
<td>HOUM</td>
<td>I</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ionactis</td>
<td>alpina</td>
<td>IOAL</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Ipomopsis</td>
<td>congesta</td>
<td>IPCO</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Juncus</td>
<td>bufonius</td>
<td>JUBU</td>
<td>N</td>
<td>AG</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Juniper</td>
<td>osteosperma</td>
<td>JUOS</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lappula</td>
<td>occidentalis</td>
<td>LAOC</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Lappula</td>
<td>redowskii</td>
<td>LARE</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Layia</td>
<td>glandulosa</td>
<td>LAGL</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lepidium</td>
<td>densiflorum</td>
<td>LEDE</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepidium</td>
<td>perfoliatum</td>
<td>LEPE</td>
<td>I</td>
<td>AF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Leptodactylon</td>
<td>pungens</td>
<td>LEPU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Lesquerella</td>
<td>sp</td>
<td>LESP</td>
<td>N</td>
<td>PF</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Leymus</td>
<td>triticoides</td>
<td>LETR</td>
<td>N</td>
<td>PG</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Linanthus</td>
<td>harknesii</td>
<td>LIHA</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Linum</td>
<td>lewisii</td>
<td>LILE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Lithophragma</td>
<td>glabrum</td>
<td>LIGL</td>
<td>N</td>
<td>PF</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lomatium</td>
<td>sp</td>
<td>LOSP</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Lupinus</td>
<td>arbustus</td>
<td>LUAR1</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Lupinus</td>
<td>argenteus</td>
<td>LUAR2</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lupinus</td>
<td>polyphyllus</td>
<td>LUPO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Lupinus</td>
<td>sp</td>
<td>LUSP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Machaeranthera</td>
<td>canescens</td>
<td>MACA</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Mentzelia</td>
<td>albicaulis</td>
<td>MEAL</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mertensia</td>
<td>oblongifolia</td>
<td>MEOB</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Microseris</td>
<td>nutans</td>
<td>MINU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Microsteris</td>
<td>gracilis</td>
<td>MIGR</td>
<td>N</td>
<td>AF</td>
<td>14</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>Mimulus</td>
<td>suksdorfii</td>
<td>MISU</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Monolepis</td>
<td>nuttalanus</td>
<td>MONU</td>
<td>N</td>
<td>AF</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Monolepis</td>
<td>spathulata</td>
<td>MOSP</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Myosotis</td>
<td>micrantha</td>
<td>MYMI</td>
<td>I</td>
<td>AF</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Myosotis</td>
<td>sp</td>
<td>MYSP</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Myosurus</td>
<td>apetalus</td>
<td>MYAP</td>
<td>W</td>
<td>AF</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Oenothera</td>
<td>caespitosa</td>
<td>OECA</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Opuntia</td>
<td>sp</td>
<td>OPSP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Penstemon</td>
<td>immanifester</td>
<td>PEIM</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
### Supplemental Table 1. (Continued)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Plant Code</th>
<th>Native/Introduced</th>
<th>Growth Form</th>
<th>Below-Ground</th>
<th>Above-Ground</th>
<th>Both</th>
</tr>
</thead>
<tbody>
<tr>
<td>Penstemon</td>
<td>kingii</td>
<td>PEKI</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Penstemon</td>
<td>speciosus</td>
<td>PESP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Phlox</td>
<td>austromontana</td>
<td>PHAU</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Phlox</td>
<td>hoodii</td>
<td>PHHO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Phlox</td>
<td>longifolia</td>
<td>PHLO</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Phlox</td>
<td>sp</td>
<td>PHSP1</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Physaria</td>
<td>sp</td>
<td>PHSP2</td>
<td>N</td>
<td>PH</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Poa</td>
<td>bulbosa</td>
<td>POBU</td>
<td>I</td>
<td>PG</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Poa</td>
<td>compressa</td>
<td>POCO</td>
<td>N</td>
<td>PG</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Poa</td>
<td>secunda</td>
<td>POSE</td>
<td>N</td>
<td>PG</td>
<td>17</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Polygonum</td>
<td>arenastrum</td>
<td>POAR</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Potentilla</td>
<td>sp</td>
<td>POSP</td>
<td>N</td>
<td>PF</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Purshia</td>
<td>tridentata</td>
<td>PUTR</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Ranunculus</td>
<td>glaberrimus</td>
<td>RAGL</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Sagina</td>
<td>saginoides</td>
<td>SASA</td>
<td>N</td>
<td>PF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Salsola</td>
<td>tragus</td>
<td>SATR</td>
<td>I</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Senecio</td>
<td>integerrimus</td>
<td>SEIN</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Sisymbrium</td>
<td>altissimum</td>
<td>SIAL</td>
<td>I</td>
<td>AF</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Stenotus</td>
<td>acaulis</td>
<td>STAC</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Symphyotrichum</td>
<td>frondosum</td>
<td>SYFR</td>
<td>N</td>
<td>AF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tetradymia</td>
<td>sp</td>
<td>TESP</td>
<td>N</td>
<td>PW</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Townsendia</td>
<td>florifer</td>
<td>TOFL</td>
<td>N</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Tragopogon</td>
<td>sp</td>
<td>TRSP1</td>
<td>I</td>
<td>AF</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Trifolium</td>
<td>sp</td>
<td>TRSP2</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Veronica</td>
<td>anagalis</td>
<td>VEAN</td>
<td>W</td>
<td>PF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Veronica</td>
<td>peregrina</td>
<td>VEPE</td>
<td>N</td>
<td>AF</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Veronica</td>
<td>sp</td>
<td>VESP</td>
<td>W</td>
<td>PF</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Viola</td>
<td>beckwithii</td>
<td>VIBE</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Vulpia</td>
<td>microstachys</td>
<td>VUMI</td>
<td>N</td>
<td>AG</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vulpia</td>
<td>octoflora</td>
<td>VUOC</td>
<td>N</td>
<td>AG</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Vulpia</td>
<td>sp</td>
<td>VUSP</td>
<td>N</td>
<td>AG</td>
<td>14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wyethia</td>
<td>sp</td>
<td>WYSP</td>
<td>N</td>
<td>PF</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Zigadenus</td>
<td>sp</td>
<td>ZISP</td>
<td>N</td>
<td>PF</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
**Supplemental Table 2** Effects of environmental characteristics on above ground richness of native species in sagebrush-steppe habitats, determined using a model averaging approach. Standardized parameter estimates from the naturally-averaged model (NA) and the zero-averaged model (ZA) are shown, with significant results ($P < 0.05$) in bold type.

<table>
<thead>
<tr>
<th>Model Category</th>
<th>Model Variables</th>
<th>NA</th>
<th>ZA</th>
<th>IMP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub Cover</td>
<td><em>Artemisia tridentata</em></td>
<td>3.07E+01</td>
<td>5.52E+00</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td>2.52E+01</td>
<td>1.73E+00</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td><em>Ericameria nauseosa</em></td>
<td>7.17E+01</td>
<td>4.85E+00</td>
<td>0.07</td>
</tr>
<tr>
<td>Ground Cover</td>
<td>Standing Dead</td>
<td>9.46E-02</td>
<td>4.32E-03</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Bare Ground</td>
<td>-7.12E-02</td>
<td>-3.59E-03</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Litter</td>
<td>-4.25E-01</td>
<td>-2.99E-02</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>-3.26E-01</td>
<td>-2.50E-02</td>
<td>0.08</td>
</tr>
<tr>
<td>Climate</td>
<td>Precipitation (mm)</td>
<td>8.61E-02</td>
<td>1.25E-02</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>Minimum Temperature (°C)</td>
<td>-3.37E+00</td>
<td>-4.21E-01</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Maximum Temperature (°C)</td>
<td>-5.12E+00</td>
<td>-4.04E+00</td>
<td>0.79</td>
</tr>
<tr>
<td>Disturbance</td>
<td>AUMs</td>
<td>5.71E-05</td>
<td>3.13E-06</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Recent Fires Nearby</td>
<td>1.75E+00</td>
<td>8.95E-02</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Past Fires Nearby</td>
<td>1.38E+01</td>
<td>9.97E+00</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>Recent Fires On-Site</td>
<td>-3.78E+00</td>
<td>-2.60E-01</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Past Fires On-Site</td>
<td>-3.02E+00</td>
<td>-3.56E-01</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Supplemental Table 3  Effects of four types of predictor variables on below-ground factors, including: (A) richness of native species, (B) richness of introduced species, and (C) evenness of introduced species in sagebrush-steppe habitats, determined using a model averaging approach run separately for variables in each category. Standardized parameter estimates from the naturally-averaged model (NA) and the zero-averaged model (ZA) are shown, as well as the estimated importance (IMP) for each factor, with significant results \( P < 0.05 \) in bold type.

<table>
<thead>
<tr>
<th>Category</th>
<th>Model Variables</th>
<th>A. Below-Ground Native Richness</th>
<th>B. Below-Ground Introduced Richness</th>
<th>C. Below-Ground Introduced Evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>NA</td>
<td>ZA</td>
<td>IMP</td>
</tr>
<tr>
<td>Shrub Cover</td>
<td>A. tridentata</td>
<td>1.2E+01</td>
<td>4.6E+00</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>C. viscidiflorus</td>
<td>9.8E+00</td>
<td>1.1E+00</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>E. nauseosa</td>
<td>9.3E+00</td>
<td>6.9E-01</td>
<td>0.07</td>
</tr>
<tr>
<td>Ground Cover</td>
<td>Standing Dead</td>
<td>3.0E-01</td>
<td>3.3E-02</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>Bare Ground</td>
<td>-1.6E-02</td>
<td>-1.3E-03</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Litter</td>
<td>-2.2E-01</td>
<td>-3.3E-02</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>1.6E-02</td>
<td>1.1E-03</td>
<td>0.07</td>
</tr>
<tr>
<td>Climate</td>
<td>Precipitation (mm)</td>
<td>2.1E-03</td>
<td>1.9E-04</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Min. Temp. (°C)</td>
<td>1.6E-01</td>
<td>-3.3E-02</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Max. Temp. (°C)</td>
<td>-3.9E-01</td>
<td>1.1E-02</td>
<td>0.08</td>
</tr>
<tr>
<td>Disturbance</td>
<td>AUMs</td>
<td>-5.9E-09</td>
<td>-4.2E-10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Recent Fires Nearby</td>
<td>3.0E+00′</td>
<td>1.5E+00</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>Past Fires Nearby</td>
<td>-1.1E+00</td>
<td>-9.4E-02</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Recent Fires On-Site</td>
<td>-2.1E+00</td>
<td>-2.9E-01</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>Past Fires On-Site</td>
<td>-1.4E+00′</td>
<td>-5.3E-01</td>
<td>0.37</td>
</tr>
</tbody>
</table>

\( t = \) trend \( P < 0.10 \)
FIGURE CAPTIONS

Fig. 1 Map of field sites showing (A) the western United States with the floristic Great Basin highlighted in gray and (B) north-eastern Nevada site locations within two sagebrush steppe dominated ecoregions, as designated by the U.S. Environmental Protection Agency (13M - Central Basin and Range, 80A - Northern Basin and Range).

