

Climate variability affects the germination strategies exhibited by arid land plants

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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 affect 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 (did populations differ in their responses to germination cues?) 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. Modeling efforts suggested 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. 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.

Keywords Seed dormancy · Great Basin · Intra-specific variation · Population-level variation · Seed traits

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).

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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 widely been 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 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 that 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 the 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 the 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 these 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 these 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 to 2014, herbarium records to estimate the geographic and environmental ranges of these species, and germination trials with field-collected seeds of ten 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 species exhibit a variety of germination strategies?
2. Did species exhibit population-level differences in seed germination?

We were also interested in whether our focal 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. Finally, 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 our focal species.

Methods

Identifying germination strategies of focal species

We selected ten 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 (Supplemental 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 of weather data. Collections were centered in Northern Nevada for 9 of 10 species (Supplemental 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 1), 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 1). Because seeds were wild-collected, there is the potential for maternal effects to influence the outcome of our germination trials (Guterman 2000; Baskin and Baskin 2014). We attempted to limit this influence by collecting seeds consistently throughout the reproductive window for these 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 1). Longer storage times may have reduced the seed dormancy of species with non-deep physiological dormancy (Baskin et al. 2006); however, most species and populations produced seed from late May to 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 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. 1). For the after-ripening treatment, seeds were placed in paper coin envelopes and were exposed to one of two treatments for 4 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 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

Table 1 Species and methodological details for ten forbs native to the Intermountain West, collected from multiple populations

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

Information includes life form (annual or perennial), seed collection time frame (in months), % viability of a subset of seeds, seed mass (mean ± SD), and sample sizes per dish for germination treatments. See text within the Methods for details regarding seed viability testing. Seed mass was estimated from a sample of ten seeds per population. Acronyms are as follows: Cool AR—cool after-ripening, Hot AR—hot after-ripening

^aSeeds for this population were procured from the National Plant Germplasm System

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 (5–20 seeds, based on availability) (Table 1), 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 2 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

2 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 (ANOVAs), using Program R (R Development Core Team 2016).

We also analyzed germination data using survival analysis to distinguish differences in the timing of germination. We accounted for seed viability in this analysis by

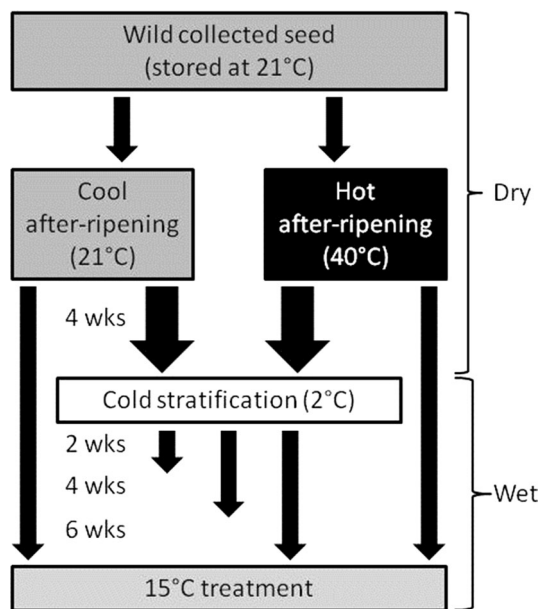


Fig. 1 Schematic of the experimental design for germination treatments. All storage and treatments took place under dark conditions. Arrow length indicates the relative amount of time of each treatment, and arrow width indicates proportion of seeds in each treatment (sample sizes in Table 2). Box color 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 and 15 °C treatments

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 Weibull distribution (Brown and Mayer 1988). We used the scale parameter and the coefficient from the AFT model to calculate the hazard ratio (HR) for these comparisons using the following equation:

$$\text{Hazard ratio} = \exp(\text{coefficient} \times -1 \times (1/\text{scale})).$$

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 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 focal 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:

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

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_{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 focal species are confined to this region, and limited 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 data set, in an attempt to limit spatial auto-correlation of 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 data analysis (Supplemental Table 3). 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 to 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 evapotranspiration (AET), potential evapotranspiration (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 $CV_{unbiased}$ 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 (Questions 3 and 4). We calculated the average value for each environmental variable across all points for each species from 1950 to 2014 and used that as a measure of the mean climate for a particular species.