Fig. 2 Mean percent composition for species and genera found in both the above and below-ground communities. Error bars show standard error across sites. Acronyms are: ACMI - Achillea millefolium, AGCR - Agropyron spicatum, ALDE - Alyssum desertorum, ARTR - Artemisia tridentata, ASCA - Astragalus calycosus, BRTE - Bromus tectorum, CTE - Ceratocephala testiculata, COPA - Collinsia parviflora, CRCI2 - Cryptantha circumscissa, CRSC - Cryptantha scoparia, CRTO - Cryptantha torreyana, DEPI - Descurainia pinnata, DESO - Descurainia sophia, DESP - Descurainia sp., DRVE - Draba verna, ELEL - Elymus elymoides, ERCH - Erigeron chrysopsidis, ERSI - Eriastrum signatum, GARA - Gayophytum ramosissimum, GIIN - Gilia inconspicua, IPCO - Ipomopsis congesta, LOSP - Lomatium sp., MIGR - Microsteris gracilis, POBU - Poa bulbosa, POSE - Poa secunda, SIAL - Sisymbrium altissimum, VUOC - Vulpia occidentalis, WYSP - Wyethia sp.

Fig. 3 Mean composition of species composing ≥ 0.5% of (A) total above-ground cover or (B) seed bank density, averaged across all sites. Error bars show standard error across sites. Acronyms are: AGCR - Agropyron cristatum, ALDE - Alyssum desertorum, ARTR - Artemisia tridentata, BRTE - Bromus tectorum, CTE - Ceratocephala testiculata, CHVI - Chrysothamnus viscidiflorus, COPA - Collinsia parviflora, CRTO - Cryptantha torreyana, DEPI - Descurainia pinnata, DRVE - Draba verna, ELEL - Elymus elymoides, ERNA - Ericameria nauseosa, ERSI - Eriastrum signatum, FEID - Festuca idahoensis, GARA - Gayophytum ramosissimum, GIIN - Gilia inconspicua, HOUM - Holosteum umbellatum, LESP - Lesquerella sp., LIGL - Lithophragma glabrum, MIGR - Microsteris gracilis, MISU - Mimulus suksdorfii, MONU - Monolepis nuttalianus, PHSP1 - Phlox sp., POCO - Poa compressa, POSE - Poa secunda, POSP - Potentilla sp., VUOC - Vulpia sp.

Fig. 4 The relationship between shrub cover of the three dominant shrub species and soil seed bank densities (seeds m⁻²) of native annual, native perennial, and introduced species. Values have been converted to standardized effect sizes for ease of comparison. Significance is indicated, with ** = P < 0.01, t = P < 0.10.

Fig. 5 The relationship between (A) shrub cover of the three dominant shrub species and the above-ground richness of native species and (B) ground cover and the above-ground richness of introduced species. Values have been converted to standardized effect sizes for ease of comparison. Significance is indicated, with * = P < 0.05, ** = P < 0.01.
**Fig. 6** Relationship between community richness and environmental characteristics, showing the relationship between (A) shrub cover of *Artemisia tridentata* and above ground richness of native species, (B) shrub cover of *Chrysothamnus viscidiflorus* and above ground richness of native species, (C) ground cover of standing dead and above ground richness of introduced species, and (D) rocky ground cover and above ground richness of introduced species. $R^2$ shows the results of the linear trendline for multiple regression.

**Fig. 7** Relationship between (A) shrub cover of the three dominant shrubs and above-ground evenness of other native species, (B) climate variables and above-ground evenness of introduced species, and (C) ground cover and below-ground evenness of native species. Significance is indicated with * = $P < 0.05$, ** = $P < 0.01$, t = $P < 0.10$.

**Fig. 8** Relationship between community evenness and environmental characteristics, showing the relationship between (A) shrub cover of *Artemisia tridentata* and above ground evenness of native species and (B) precipitation and above ground evenness of introduced species. $R^2$ shows the results of the linear trendline for multiple regression.

**Fig. 9** Relationships between (A) shrub cover of the three dominant shrubs and the number of rare species above and below-ground, (B) *C. viscidiflorus* cover and the number of above-ground rare species, and (C) *A. tridentata* cover and the number of below-ground rare species. Significance is indicated as * = $P < 0.05$, ** = $P < 0.01$, and $R^2$ values are for the linear trendline for the single regression between number of rare species and shrub cover.

**Fig. 10** Above and below-ground similarity in community composition as predicted by (A) ground cover and (B) disturbance history. In (A), values are standardized Brays-Curtis similarity indices based on presence/absence of species in the above- and below-ground communities, with higher numbers indicating greater similarity. In (B), values are Brays-Curtis dissimilarity indices based on species densities, with lower numbers indicating greater similarity. Significance is indicated as * = $P < 0.05$. 
Fig. 1
N = native, I = introduced, A = annual, P = perennial, F = forb, G = grass, W = woody

Fig 3.
Fig. 4

The figure displays a bar graph showing the standardized effect size of seeds (m$^{-2}$) for different shrub cover types: A. tridentata, C. viscidiflorus, and E. nauseosa. The x-axis represents the shrub cover, while the y-axis shows the standardized effect size. The graph includes bars for native annuals, native perennials, and introduced species, with statistical significance indicated by stars (**) and a letter (t).
Fig. 5

A. Native Species

B. Introduced Species

Shrub Cover

Ground Cover

A. tridentata  C. viscidiflorus  E. nauseosa

Bare Ground  Litter  Rock  Standing Dead

Standardized Effect Size

Above-Ground Richness

*  **
Fig. 6
Fig. 7

A. Above-ground, native species

B. Above-ground, introduced species

C. Below-ground, native species

- A. tridentata
- C. viscidiflorus
- E. nauseosa

Shrub Cover

Maximum Temp. (°C)

Minimum Temp. (°C)

Precipitation (mm)

Climate

- Bare Ground
- Litter
- Rock
- Standing Dead

Ground Cover

**

*
Fig. 8

A. Above Ground Evenness of Natives

B. Above Ground Evenness of Introduced Species

A. tridentata Cover

Precipitation (mm)
Fig. 9

A. Bar chart showing the standardized effect size and number of rare species for shrub cover. The bars are color-coded for above-ground and below-ground conditions. The species included are A. tridentata, C. viscidiflorus, and E. nauseosa.

B. Above-ground graph showing the relationship between C. viscidiflorus cover and the number of rare species, with $R^2 = 0.185$.

C. Below-ground graph showing the relationship between A. tridentata cover and the number of rare species, with $R^2 = 0.391$. ** indicates a significant effect at the 0.01 level, * indicates a significant effect at the 0.05 level.
A. Similarity by presence/absence

B. Dissimilarity by density

Fig. 10
Chapter IV: Climate variability affects the germination strategies exhibited by arid land plants

ABSTRACT

Spatial and temporal environmental variability can lead to variation in selection pressures across a landscape. Strategies for coping with environmental heterogeneity range from specialized phenotypic responses to a narrow range of conditions to generalist strategies that function under a range of conditions. Here, we ask how mean climate and climate variation at individual sites and across a species’ range affects the specialist-generalist spectrum of germination strategies exhibited by 10 arid land forbs. We investigated these relationships using climate data for the western United States, occurrence records from herbaria, and germination trials with field-collected seeds, and predicted that generalist strategies would be most common in species that experience a high degree of climate variation or occur over a wide range of conditions. We used two metrics to describe variation in germination strategies: a) selectivity (did seeds require specific cues to germinate?) and b) population-level variation in germination displayed by each species. Species exhibited distinct germination strategies, with some species demonstrating as much among-population variation as we observed among species. Our modeling efforts suggest that generalist strategies evolve in response to higher spatial variation in actual evapo-transpiration (AET) at a local scale and in available water in the spring and annual precipitation at a range-wide scale. Describing the conditions that lead to variation in early life history traits is important for understanding the evolution of diversity in natural systems, as well as the possible responses of individual species to global climate change.
INTRODUCTION

Across the range of many plant species, environmental conditions vary spatially and temporally, resulting in variation in selection pressures that can affect their growth and establishment (Lechowicz and Bell 1991; Levine and Rees 2004; Adler et al. 2006; Treurnicht et al. 2016). The first interaction that a plant has with its environment occurs during the critical process of seed germination, with the reliance on environmental cues at this life-history stage acting as a potential population bottleneck (Menges 1991). Thus, climate plays a role in shaping the evolution of seed traits (Cochrane et al. 2015; Rosbakh and Poschlod 2015), and the interactions between seeds and climate determine the subsequent conditions and selection pressures experienced during plant growth and establishment (Donohue et al. 2010; Poschlod et al. 2013; Fraaije et al. 2015; Mondoni et al. 2015; Jiménez-Alfaro et al. 2016). Given that climate varies across space and through time, it has the potential to differentially influence the life-history strategies of populations across the geographic range of a species (Sher et al. 2004). Both the type and scale of environmental variation can affect the evolution of plant life-history strategies. For example, divergent selection in highly contrasting environments can lead to population differentiation (Kawecki and Ebert 2004; Sambatti and Rice 2006; Leimu and Fischer 2008; Hereford 2009), whereas high levels of environmental stochasticity at small spatial scales can lead to the development of characteristics that would be beneficial under a variety of conditions (Reboud and Bell 1997; Kassen 2002; Condon et al. 2014).

Strategies for coping with environmental heterogeneity range from increased specialization to a narrow range of conditions, i.e. producing a fixed phenotype, to development of the ability to exploit a broader range of conditions through a more generalist strategy, i.e. producing a range of phenotypes under contrasting conditions. Specialization can be particularly
advantageous if the costs of being a generalist are high, e.g. if specialization allows for higher resource use efficiency (Futuyma and Moreno 1988). In contrast, by adopting a generalist strategy, some plants may be able to change architectural, physiological, or phenological traits in response to year-to-year changes in environmental indicators of resource availability (Sultan 2000). This type of phenotypic plasticity is thought to be adaptive when it results in higher fitness across a range of environmental conditions (Bradshaw 1965; Sultan 1987). Both specialist and generalist strategies have been widely documented in natural populations (Cook and Johnson 1968; Nagy and Rice 1997; Kassen 2002; Heschel et al. 2004; Sambatti and Rice 2006). In fact, given the variation in plant life histories and the ubiquity of environmental heterogeneity, it is highly likely that most plant species achieve some balance between specialization and phenotypic plasticity among individuals in natural plant populations (Bell et al. 2000).

Establishment from seed is a key process in plant life cycles, and many plants have developed some degree of seed dormancy in order to cope with uncertainty in their environment at this stage (Cohen 1966; Ellner 1985; Gremer et al. 2016). In arid systems, for example, high levels of inter-annual climatic variability, in addition to inherent water-limitations, have a strong influence on germination and seedling survival (Clauss and Venable 2000; Chesson et al. 2004; Torres-Martinez et al. 2016). Moisture and temperature cues are the most common dormancy breaking mechanisms for desert plants (Baskin and Baskin 2014). Seed dormancy affects the seasonal timing of germination for many desert plants (Baskin and Baskin 2014), and germination timing influences the environmental conditions seedlings will experience and when and with whom they will compete for resources (Freas and Kemp 1983; Weinig 2000; Chesson et al. 2004; Kos and Poschlod 2007). In the Great Basin, where our work is focused, germination
generally occurs in either fall/winter or spring, with some species acting as facultative winter-germinators, meaning that if they do not experience the appropriate conditions to stimulate germination in fall/winter, then they may delay germination until the spring. Most seed germination is stimulated by pulsed rain events that occur in fall or winter; however, the timing and quantity of precipitation events in arid systems is notoriously variable (Comstock and Ehleringer 1992; Schwinning et al. 2004). Therefore, the evolution of seed dormancy in these species is potentially related to the level of environmental variability a species or population experiences, and the environmental cues that indicate the level of resource availability at different times of the year.

In general, it is predicted that for species that experience higher levels of variation across their range (spatial variation) than year-to-year variation within populations (temporal variation), natural selection would favor specialized, fixed life-history strategies and greater differences among populations (Kawecki and Ebert 2004); alternately, for species that experience high levels of year-to-year variation in combination with reliable signals of future conditions, natural selection would favor phenotypically plastic responses, and possibly more similarity among populations (Via et al. 1995; Gabriel et al. 2005; Valladares et al. 2007). Meyer et al. (1995) demonstrated this pattern in *Penstemon* species that vary in their niche breadth and have evolved habitat specific germination strategies at locations across their range, with species possessing broader niches or from more unpredictable habitats exhibiting a broader range of germination strategies. Germination strategies may also be affected by variation at different spatial scales, due to differences in local vs. range-wide dynamics. Range size, and the associated breadth of habitats encompassed by larger ranges, may influence both the overall germination strategy of a species and the amount of population-level variation in germination
strategies exhibited by a species, with generalist species typically having larger ranges (Brändle et al. 2003; Luna et al. 2012). Thus, range-wide climate variability and range size may also be predictive of the specialist-generalist spectrum of germination strategies exhibited by different species.

Here, our goals were to examine overall differences in germination strategies among a suite of Great Basin forb species, and to relate the relative degree of specialization in their germination strategies to environmental characteristics at both local and range-wide scales. We used two metrics to quantify the germination responses of our species: a) the degree of selectivity, describing whether species were able to germinate across a wide variety of treatments or if they responded primarily to specific cues, and b) the amount of population-level variation in germination strategies exhibited by each species. This allowed us to describe species along a specialist-generalist spectrum, relative to the breadth of cues that resulted in germination, and to describe among-population differences in these germination strategies. We next asked whether there was evidence that mean climate characteristics, climate variability, or range size plays a role in shaping the specialist-generalist spectrum of germination strategies exhibited by our short-lived forbs, and which climate characteristics were most strongly associated with different germination strategies at different scales. We investigated these relationships using climate data for the western United States from 1950-2014, herbarium records to estimate the geographic and environmental ranges of our species, and germination trials with field-collected seeds of 10 Great Basin forb species, including: Agoseris grandiflora, Blepharipappus scaber, Chaenactis douglasii, Collinsia parviflora, Crepis intermedia, Cryptantha pterocarya, Gilia inconspicua, Mentzelia albicaulis, Microsteris gracilis, and Phacelia hastata. Specifically, we asked the following research questions:
1) Did our species exhibit a variety of germination strategies?

2) Did our species exhibit population-level differences in seed germination?

We were also interested in whether our species exhibited relationships between germination responses and environmental characteristics, asking if there was a relationship between the following predictors and the degree of either a) selectivity or b) population-level variation in germination strategies for each species:

3) spatial climate variability or climate mean values experienced at a local scale (i.e. differences in climate at seed collection locations),

4) spatial climate variability or climate mean values experienced at a range-wide scale

5) spatial and temporal (inter-annual) variation at a local scale or across the range of a species

We expected that species would differ in their germination responses, with species expressing a higher degree of selectivity experiencing lower levels of inter-annual variation across their range. We also predicted that species with less population-level variation in germination strategies would experience higher levels of both spatial and inter-annual climate variability.

Lastly, given the primacy of this resource in the desert, we expected that water-related variables would be the most influential in shaping the germination strategies of these species.

METHODS

IDENTIFYING GERMINATION STRATEGIES OF FOCAL SPECIES:

We selected 10 forbs that are commonly found co-occurring in sagebrush steppe ecosystems in the western Great Basin, and are of interest as part of the spring and summer flora that provide forage and cover for wildlife in these systems. Seeds were wild-collected
(Table 1) from 3 populations of 9 species and 2 populations for 1 species (*B. scaber*) from areas with 226-757 mm of annual precipitation, with a mean of 406 mm, across the past 64 years. Collections were centered in Northern Nevada for 9 of 10 species (Fig. 1). Sites were visited weekly for the purpose of seed collection throughout the reproductive window for each species, between February 2013 and September 2013 (Table 2), and seeds were stored in the dark at room temperature (~21°C) until germination trials began. Due to low regional availability, *Phacelia hastata* seeds from the National Plant Germplasm System (United States Department of Agriculture) collections were used to supplement collections made in 2013; these collections came from two areas in south-eastern Oregon. All seeds from an individual site were a mixture from at least 50 maternal plants. Fifteen to forty seeds from each population (based on seed availability) were sent to the Colorado Seed Lab (http://seeds.agsci.colostate.edu/seedlab/home-2/) for tetrazolium testing to determine seed viability (Table 2). Because seeds were wild-collected, there is the potential for maternal effects to influence the outcome of our germination trials (Gutterman 2000; Baskin and Baskin 2014), we attempted to limit this influence by collecting seeds consistently throughout the reproductive window for our species. In addition, the seeds of species that reproduced in the spring were stored at room temperature for a longer period of time before the start of the trial than the seeds of species that reproduced in the late spring/summer (Table 2). Longer storage times may have reduced the seed dormancy of species with non-deep physiological dormancy (Baskin et al. 2006); however, most of our species and populations produced seed from late May through mid-June. In the case of *P. hastata*, extended periods of time in cold storage, as often occurs in seed preservation, may also have affected their response to our germination treatments (Baskin et al. 2006), despite the fact that the seeds retained high viability.
Our germination methods loosely followed those of Forbis (2010), with treatments varying after-ripening temperature and length of cold stratification (Fig. 2). For the after-ripening treatment, seeds were placed in paper coin envelopes and were exposed to one of two treatments for four weeks, either a dark 40°C germination chamber or in the dark at room temperature (~21°C), to test whether exposure to summer conditions was a dormancy breaking requirement. Seeds were then tested for germination in response to cold temperatures and moist conditions, indicative of a requirement for exposure to fall or winter conditions in order to break dormancy. After-ripened seeds were divided into four cold stratification groups and placed in a dark growth chamber at 2°C for 2, 4, or 6 weeks, and then transferred to a dark 15°C chamber for the remainder of the study; these treatments are hereafter referred to as 2C2, 2C4, and 2C6. The fourth group of seeds was placed directly into the 15°C chamber to test whether seeds would germinate in the absence of cold stratification; this treatment is referred to as 15C. For each population, equal numbers of seeds (5 to 20 seeds, based on availability) (Table 2), were placed on filter paper (Whatman #597) in five replicate 90 mm petri dishes and moistened with deionized water. Dishes were checked weekly for germination and deionized water was added as needed; the cold and warm chambers were switched every two weeks to avoid inadvertent chamber effects. Seeds germinated in both the 2°C the 15°C chambers. Germination experiments were conducted from late September to late December 2013, at the point where no seeds had germinated in any dish for over two weeks. Total germination percentage was calculated for each species as follows:

Percent germination = \( \frac{\text{number of germinated seeds}}{\text{(number of seeds per treatment} \times \text{percent viability})} \times 100 \)
We determined differences in the total fraction of seeds germinated in each treatment for all populations using one-way analysis of variance (ANOVARs), using Program R (R Development Core Team 2016).

We also analyzed our germination data using survival analysis to distinguish differences in the timing of germination. We accounted for seed viability in this analysis by multiplying the number of seeds in each treatment group (after-ripening and cold stratification combination) by the percent viability of each population and removing the appropriate number of seeds from the data set. We removed un-germinated seeds first, and when needed, removed germinated seeds (selected randomly). We used the Survival package (Therneau 2015) within Program R (3.3.1) (R Development Core Team 2016) to model germination timing using the Surv function with interval censoring (type = interval2), enabling us to calculate the survival function for each seed treatment and for each population. Germination probabilities were calculated using the function survfit and the resulting germination curves were compared with accelerated failure time (AFT) regressions using the survreg function with a Wiebull distribution (Brown and Mayer 1988). We used the scale parameter and the coefficient from the AFT model to calculate the hazard ratio (HR) for our comparisons using the following equation:

\[
\text{Hazard Ratio} = \exp(\text{coefficient} \times \frac{1}{\text{scale}})
\]

Here, the HR is a ratio of the rate of germination in one treatment relative to a comparison treatment. For example, if seeds experiencing the hot after-ripening treatment germinated at twice the rate of the cool after-ripened seeds, then the HR for that comparison would be 2.

Describing variation in germination strategies of focal species:

For each species, we calculated metrics to describe the variability in total germination response to our treatments, including: differences in percent germination across populations.
(population-level differences) and differences in the percent germination for each population across all germination treatments (selectivity). Our species are both annual and perennial forbs, and while we did not aim to differentiate germination strategies between perennial and annual species, we have organized our results to allow qualitative inspection of differences between these life history strategies. We used the coefficient of variation (CV) as our method for quantifying variability in percent germination, generally calculated as the standard deviation divided by the mean, with higher values indicating a higher degree of variation. To account for differences in sample sizes when calculating the CV across different groups (e.g. one species had only two populations), we calculated an unbiased CV using the methods of Abdi (2010), as follows:

\[
CV_{\text{unbiased}} = \left( 1 + \frac{1}{4+N} \right) * CV
\]

where \( N \) is the number of samples from the group being measured.

We quantified the degree of population-level variation for each species as the \( CV_{\text{unbiased}} \) of the percent germination across populations in response to all treatments. For this response, lower CV values indicate that all populations of a species experienced similar values for total percent germination, and may indicate either uniform levels of germination or uniform lack of germination across treatments. Conversely, higher CV values indicate that populations differed in their response to the germination treatments.

We quantified the degree of selectivity of a population to particular germination treatments by calculating the CV for each population across all germination treatments. For this measure, lower CV values indicate that seeds from a particular population germinated in roughly equal quantities in response to all germination treatments, while higher CV values indicate that seeds of that population experienced different levels of germination in different
treatments. We then calculated the mean CV across all populations of a species to estimate the degree of selectivity of the species. Thus, if there was germination, a lower mean CV indicates a more flexible germination strategy, while a higher mean CV indicates a more specialist germination strategy.