Second, 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 to 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 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 (Supplement 1). The Pearson's correlation between niche breadth and range size was 0.97, so we chose to exclude niche breadth from these 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 ($R > \pm 0.7$) across our collective species' ranges, and narrowed the focal set of variables down to a subset of uncorrelated variables for each model (Supplemental Table 2). When selecting variables for each 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 bioclimatic

variables (Questions 3 and 4), models examining mean values of 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 question. 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 Akaike 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 focal species exhibit a variety of germination strategies (Question 1)?

Overall, focal species exhibited distinct differences in the total number of seeds that germinated in response to treatments (Fig. 2). 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 to completely break dormancy. The remaining species fell somewhere in-between. Two species preferred longer periods of cold stratification (*C. intermedia*

and *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 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 2). For *C. douglasii*, cool after-ripening resulted in both faster germination and higher total number of germinated seeds (Table 2).

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 2). *A. 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 a little difference between the rates of germination in the cold stratification treatments (Table 2). Some species germinated more quickly in warmer temperatures after exposure to cold stratification (Table 2): *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 2). Only *G. inconspicua* exhibited a higher rate of germination coupled with higher overall seed germination when placed directly into 15 °C (Table 2). 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 2).

Did 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 2; Fig. 3). Two species with generalist strategies, *A. grandiflora* and *C. pterocarya*, exhibited significant differences in the rates of germination