**MEASURING LOCAL AND RANGE-WIDE ENVIRONMENTAL CHARACTERISTICS FOR EACH SPECIES:**

We obtained location information across the western United States using herbarium records downloaded from three websites: The Intermountain Region Herbarium Network (http://intermountainbiota.org/portal/), The Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/), and the Burke Museum at the University of Washington (http://www.burkemuseum.org/research-and-collections/botany-and-herbarium/collections/database/). We focused the extent of our study area on the western United States, as many of our species are confined to this region, and limited our points to those representing plants that were found from 1950 to the present, due to frequent uncertainty about the locations of older specimens. For each species, we performed geographic filtering of the occurrence points collected from the herbarium data, to reduce collection bias (Kramer-Schadt et al. 2013; Boria et al. 2014). Specifically, we used the SDM Toolbox for ArcGIS (Brown 2014) to remove points if their occurrence was within a 20 km buffer of another point included in the dataset, in an attempt to limit spatial auto-correlation of our measurements of the environmental variables. We gathered environmental data in two ways. First, we tabulated 29 biologically relevant variables for each point for use in our data analysis (Supplemental Table 1). Environmental variables included precipitation and temperature, as well as a suite of bioclimatic variables (Booth et al. 1989) derived from monthly temperature and precipitation data, obtained from the PRISM Climate Group at the University of Oregon, for the western United
States from 1950 – 2014 (Daly et al. 2008), creating 64-year averages. We also calculated a suite of variables using a Thornthwaite water balance approach, which considers the simultaneous availability of water and energy for plants (Stephenson 1998; Lutz et al. 2010). Many of the variables were derived from measures of actual evapo-transpiration (AET), potential evapo-transpiration (PET), water supply (WS), soil water balance (SWB), and climate water deficit (CWD); most of these variables were calculated using the methods outlined in Dilts et al. (2015).

Values for each environmental variable were extracted in ArcMap 10.1 for each point for each species, including locations based on herbarium records (range-wide points) and the seed collection locations (local points). We then calculated the $\text{CV}_{\text{unbiased}}$ for each environmental variable across locations for each species and used that as a measure of spatial climate variability for a particular species. These measures were used to describe spatial climate variation experienced at the local scale (i.e. differences in average climate between the specific seed collection locations, Question 3) and across each species’ range (i.e. the amount of variation in average climate between species occurrences documented by herbarium collections, Question 4). They were also used to examine how mean values for climate variables may influence germination patterns (Question 3 and 4). We calculated the average value for each environmental variable across all points for each species from 1950-2014 and used that as a measure of the mean climate for a particular species.

Secondly, for models examining inter-annual variation in climate variables (Question 5), we extracted monthly PRISM data for precipitation, minimum temperature, and maximum temperature from both seed collection locations (local) and herbarium record locations (range-wide) for each species, from 1950-2014. Because these calculations were more computationally intensive, we focused on a subset of easily summarized variables, rather than calculating
variation in composite and derived variables described above. We summed the precipitation over the months of each season for each year and averaged the minimum temperatures and maximum temperatures over the months of each season for each year. We calculated spatial variation for each species by calculating the $CV_{unbiased}$ across all points for each season of each year and taking the mean of these values across all years for each season. We calculated the temporal variation for each species by calculating the $CV_{unbiased}$ across all years for each season at each point and taking the mean of these values across all points. Finally, we estimated range size and niche breadth for each species.

We estimated range size and niche breadth for each species. Due to our inability to predict true absences for our species from herbarium records, Maxent modeling is among the most commonly used and best performing presence-background modeling approaches (Elith et al. 2006). We used Maxent (version 3.3.3k, Phillips et al. 2006) to identify the best model or models of the potential habitat for our species across the western United States. We relied upon Maxent’s internal variable selection (Elith et al. 2011). Thus, rather than removing highly correlated variables through a pre-screening process, we allowed the program to converge on the most predictive combination of climate variables for each species using our entire collection of climate variables and interpreted models keeping in mind that correlations exist. Model selection involved species-specific model optimization by adjusting the regularization parameter (1-5) and the Maxent feature types (Anderson and Gonzalez 2011; Warren and Seifert 2011). We selected the best model or models for each species using the Akaike’s information criterion (AIC) scores, calculated using ENMTools (Warren et al. 2010). The model with the lowest AIC score was considered the best model and models with AIC scores <2 from the lowest AIC score were considered comparable to the best model. For species with multiple top models, we
overlapped the binary maps for all top models, using the maximum sensitivity-specificity method (Liu et al. 2013), and considered an area to be part of a species’ range if it was predicted as potential habitat by two or more top models. We calculated niche breadth for each of our species using ENMTools (Warren et al. 2010). However, the Pearson’s correlation between niche breadth and range size was 0.97, so we chose to exclude it from our models and retain range size, as this variable produces an intuitive measure in units that can be easily compared among species and across studies.

IDENTIFYING RELATIONSHIPS BETWEEN GERMINATION STRATEGIES AND ENVIRONMENTAL CHARACTERISTICS AT LOCAL AND RANGE-WIDE SCALES:

We used generalized linear models to determine relationships between environmental characteristics, range size, and seed germination strategies. We performed a Pearson’s correlation analysis to determine which variables were highly correlated (R > ±0.7) across our collective species’ ranges, and narrowed our focal set of variables down to a subset of uncorrelated variables for each of our models (Table 2). When selecting variables for our model, we placed an emphasis on maintaining similar variables across models. Once a group of variables was selected, Q-Q plots were used to confirm a normal distribution within the data parameters and plots of residual versus fitted values were used to check for trends within the residuals for each of the models, and values were transformed as needed.

To address our questions, we created three sets of generalized linear models. These included: models examining spatial climate variability from 64-year averages of our bioclimatic variables (Questions 3 and 4), models examining mean values of our bioclimatic variables (Questions 3 and 4), and models examining spatial and temporal climate variability from monthly measures of precipitation and temperature (Question 5). For each set of questions, we
ran separate models that used either a) selectivity or b) population-level differences in germination strategies as response variables.

We analyzed these generalized linear models using multi-model inference, performed using the package MuMIn for program R (Barton 2016). We performed model selection using the dredge function to generate a set of candidate models, each containing no more than five terms, using combinations of the variables from the previously described global models for each of our questions. We then performed model averaging across all models produced by the model selection process. This allows us to obtain estimates of the regression coefficients that are averaged across all models, with each value weighted by the corrected Aikake information criterion (AICc) scores for the models that contained it. We used both zero averaging (ZA; assigns a parameter estimate of zero to predictor variables that are excluded from a particular model and includes those zero values when performing model averaging) and natural averaging (NA, only averages across models that contain that particular predictor variable) to estimate individual parameters. The ZA approach is better for assessing the relative importance of all parameters from the global model, whereas the NA approach is better for determining the importance of an individual parameter (Burnham and Anderson 2002; Grueber et al. 2011). Model averaging also provides an estimate of parameter importance (IMP) for each of the predictor variables, which is based on the proportion of highly predictive models that contain the focal parameter. Higher IMP values indicate that a parameter was either included in more models and/or was included in highly predictive models.

RESULTS

Did our focal species exhibit a variety of germination strategies (Question 1)?
Overall, our species exhibited distinct differences in the total number of seeds that germinated in response to our treatments (Fig. 3). Four species (A. grandiflora, C. parviflora, C. pterocarya, and M. gracilis) appeared to possess generalist germination strategies and experienced very high levels of germination in response to all treatments. Two other species, P. hastata and M. albicaulis, experienced very low levels of germination in all treatments, indicating that they may require additional cues in order to completely break dormancy. The remaining species fell somewhere in-between. Two species preferred longer periods of cold stratification (C. intermedia, C. douglasii), one species preferred no cold stratification (G. inconspicua), and one species achieved a moderate level of germination in all treatments (B. scaber).

Our results indicated that hot, summer temperatures were more likely to affect the timing of germination, rather than the total quantity of germinated seeds. While hot after-ripening stimulated faster germination in A. grandiflora, M. gracilis, and P. hastata, the total number of germinated seeds did not differ between after-ripening treatments (Table 3). For C. douglasii, cool after-ripening resulted in both faster germination and higher total number of germinated seeds (Table 3).

Our results also indicated that winter and spring conditions have the potential to affect both the rate of germination and the total number of germinated seeds, a result consistent with other germination research (Meyer et al. 1995; Forbis 2010; Baskin and Baskin 2014). Species with high levels of germination during cold stratification (potential winter germinators) included A. grandiflora, B. scaber, C. parviflora, C. pterocarya, and M. gracilis. None of these species experienced significant differences in total germination in response to the cold stratification treatments, although they did show differences in their rates of germination (Table 3).
*grandiflora* germinated more quickly in the 15°C treatment, *B. scaber* experienced faster germination in the cold stratification treatments, and *C. pterocarya* experienced a high initial rate of germination in 15°C, with little difference between the rates of germination in the cold stratification treatments (Table 3). Some species germinated more quickly in warmer temperatures after exposure to cold stratification (Table 3): *C. douglasii*, *C. intermedia*, and *P. hastata*. These species also exhibited significant differences in total germination in response to the cold stratification treatments, with *C. douglasii* experiencing higher germination with longer periods of cold stratification, and *C. intermedia* and *P. hastata* experiencing higher germination in all cold stratification treatments (Table 3). Only *G. inconspicua* exhibited a higher rate of germination coupled with higher overall seed germination when placed directly into 15°C (Table 3). Although *M. albicaulis* experienced a relatively high rate of germination in the 15°C treatment, it exhibited very low levels of germination overall, with no significant difference in total germination between cold stratification treatments (Table 3).

**Did our focal species exhibit population-level variation in seed germination (Question 2)?**

All but one species, *C. parviflora*, experienced significant population-level differences in the rate of germination and/or the total seeds germinated (Table 3, Fig. 4). Two species with generalist strategies, *A. grandiflora* and *C. pterocarya*, exhibited significant differences in the rates of germination between populations without exhibiting differences in the total number of seeds germinated (Table 3). Another species with a generalist strategy, *M. gracilis*, exhibited both population-level differences in germination rates and in the total number of seeds germinated (Table 3). The most dramatic population-level differences were exhibited by *C. intermedia* in both germination rate and total germinated seeds (Table 3). *B. scaber* exhibited population-level differences in both the rate and the total seeds germinated (Table 3). Two
other species, *C. douglasii* and *G. inconspicua*, had one of their populations germinate at a much faster rate than the other two populations, as well as a higher level of germination (Table 3). Finally, the two species that exhibited low levels of germination, *P. hastata* and *M. albicaulis*, still showed population-level differences in germination rates and total seeds germinated, but may have required additional cues in order to completely break dormancy (Table 3, Fig. 4). We quantified both species and population-level variation in the fraction of seeds germinated (Table 4).

**ARE THERE RELATIONSHIPS BETWEEN GERMINATION RESPONSES AND ENVIRONMENTAL CHARACTERISTICS?**

**Spatial climate variability and mean climate experienced at a local scale (Question 3):**

At the local scale, the natural average (NA) of spatial variation in cumulative AET was negatively correlated with both selectivity (Question 3a) and population-level differences in germination (Question 3b) (Table 5A), indicating that species collected from environments with greater spatial variation in annual productivity had more generalist germination strategies and smaller differences among populations. In contrast, mean values of these bioclimatic variables had no association with either selectivity (Question 3a) or population-level variation (Question 3b) at the local scale (see Supplemental Table 2a).

**Spatial climate variability and mean climate experienced at a range-wide scale (Question 4):**

At a range-wide scale, variation in available water in the spring and annual precipitation were negatively correlated with selectivity (Question 4a) (Table 5B), indicating that species that experienced higher spatial variability in the amount of water available for runoff and deep percolation in the spring and in total annual precipitation across their range were more likely to have generalist strategies. At the range-wide scale, none of the variables from our global model were significantly correlated with population-level variation in germination (Question 4b). Mean
values of these bioclimatic variables had no association with either selectivity (Question 4a) or population-level variation (Question 4b) at the range-wide scale (see Supplemental Table 2b).

**Spatial and temporal (inter-annual) variation at a local scale and range-wide scale (Question 5):**

Our models did not indicate a significant relationship between the degree of spatial or temporal (inter-annual) variation in our seasonal variables (precipitation, minimum temperature, or maximum temperature) and either selectivity or population level differences at either a local or a range-wide scale (see Supplemental Table 3).

**DISCUSSION**

Seed germination is a key element of a plant’s response to its environment, and variation in seed germination strategies is commonly observed among species (Meyer et al. 1995; Petru and Tielborger 2008; Forbis 2010; Baskin and Baskin 2014). Consistent with these observations, we found that our species exhibited a variety of germination strategies, encompassing both generalist and specialist germination traits. Much less work has been done describing differences among populations, though this type of variation may be important for species persistence in response to climate variability (Cochrane et al. 2015). We found evidence for population-level differences in germination strategies for nine out of ten of our species, all except for *C. parviflora*. Given that our seeds were collected over a small area, relative to the potential ranges of these species, it is interesting to discover that populations can exhibit dramatic differences in germination strategies at this small spatial scale. Our results support the findings of other research reporting population-level differences in plant traits (Sambatti and Rice 2006; Becker et al. 2008; Banta et al. 2012; Granado-Yela et al. 2013; Prendeville et al. 2013; Torres-Martinez et al. 2016), and there is increasing interest in research focusing on
population-level variation in plant early life history traits (Cochrane et al. 2015; Jiménez-Alfaro et al. 2016).

As we predicted, there were relationships between germination strategies and climate variability at different spatial scales, primarily related to water availability and the simultaneous availability of water and energy (AET). We found evidence that spatial variation in AET at a local scale influenced both the selectivity in germination response and the degree of population-level differences in germination exhibited by our species, with increases in spatial variation in AET associated with decreases in both selectivity and population-level differences. Given that AET is a proxy for productivity, this supports the idea that natural selection would favor a generalist strategy in populations that experience high spatial variability in resource availability. This may be due to population-level variation in competitive pressures (Kadmon and Shmida 1990), but may also be due to other local characteristics, such as edaphic factors (Wright et al. 2006) or other biotic and abiotic factors (Linhart and Grant 1996).

At the range-wide scale, species that experienced higher spatial variation in available water in the spring and annual precipitation across their range had more generalist germination strategies, with seeds ready to germinate in response to available moisture, rather than waiting for specific temperature/moisture combinations. The fact that different variables were important at local and range-wide scales supports the idea that resource availability, mediated by factors such as competition and edaphic characteristics, are generally more influential on plant fitness at smaller spatial scales (Turkington and Harper 1979; Snaydon and Davies 1982; Becker et al. 2008), while climate factors are generally more influential at larger spatial scales (Santamaria et al. 2003; Macel et al. 2007, but see Carta et al. 2016). We did not find evidence linking population-level variation in germination response with range-wide climate variability;
this may be due to the fact that these arid land species may cue into different aspects of climate (Chesson et al. 2004), leading to individualized responses that make it difficult to find general patterns between specific climate variables and variation in germination strategies. This emphasizes the importance of studying the unique natural histories and adaptations of individual species (Macel et al. 2007), in addition to searching for large-scale patterns in life history strategies.

Germination strategies can provide a means for tracking suitable conditions through time by delaying seed germination until conditions improve (Gremer et al. 2016). Bet hedging is a germination strategy where plants sacrifice their mean fitness in a single year in order to increase their long-term fitness across years (Cohen 1966; Venable 2007). With this strategy, a plant produces seeds that can be separated into different groups, or seed fractions, that each germinate in response to different cues, enabling the plant to spread germination across several years and the risk of seedling failure through time. This strategy is thought to be an adaptive response to environmental variability (Nevoux et al. 2010), and is well documented in desert annuals (Cohen 1966; Venable 2007; Gremer et al. 2016). It is possible that some germination strategies may integrate elements of both bet hedging and phenotypic plasticity (Simons 2014; Botero et al. 2015). Thus, some of our species may have displayed population-level variation in their germination strategies due to bet hedging; most notably, B. scaber exhibited a moderate level of germination in response to most of our germination cues, a pattern that would be consistent with a bet hedging strategy. Further research on the survival of germinating seeds in contrasting habitats could be used to model overall success of the generalist/specialist strategies we observed among these species.
Finally, we know that different germination strategies can involve variation in the timing of germination, and that this can affect seedling success (Rathcke and Lacey 1985; Pake and Venable 1996; Donohue et al. 2005) and have lasting consequences over the lifetime of a plant (Rathcke and Lacey 1985). In general, facultative winter germination and winter germination prioritize appearing early in the growing season; these are strategies adopted by species that are highly competitive (Raynal et al. 1975; Winsor 1983) or that grow in areas where competition for resources is inherently low. In contrast, species with spring germination may be better at tolerating harsh, summer conditions and may benefit from the lower level of competition for resources presented later in the growing season. At shorter timescales, differences in timing of days to weeks can also affect overall plant survival and fitness, both in general (Baskin and Baskin 1972; Warwick and Briggs 1978; Marks and Prince 1981) and in arid systems in particular (Leger et al. 2009; Kulpa and Leger 2013). There is also evidence that the order of emergence may be more important than the emergence date in determining seedling success for some species (Warwick and Briggs 1978; Weaver and Cavers 1979). Thus, species may partition resources in space and time by expressing different germination strategies, allowing for a diversity of plants to persist in resource limited systems (Chesson et al. 2004; Moreira et al. 2012).

In summary, our research demonstrates a link between climate variability and generalist life-history strategies, and demonstrates how climate may influence intra-specific variability in seed germination. As expected, species experiencing higher levels of environmental variation exhibited more generalist strategies, and variation in water-related variables were important predictors of where species occurred along the specialist-generalist spectrum of life history strategies. We also observed that co-occurring species can possess distinct germination
strategies, and that populations can also vary in their germination strategies as much or more than the strategies of different species. Because of the key role that early life history characteristics play in a species’ interactions with its environment and the influence of germination timing on plant species persistence, knowledge of these strategies will become increasingly important in the face of climate change (Cochrane et al. 2015; Mondoni et al. 2015; Jiménez-Alfaro et al. 2016; Doherty et al. 2017).

ACKNOWLEDGEMENTS

We would like to thank the Great Basin Native Plant Project for their generous funding and the Germplasm Research Information Network/National Plant Germplasm System (GRIN/NPGS) for providing me with hand-collected seeds for my work with Phacelia hastata. Brittany Trimble, Lyndsey Boyer, Travis Allen, Vicki Thill, and Brianna Koorman provided valuable assistance with seed germination monitoring.
REFERENCES


Lechowicz MJ, Bell G (1991) The ecology and genetics of fitness in forest plants. II. Microspatial


R Development Core Team (2016) R: A Language and Environment for Statistical Computing. R http://www.r-project.org/, Vienna, Austria


Schwinning S, Sala OE, Loik ME, Ehleringer JR (2004) Thresholds, memory, and seasonality:


Treurnicht M, Pagel J, Esler KJ, Schutte-Vlok A, Nottebrock H, Kraaij T, Rebelo AG, Schurr FM


Table 1 Seed collection site descriptions and characteristics for each population of ten forb species native to the Intermountain West

<table>
<thead>
<tr>
<th>Species</th>
<th>Range Size (1000 km²)</th>
<th>Population Locality</th>
<th>Latitude¹</th>
<th>Longitude²</th>
<th>Elevation (m)</th>
<th>1→2</th>
<th>1→3</th>
<th>2→3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agoseris grandiflora</em></td>
<td>650</td>
<td>1. Hunter Creek, Washoe County, NV</td>
<td>39.4901</td>
<td>-119.9008</td>
<td>1544</td>
<td>12656</td>
<td>10726</td>
<td>8345</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (5774 ft), Washoe County, NV</td>
<td>39.6041</td>
<td>-119.9009</td>
<td>1760</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (7769 ft), Washoe County, NV</td>
<td>39.5827</td>
<td>-119.9361</td>
<td>2368</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Blepharipappus scaber</em></td>
<td>490</td>
<td>1. Hoge Road, Washoe County, NV</td>
<td>39.5729</td>
<td>-119.845</td>
<td>1603</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Hunter Creek, Washoe County, NV</td>
<td>39.4901</td>
<td>-119.9008</td>
<td>1554</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chaenactis douglasii</em></td>
<td>1400</td>
<td>1. Thomas Creek, Washoe County, NV</td>
<td>39.3922</td>
<td>-119.8423</td>
<td>1863</td>
<td>24060</td>
<td>21832</td>
<td>3832</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (5774 ft), Washoe County, NV</td>
<td>39.6041</td>
<td>-119.9009</td>
<td>1760</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (7349 ft), Washoe County, NV</td>
<td>39.5771</td>
<td>-119.9287</td>
<td>2240</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>1508</td>
<td>1. Keystone Canyon, Washoe County, NV</td>
<td>39.5528</td>
<td>-119.8489</td>
<td>1506</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (6102 ft), Washoe County, NV</td>
<td>39.5934</td>
<td>-119.9023</td>
<td>1860</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (7349 ft), Washoe County, NV</td>
<td>39.5781</td>
<td>-119.9264</td>
<td>2240</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crepis intermedia</em></td>
<td>1581</td>
<td>1. Ball's Canyon, Sierra County, CA</td>
<td>39.6566</td>
<td>-120.0537</td>
<td>1684</td>
<td>21088</td>
<td>19822</td>
<td>3491</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road, Washoe County, NV</td>
<td>39.5828</td>
<td>-119.8414</td>
<td>1586</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cryptantha pterocarya</em></td>
<td>844</td>
<td>1. Prison Hill, Carson City County, NV</td>
<td>39.1378</td>
<td>-119.7147</td>
<td>1411</td>
<td>53102</td>
<td>50898</td>
<td>5311</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (6102 ft), Washoe County, NV</td>
<td>39.5934</td>
<td>-119.9023</td>
<td>1860</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road, Washoe County, NV</td>
<td>39.5856</td>
<td>-119.8413</td>
<td>1590</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gilia inconspicua</em></td>
<td>1083</td>
<td>1. Hoge Rd, Washoe County, NV</td>
<td>39.5703</td>
<td>-119.8456</td>
<td>1613</td>
<td>1445</td>
<td>27895</td>
<td>29181</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Yorkshire Road, Washoe County, NV</td>
<td>39.5849</td>
<td>-119.8414</td>
<td>1586</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Washoe Valley, Washoe County, NV</td>
<td>39.3237</td>
<td>-119.8036</td>
<td>1540</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mentzelia albicaulis</em></td>
<td>1833</td>
<td>1. Red Rock Road, Washoe County, NV</td>
<td>39.8626</td>
<td>-119.9401</td>
<td>1450</td>
<td>52902</td>
<td>31722</td>
<td>21649</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Thomas Creek, Washoe County, NV</td>
<td>39.3922</td>
<td>-119.8423</td>
<td>1863</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road, Washoe County, NV</td>
<td>39.5872</td>
<td>-119.8418</td>
<td>1590</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Microsteris gracilis</em></td>
<td>1689</td>
<td>1. Hoge Road, Washoe County, NV</td>
<td>39.5725</td>
<td>-119.8453</td>
<td>1603</td>
<td>5651</td>
<td>20088</td>
<td>21113</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (6965 ft), Washoe County, NV</td>
<td>39.5783</td>
<td>-119.9104</td>
<td>2123</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Thomas Creek, Washoe County, NV</td>
<td>39.3923</td>
<td>-119.8593</td>
<td>1956</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>1388</td>
<td>1. North Owyhee River, Malheur County, OR</td>
<td>43.67405</td>
<td>-117.23945</td>
<td>719</td>
<td>39792</td>
<td>522747</td>
<td>485204</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. South Owyhee Lake, Malheur County, OR</td>
<td>43.3184</td>
<td>-117.29753</td>
<td>940</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Thomas Creek, Washoe County, NV</td>
<td>39.3922</td>
<td>-119.8423</td>
<td>1863</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹ Range size estimated using Maxent modeling and herbarium records, for details see the Methods section
² Location information was collected in the NAD83 reference system at the center of abundance for each species
³ Distance between sites was measured as direct point-to-point distances
Table 2 Species characteristics and methodological details for ten forbs native to the Intermountain West, collected from multiple populations. Information includes life form (annual or perennial), seed collection time frame (in months), % viability of a subset of seeds, seed mass (means and standard deviation), and sample sizes per dish in germination treatments.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life Form</th>
<th>Population</th>
<th>Collection Months</th>
<th>Viability (%)</th>
<th>Seed Mass (mg)</th>
<th>Seeds/Dish</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agoseris grandiflora</em></td>
<td>Perennial</td>
<td>1. Hunter Creek</td>
<td>June-July</td>
<td>100</td>
<td>1.7 ± 0.2</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (~5000 ft)</td>
<td>June-July</td>
<td>97.5</td>
<td>1.6 ± 0.2</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (~7500 ft)</td>
<td>July-August</td>
<td>90</td>
<td>1.6 ± 0.3</td>
<td>20</td>
</tr>
<tr>
<td><em>Blepharipappus scaber</em></td>
<td>Annual</td>
<td>1. Hoge Road</td>
<td>June-July</td>
<td>97.5</td>
<td>1.4 ± 0.3</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Hunter Creek</td>
<td>June-July</td>
<td>92.5</td>
<td>1.5 ± 0.3</td>
<td>20</td>
</tr>
<tr>
<td><em>Chaenactis douglasii</em></td>
<td>Perennial</td>
<td>1. Thomas Creek</td>
<td>June-July</td>
<td>97.5</td>
<td>3.1 ± 0.4</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (~5000 ft)</td>
<td>June-July</td>
<td>90</td>
<td>2.9 ± 0.8</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (~7400 ft)</td>
<td>July-August</td>
<td>90</td>
<td>2.9 ± 0.5</td>
<td>20</td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>Annual</td>
<td>1. Keystone Canyon</td>
<td>April-May</td>
<td>90</td>
<td>2.0 ± 0.4</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (~5100 ft)</td>
<td>April-May</td>
<td>77</td>
<td>1.4 ± 0.4</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Peavine (~7100 ft)</td>
<td>May-June</td>
<td>87.5</td>
<td>1.7 ± 0.4</td>
<td>15</td>
</tr>
<tr>
<td><em>Crepis intermedia</em></td>
<td>Perennial</td>
<td>1. Ball’s Canyon</td>
<td>June-July</td>
<td>72.5</td>
<td>4.5 ± 1.4</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Keystone Canyon</td>
<td>June-July</td>
<td>42.5</td>
<td>4.3 ± 1.9</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road</td>
<td>June-July</td>
<td>60</td>
<td>4.9 ± 1.4</td>
<td>20</td>
</tr>
<tr>
<td><em>Cryptantha pterocarya</em></td>
<td>Annual</td>
<td>1. Prison Hill</td>
<td>June-July</td>
<td>85.7</td>
<td>0.4 ± 0.1</td>
<td>Cool AR 10</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hot AR 15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (~5100 ft)</td>
<td>June-July</td>
<td>100</td>
<td>0.5 ± 0.1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road</td>
<td>June-July</td>
<td>86.7</td>
<td>0.4 ± 0.2</td>
<td>15</td>
</tr>
<tr>
<td><em>Gilia inconspicua</em></td>
<td>Annual</td>
<td>1. Hoge Rd</td>
<td>May-June</td>
<td>90</td>
<td>0.9 ± 0.2</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Yorkshire Road</td>
<td>May-June</td>
<td>95</td>
<td>0.8 ± 0.2</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Washoe Valley</td>
<td>May-June</td>
<td>87.5</td>
<td>0.6 ± 0.2</td>
<td>Cool AR 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hot AR 10</td>
</tr>
<tr>
<td><em>Mentzelia albicaulis</em></td>
<td>Annual</td>
<td>1. Red Rock Road</td>
<td>June-July</td>
<td>95</td>
<td>0.4 ± 0.1</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Thomas Creek</td>
<td>June-July</td>
<td>97.5</td>
<td>0.5 ± 0.1</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Yorkshire Road</td>
<td>June-July</td>
<td>100</td>
<td>0.5 ± 0.2</td>
<td>20</td>
</tr>
<tr>
<td><em>Microsteris gracilis</em></td>
<td>Annual</td>
<td>1. Hoge Road</td>
<td>April-June</td>
<td>100</td>
<td>1.9 ± 0.3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. Peavine (~6800 ft)</td>
<td>April-June</td>
<td>100</td>
<td>1.8 ± 0.3</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Thomas Creek</td>
<td>June-July</td>
<td>100</td>
<td>2.0 ± 0.3</td>
<td>5</td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>Perennial</td>
<td>1. North Owyhee River1</td>
<td>June-July</td>
<td>95</td>
<td>1.1 ± 0.3</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2. South Owyhee Lake3</td>
<td></td>
<td>95</td>
<td>1.0 ± 0.2</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3. Thomas Creek</td>
<td>June-July</td>
<td>80</td>
<td>0.9 ± 0.1</td>
<td>5</td>
</tr>
</tbody>
</table>

1 Seed viability determined by tetrazolium tests performed by the Colorado Seed Laboratory  
2 Seed mass was estimated from a sample of ten seeds from each population  
3 Seeds for this population were procured from the National Plant Germplasm System
### Table 3 Statistical results for differences in rate and total germination in response to our treatments and among populations for (a) perennials and (b) annuals

Hazard ratios (HR) from the survival analysis indicate pair-wise differences between the rates of germination, with numbers greater than one indicating faster germination and numbers less than 1 indicating slower germination for the treatment in the numerator of the comparison. For example, the HR - Hot/Cool value for *Agoseris grandiflora* of 1.15 indicates that the hot after-ripening treatment germinated 1.15 times faster than the cool treatment. Significant results in total germination from ANOVAs are indicated as follows:

- \( P < 0.10 \)
- \( P < 0.05 \)
- \( P < 0.01 \)
- \( P < 0.001 \)

Arrows indicate whether treatments increased or decreased germination. The total germination column in the Population Differences analysis indicates when populations (Pop) differed in total germination. A “-” indicates no differences among treatments or populations.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>After-ripening</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agoseris grandiflora</em></td>
<td>1.15***</td>
<td>0.36***</td>
<td>0.44***</td>
<td>0.40***</td>
<td>1.18***</td>
<td>-</td>
</tr>
<tr>
<td><em>Chaenactis douglasii</em></td>
<td>0.68***</td>
<td>1.00***</td>
<td>4.24***</td>
<td>6.57***</td>
<td>1.10***</td>
<td>1.85*** 1.69***</td>
</tr>
<tr>
<td><em>Crepis intermedia</em></td>
<td>0.94</td>
<td>2.16***</td>
<td>4.58***</td>
<td>3.70***</td>
<td>3.43***</td>
<td>5.93*** 1.73***</td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>1.36*</td>
<td>3.31***</td>
<td>4.24***</td>
<td>5.89***</td>
<td>0.56**</td>
<td>2.18*** 3.92***</td>
</tr>
<tr>
<td><strong>Cold Stratification</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Blepharipappus scaber</em></td>
<td>1.03</td>
<td>1.33**</td>
<td>1.45***</td>
<td>1.37**</td>
<td>0.50***</td>
<td>N/A N/A</td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>1.00</td>
<td>0.85†</td>
<td>0.87‡</td>
<td>0.78**</td>
<td>0.92</td>
<td>1.00 1.08</td>
</tr>
<tr>
<td><em>Cryptantha pterocarya</em></td>
<td>0.99</td>
<td>0.31***</td>
<td>0.29***</td>
<td>0.30***</td>
<td>1.52***</td>
<td>0.50*** 0.33***</td>
</tr>
<tr>
<td><em>Gilia inconspicua</em></td>
<td>0.87</td>
<td>0.07***</td>
<td>0.07***</td>
<td>0.14***</td>
<td>1.03</td>
<td>3.05*** 2.95***</td>
</tr>
<tr>
<td><em>Mentzelia albicaulis</em></td>
<td>1.02</td>
<td>0.42**</td>
<td>0.40***</td>
<td>0.69†</td>
<td>0.17***</td>
<td>0.26*** 1.49</td>
</tr>
<tr>
<td><em>Microsteris gracilis</em></td>
<td>1.18</td>
<td>0.36***</td>
<td>0.38***</td>
<td>0.45***</td>
<td>1.57***</td>
<td>1.69*** 1.07</td>
</tr>
</tbody>
</table>

Hazard ratios (HR) from the survival analysis indicate pair-wise differences between the rates of germination, with numbers greater than one indicating faster germination and numbers less than 1 indicating slower germination for the treatment in the numerator of the comparison. For example, the HR - Hot/Cool value for *Agoseris grandiflora* of 1.15 indicates that the hot after-ripening treatment germinated 1.15 times faster than the cool treatment. Significant results in total germination from ANOVAs are indicated as follows:

1. \( P < 0.10 \)
2. \( P < 0.05 \)
3. \( P < 0.01 \)
4. \( P < 0.001 \)

Arrows indicate whether treatments increased or decreased germination. The total germination column in the Population Differences analysis indicates when populations (Pop) differed in total germination. A “-” indicates no differences among treatments or populations.

1. \( F\) \(_{(1,118)}\)
2. \( F\) \(_{(3,116)}\)
3. \( F\) \(_{(2,117)}\)
4. \( F\) \(_{(1,78)}\)
Table 4 Coefficient of variation (CV) of fraction of total germinated seeds for (a) perennial and (b) annual forbs, with population numbers as described in Tables 1 and 2

<table>
<thead>
<tr>
<th></th>
<th>Agoseris grandiflora</th>
<th>Chaenactis douglasii</th>
<th>Crepis intermedia</th>
<th>Phacelia hastata</th>
</tr>
</thead>
<tbody>
<tr>
<td>CV by Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across treatments:</td>
<td>0.010</td>
<td>0.773</td>
<td>0.455</td>
<td>0.788</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV by Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across treatments:</td>
<td>0.009</td>
<td>0.675</td>
<td>0.912</td>
<td>0.620</td>
</tr>
<tr>
<td>1</td>
<td>1.056</td>
<td>0.281</td>
<td>0.705</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.111</td>
<td>0.687</td>
<td>0.116</td>
<td>0.554</td>
</tr>
<tr>
<td>Selectivity:</td>
<td>0.010</td>
<td>0.806</td>
<td>0.436</td>
<td>0.626</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraction Germinated</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>by Population:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.989</td>
<td>0.273</td>
<td>0.480</td>
<td>0.143</td>
</tr>
<tr>
<td>2</td>
<td>0.994</td>
<td>0.307</td>
<td>0.843</td>
<td>0.083</td>
</tr>
<tr>
<td>3</td>
<td>0.986</td>
<td>0.450</td>
<td>0.944</td>
<td>0.281</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV by species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across populations:</td>
<td>0.004</td>
<td>0.296</td>
<td>0.350</td>
<td>0.652</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Blepharipappus scaber</th>
<th>Collinsia parviflora</th>
<th>Cryptantha pterocarya</th>
<th>Gilia inconspicua</th>
<th>Mentzelia albicaulis</th>
<th>Microsteris gracilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>CV by Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across treatments:</td>
<td>0.349</td>
<td>0.000</td>
<td>0.017</td>
<td>0.957</td>
<td>1.147</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV by Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across treatments:</td>
<td>0.396</td>
<td>0.000</td>
<td>0.000</td>
<td>1.392</td>
<td>0.721</td>
<td>0.018</td>
</tr>
<tr>
<td>1</td>
<td>0.094</td>
<td>0.000</td>
<td>0.000</td>
<td>0.601</td>
<td>0.914</td>
<td>0.000</td>
</tr>
<tr>
<td>2</td>
<td>0.000</td>
<td>0.027</td>
<td>1.137</td>
<td>0.447</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Selectivity:</td>
<td>0.245</td>
<td>0.000</td>
<td>0.009</td>
<td>1.044</td>
<td>0.694</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraction Germinated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>by Population:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.371</td>
<td>1.000</td>
<td>1.000</td>
<td>0.231</td>
<td>0.113</td>
<td>0.983</td>
</tr>
<tr>
<td>2</td>
<td>0.639</td>
<td>1.000</td>
<td>1.000</td>
<td>0.239</td>
<td>0.020</td>
<td>1.000</td>
</tr>
<tr>
<td>3</td>
<td>1.000</td>
<td>0.983</td>
<td>0.526</td>
<td>0.030</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV by species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>across populations:</td>
<td>0.307</td>
<td>0.000</td>
<td>0.011</td>
<td>0.549</td>
<td>1.007</td>
<td>0.011</td>
</tr>
</tbody>
</table>

CV by Species measures variation across all treatments, and CV by Population measures variation across all treatments for each population of a species. Selectivity was calculated as the mean value of CV by population. CVs by species across populations, or population-level differences, were calculated as the CV of the fraction of seeds germinated across populations of a species. Higher numbers indicate higher variation in total seed germination among treatments or populations. The CV values presented are adjusted to account for variation in the number of populations representing each species.
Table 5 Effects of (a) local and (b) rangewide spatial climate variability on the degree of selectivity in response to treatments and the population-level differences in seed germination demonstrated by ten forb species native to the Intermountain West, determined using a model averaging approach. Standardized parameter estimates from the naturally-averaged model (NA) and the zero-averaged model (ZA) are shown.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Selectivity</th>
<th>Population-level Difference</th>
<th>IMP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NA</td>
<td>ZA</td>
<td></td>
</tr>
<tr>
<td>Range Size</td>
<td>3.38E-04</td>
<td>6.20E-05</td>
<td>0.18</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>9.02E-01</td>
<td>4.18E-02</td>
<td>0.05</td>
</tr>
<tr>
<td>Available Water in the Spring</td>
<td>9.69E-01</td>
<td>1.38E-01</td>
<td>0.14</td>
</tr>
<tr>
<td>SWB</td>
<td>-1.37E-01</td>
<td>-7.58E-03</td>
<td>0.06</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>9.70E+01</td>
<td>8.41E+00</td>
<td>0.09</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>1.71E+00</td>
<td>1.82E-01</td>
<td>0.11</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>-1.49E+00</td>
<td>-2.46E-01</td>
<td>0.17</td>
</tr>
<tr>
<td>AET</td>
<td>-2.15E+00</td>
<td>-1.41E+00</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>3.40E-04</td>
<td>7.74E-05</td>
<td>0.23</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>8.80E-01</td>
<td>4.02E-02</td>
<td>0.05</td>
</tr>
<tr>
<td>Available Water in the Spring</td>
<td>1.01E+00</td>
<td>3.29E-01</td>
<td>0.32</td>
</tr>
<tr>
<td>SWB</td>
<td>-1.30E+02</td>
<td>-1.12E+01</td>
<td>0.09</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>3.03E-01</td>
<td>1.15E-02</td>
<td>0.04</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>-4.07E-01</td>
<td>-3.16E-02</td>
<td>0.08</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>-4.07E-01</td>
<td>-3.16E-02</td>
<td>0.08</td>
</tr>
<tr>
<td>AET</td>
<td>-1.79E+00</td>
<td>-1.11E+00</td>
<td>0.62</td>
</tr>
</tbody>
</table>

Values in bold indicate a significant relationship ($P < 0.05$). The relative parameter importance (IMP) from the zero-averaged models indicates the proportion of models that contained that parameter, weighted by the AICc values of the models in which the parameter appears. Selectivity was estimated as the mean of the coefficients of variation across all treatments for each of the populations sampled of a particular species. See Supplemental Table 1 for definitions of model variables. Local climate variability was measured across the seed collection locations for each species and rangewide climate variability was measured across herbarium records for each species, with each species represented by a different number of records as follows: *Agoseris grandiflora* (142), *Chaenactis douglasii* (456), *Crepis intermedia* (173), *Phacelia hastata* (469), *Blepharipappus scaber* (81), *Collinsia parviflora* (559), *Cryptantha pterocarya* (401), *Gilia inconspicua* (214), *Mentzelia albicaulis* (568), and *Microsteris gracilis* (515).
Supplemental Table 1  Climate variables considered as potential predictors in generalized linear models of variation in selectivity and population-level differences in response to germination treatments for 10 forb species. All water-based variables are in units of millimeters; all temperature-based variables are in units of degrees Celsius. Variables incorporated into the models for each research question are indicated in black within the center portion of the table. Questions 3 and 4 only incorporated variation in precipitation and temperature variables, variables excluded from those models are indicated in gray in the center portion of the table. Interpretation of composite variables is also presented.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Research Question</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET - annual actual evapo-transpiration</td>
<td></td>
</tr>
<tr>
<td>CWD - annual climate water deficit</td>
<td></td>
</tr>
<tr>
<td>PET - annual potential evapo-transpiration</td>
<td></td>
</tr>
<tr>
<td>SWB - annual soil water balance</td>
<td></td>
</tr>
<tr>
<td>WS - annual water supply</td>
<td></td>
</tr>
<tr>
<td>Coefficient of variation of annual precipitation</td>
<td></td>
</tr>
<tr>
<td>AET:CWD ratio</td>
<td></td>
</tr>
<tr>
<td>PET:AET ratio</td>
<td></td>
</tr>
<tr>
<td>SWB:AET ratio</td>
<td></td>
</tr>
<tr>
<td>WS:AET ratio</td>
<td></td>
</tr>
<tr>
<td>Positive difference between AET and SWB</td>
<td></td>
</tr>
<tr>
<td>Positive difference between WS and the greater of AET or SWB</td>
<td></td>
</tr>
<tr>
<td>Spring ratio of WS and the greater of AET or SWB</td>
<td></td>
</tr>
<tr>
<td>Total Annual Precipitation</td>
<td></td>
</tr>
<tr>
<td>Winter precipitation</td>
<td></td>
</tr>
<tr>
<td>Spring precipitation</td>
<td></td>
</tr>
<tr>
<td>Summer precipitation</td>
<td></td>
</tr>
<tr>
<td>Fall precipitation</td>
<td></td>
</tr>
<tr>
<td>Temperature range</td>
<td></td>
</tr>
<tr>
<td>Annual minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Winter minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Spring minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Summer minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Fall minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Annual maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Winter maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Spring maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Summer maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Fall maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Range Size</td>
<td></td>
</tr>
</tbody>
</table>
**Supplemental Table 1 (continued)**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Biological Relevance and Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET - annual actual evapo-transpiration</td>
<td>Proxy for productivity</td>
</tr>
<tr>
<td>CWD - annual climate water deficit</td>
<td>Proxy for drought stress</td>
</tr>
<tr>
<td>PET - annual potential evapo-transpiration</td>
<td>Climatic demand for water, excluding water availability</td>
</tr>
<tr>
<td>SWB - annual soil water balance</td>
<td>Quantity of water stored in the soil from one month to the next</td>
</tr>
<tr>
<td>WS - annual water supply</td>
<td>Total water supply for the year</td>
</tr>
<tr>
<td>Coefficient of variation of annual precipitation</td>
<td>Seasonality of precipitation</td>
</tr>
<tr>
<td>AET:CWD ratio</td>
<td>Relative CWD; values &gt; 1 are more mesic, values &lt; 1 are more xeric</td>
</tr>
<tr>
<td>PET:AET ratio</td>
<td>Relative drought indicator; values &gt; 1 indicate an unmet demand for water</td>
</tr>
<tr>
<td>SWB:AET ratio</td>
<td>Values &gt; 1 indicate more soil water storage than AET</td>
</tr>
<tr>
<td>Positive difference between AET and SWB</td>
<td>Values &gt; 1 indicate more water for soil water storage, runoff, or deep percolation than used in AET</td>
</tr>
<tr>
<td>Positive difference between WS and the greater of AET or SWB</td>
<td>Fraction of AET from month’s precipitation, not from soil water</td>
</tr>
<tr>
<td>Spring ratio of WS and the greater of AET or SWB</td>
<td>Cumulative water available for runoff or deep percolation</td>
</tr>
<tr>
<td>Total Annual Precipitation</td>
<td>Spring water available for runoff or deep percolation</td>
</tr>
<tr>
<td>Winter precipitation</td>
<td></td>
</tr>
<tr>
<td>Spring precipitation</td>
<td></td>
</tr>
<tr>
<td>Summer precipitation</td>
<td></td>
</tr>
<tr>
<td>Fall precipitation</td>
<td></td>
</tr>
<tr>
<td>Temperature range</td>
<td></td>
</tr>
<tr>
<td>Annual minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Winter minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Spring minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Summer minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Fall minimum temperature</td>
<td></td>
</tr>
<tr>
<td>Annual maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Winter maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Spring maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Summer maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Fall maximum temperature</td>
<td></td>
</tr>
<tr>
<td>Range Size</td>
<td></td>
</tr>
</tbody>
</table>

* Climate Variation
** Climate Mean Values
Local
Rangewide
† To improve the distribution of the model residuals, we log transformed total annual precipitation for Questions 4a** and we log transformed summer precipitation for Question 4b**.

1 See Dilts et al. 2015 for method of calculation
2 Summed for all months
3 Average for all months
4 Winter (Dec, Jan, Feb), Spring (Mar, Apr, May), Summer (Jun, Jul, Aug), Fall (Sep, Oct, Nov)
Supplemental Table 2  Effects of (a) local and (b) rangewide spatial climate means on the degree of selectivity to treatments and the population-level differences in seed germination demonstrated by our focal species, determined using generalized linear models. Standardized parameter estimates from the naturally-averaged model (NA) and the zero-averaged model (ZA) are shown. Values in bold indicate a significant relationship ($P < 0.05$). The relative parameter importance (IMP), from the zero-averaged models, indicates the proportion of models that contained that parameter, weighted by the AICc values of the models in which the parameter appears. Selectivity was estimated as the mean of the coefficients of variation across all treatments for each of the populations sampled of a particular species. See Table 2 for definitions of the model variables.

<table>
<thead>
<tr>
<th></th>
<th>Local</th>
<th>Population-level Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>3.50E-01</td>
<td>3.95E-02</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>7.54E-03</td>
<td>7.20E-04</td>
</tr>
<tr>
<td>Range Size</td>
<td>2.07E-04</td>
<td>2.28E-05</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>-4.50E-02</td>
<td>-5.75E-03</td>
</tr>
<tr>
<td>Available Water in the Spring</td>
<td>-3.85E-03</td>
<td>-3.14E-04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th>Local</th>
<th>Population-level Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>NA</td>
<td>ZA</td>
</tr>
<tr>
<td>Minimum Temperature</td>
<td>-6.93E-02</td>
<td>-2.34E-02</td>
<td>0.34</td>
</tr>
<tr>
<td>Fraction of AET from Precipitation</td>
<td>2.66E-03</td>
<td>1.84E-04</td>
<td>0.19</td>
</tr>
<tr>
<td>Range Size</td>
<td>1.83E-04</td>
<td>1.47E-05</td>
<td>0.08</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>-9.12E-04</td>
<td>-1.56E-04</td>
<td>0.17</td>
</tr>
<tr>
<td>AET: CWD</td>
<td>-5.34E-03</td>
<td>-9.90E-04</td>
<td>0.07</td>
</tr>
<tr>
<td>AET</td>
<td>-2.98E-05</td>
<td>-2.96E-06</td>
<td>0.10</td>
</tr>
</tbody>
</table>
**Supplemental Table 3** Effects of temporal and spatial climate variability and range size on the degree of selectivity and the population-level differences in seed germination demonstrated by our focal species at a A) local and B) range-wide scale, determined using generalized linear models. Standardized parameter estimates from the naturally-averaged model (NA) and the zero-averaged model (ZA) are shown. The relative parameter importance (IMP), from the zero-averaged models, indicates the proportion of models that contained that parameter, weighted by the AICc values of the models in which the parameter appears. See Table 2 for definitions of model variables.

<table>
<thead>
<tr>
<th>Variation Type</th>
<th>Selectivity</th>
<th>Population-level Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NA</td>
<td>ZA</td>
</tr>
<tr>
<td>Fall Precipitation</td>
<td>Spatial</td>
<td>6.80E-01</td>
</tr>
<tr>
<td>Fall Precipitation</td>
<td>Temporal</td>
<td>2.06E+00</td>
</tr>
<tr>
<td>Summer Precipitation</td>
<td>Temporal</td>
<td>6.24E+00</td>
</tr>
<tr>
<td>Fall Minimum Temperature</td>
<td>Temporal</td>
<td>-1.60E+03</td>
</tr>
<tr>
<td>Winter Maximum Temperature</td>
<td>Temporal</td>
<td>8.15E+03</td>
</tr>
<tr>
<td>Range Size</td>
<td></td>
<td>2.24E-04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variation Type</th>
<th>Selectivity</th>
<th>Population-level Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NA</td>
<td>ZA</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>Spatial</td>
<td>-1.68E+00</td>
</tr>
<tr>
<td>Annual Precipitation</td>
<td>Temporal</td>
<td>3.96E+00</td>
</tr>
<tr>
<td>Annual Minimum Temperature</td>
<td>Spatial</td>
<td>-3.97E+00</td>
</tr>
<tr>
<td>Annual Minimum Temperature</td>
<td>Temporal</td>
<td>1.03E+04</td>
</tr>
<tr>
<td>Spring Precipitation</td>
<td>Spatial</td>
<td>-1.83E+00</td>
</tr>
<tr>
<td>Winter Minimum Temperature</td>
<td>Spatial</td>
<td>-2.71E+01</td>
</tr>
<tr>
<td>Range Size</td>
<td></td>
<td>2.94E-04</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

**Fig. 1** Map of seed collection sites with (a) western United States showing the floristic Great Basin in dark gray, (b) eastern Oregon locations, and (c) Reno area locations

**Fig. 2** Schematic of the experimental design for germination treatments. All storage and treatments took place under dark conditions. Arrow length indicates the relative amount of time of each treatment, and arrow width indicates proportion of seeds in each treatment (sample sizes in Table 2). Box color indicates relative temperature from high (black) to low (white). Storage and after-ripening were performed under dry conditions, while cold stratification and the 15°C treatment were performed with seeds in petri dishes on moist filter paper. Seeds germinated in both the 2°C and 15°C treatments

**Fig. 3** Mean fraction of germinated seeds for each species/treatment combination for (a) perennial species and (b) annual species, after accounting for seed viability for each population. Error bars represent the standard error across all populations of each species. Treatments included either hot or cool after-ripening, followed by cold stratification for zero (15°C), two (2C2), four (2C4), or six (2C6) weeks. Species acronyms indicate the following species: AGGR - Agoseris grandiflora, CHDO - Chaenactis douglasii, CRIN - Crepis intermedia, PHHA - Phacelia hastata, BLSC - Blepharipappus scaber, COPA - Collinsia parviflora, CRPT - Cryptantha pterocarya, GIIN - Gilia inconspicua, MEAL - Mentzelia albicaulis, and MIGR - Microsteris gracilis

**Fig. 4** Time to event plots of seed germination for each population of perennial (a-d) and annual (e-j) species across all treatments. Ninety-five percent confidence intervals are indicated by the colored area around the curves for each population
Fig. 1

a.
b.
Fig. 1 (continued)
Fig. 2
Fig. 3
Fig. 4
Fig. 4
(continued)
Chapter V: Conclusions

This dissertation used sagebrush steppe plant communities to study how plants respond to environmental heterogeneity. Desert systems, such as the Great Basin, are suited for addressing questions related to environmental heterogeneity due to the high amount of environmental variability they experience, such as: temperature shifts from day to night, spatial patchiness in precipitation patterns, and inter-annual variability in climate. The Great Basin also possesses a complex disturbance history, which includes, but is not limited to, introductions of exotic invasive species, grazing, and fire. This work explored the ecology and evolution of understory herbaceous species in this highly variable environment, and asked how this information can be used to inform restoration and land management efforts.

In Chapter II, we used herbarium records and ecological niche models to compare the climate niche and area of occupancy of ten co-occurring understory forbs common to sagebrush steppe systems, asking how climate niches may differ among them. We found that species varied in niche breadth and in the size and spatial distribution of their areas of occupancy. We also found that species varied in the climate variables that predicted their suitable habitat and in the degree of climate variability experienced across areas where they grow, with only two of the ten species sharing a comparable climate niche. This work suggests that herbarium records could be used to better understand the ecology of under-studied, cryptic, or non-dominant species. These methods could be used to guide the selection of restoration species and aid in the identification of species that may be most vulnerable to climate change. This work also highlights potential mechanisms for species co-existence of understory forbs in this system, with climate cues acting as a potential means for the temporal partitioning of resources among species; although, further research would be needed to substantiate this hypothesis.
In Chapter III, we investigated seed bank dynamics in sagebrush steppe areas that differed in their disturbance history, asking whether shrub cover, ground cover, local climate, or disturbance (fire and grazing history) were predictive of a variety of measures of seed bank dynamics. In general, we found that coarse measures of fire and grazing commonly available to government agencies were not strong predictors of seed bank dynamics; although, fire on a site <10 years ago was predictive of the similarity between the above and below-ground community composition of an area. Instead, we found that shrub cover was a strong predictor of several measures of seed bank dynamics, including: the densities of seeds in the soil, above-ground and below-ground richness of native species, above-ground evenness of native species, and above-ground and below-ground presence of rare species. This research indicates that the identity and density of shrubs in an area may be reflective of the successional stage of an area after disturbance, with shrub cover of early seral shrubs, like rabbitbrush species, predictive of patterns consistent with moderate disturbance or recovery, and later seral species, like sagebrush, producing patterns consistent with a lack of disturbance. Differences in the seed bank densities between areas containing the two common rabbitbrush species, *Chrysothamnus viscidiflorus* and *Ericameria nauseosa*, indicate that future work is needed to identify potential differences in their ecology and influence on understory plant communities.

In Chapter IV, we explored the specialist-generalist spectrum of germination strategies exhibited by a group of ten arid land forbs, asking whether there were potential relationships between these strategies and climate at a local or range-wide scale. We performed germination trials and assessed the germination strategies of our species using two metrics: selectivity (whether seeds required specific cues to germinate) and population-level variation. We found that these co-occurring species exhibited distinct germination strategies, with nine out of ten of
our species demonstrating population-level differences. Our modeling efforts indicated that
generalist strategies evolve in response to higher spatial variation in actual evapotranspiration
at a local scale and in available water in the spring and annual precipitation at a range-wide
scale. This work contributes to our understanding of the relationship between climate variability
and life-history strategies, including intraspecific variability in seed germination. This work also
provides an approach for land managers to select appropriate restoration species, based on the
life history of desired species and environmental conditions occurring at focal locations.