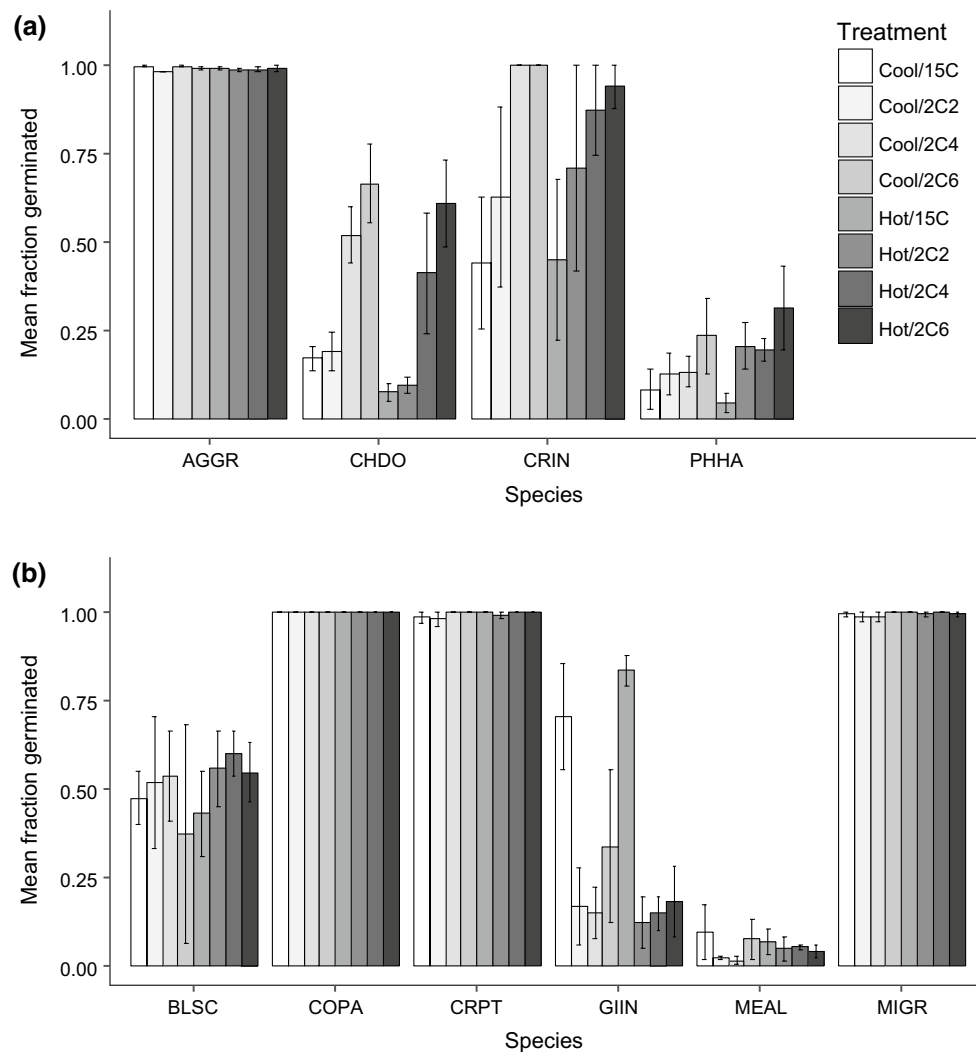


Fig. 2 Fraction of germinated seeds for each species/treatment combination (mean $\pm$ SE across all populations of each species) for **a** perennial species and **b** annual species, after accounting for seed viability for each population. Treatments included either hot or cool after-ripening, followed by cold stratification for 0 (15C), 2 (2C2), 4 (2C4), or 6 (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*

between populations without exhibiting differences in the total number of seeds germinated (Table 2). 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 2). The most dramatic population-level differences were exhibited by *C. intermedia* in both germination rate and total germinated seeds (Table 2). *B. scaber* exhibited population-level differences in both the rate and the total seeds germinated (Table 2). Two other species, *C. douglasii* and *G. inconspicua*, had one of their populations which germinate at a much faster rate than the other two populations, as well as a higher level of germination (Table 2). 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 to completely break dormancy (Table 2; Fig. 3). We quantified both species and population-level variation in the fraction of seeds germinated (Table 3).

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

Table 2 Statistical results for differences in rate and total germination in response to treatments and among populations for (a) perennials and (b) annuals

Species	Treatments				Population differences					
	After-ripening		Cold stratification							
	Rate (HR)		Rate (HR)		Rate (HR)					
	Hot/cool	Total germination	2C2/15C	2C4/15C	2C6/15C	Total germination	Pop 2/Pop 1	Pop 3/Pop 1	Pop 3/Pop 2	Total germination
(a)										
<i>Agoseris grandiflora</i>	1.15***	–	0.36***	0.44***	0.40***	–	1.18**	0.82***	0.69***	–
<i>Chaenactis douglasii</i>	0.68***	↑ _{cool} 4.04 ¹ *	1.00	4.24***	6.57***	↓ _{15C} 65.34 ² ***	1.10	1.85***	1.69***	↑ _{Pop3} 4.60 ³ *
<i>Crepis intermedia</i>	0.94	–	2.16***	4.58***	3.70***	↓ _{15C} 22.75 ² ***	3.43***	5.93***	1.73***	↓ _{Pop1} ↑ _{Pop3} 27.24 ³ ***
<i>Phacelia hastata</i>	1.36*	–	3.31***	4.24***	5.89***	↓ _{15C} 8.12 ² ***	0.56**	2.18***	3.92***	↓ _{Pop2} ↑ _{Pop3} 14.52 ³ ***
(b)										
<i>Blepharipappus scaber</i>	1.03	–	1.33**	1.45***	1.37**	–	0.50***	N/A	N/A	↓ _{Pop1} 81.66 ⁴ ***
<i>Collinsia parviflora</i>	1.00	–	0.85*	0.87 ¹	0.78**	–	0.92	1.00	1.08	–
<i>Cryptantha pterocarya</i>	0.99	–	0.31***	0.29***	0.30***	–	1.52***	0.50***	0.33***	↓ _{Pop3} ↑ _{Pop2} 2.93 ^{3†}
<i>Gilia inconspicua</i>	0.87	–	0.07***	0.07***	0.14***	↑ _{15C} 62.22 ² ***	1.03	3.05***	2.95***	↑ _{Pop3} 12.72 ³ ***
<i>Mentzelia albicaulis</i>	1.02	–	0.42**	0.40***	0.69 ¹	↑ _{15C} 2.42 ^{2†}	0.17***	0.26***	1.49	↑ _{Pop1} 21.71 ³ ***
<i>Microsteris gracilis</i>	1.18*	–	0.36***	0.38***	0.45***	–	1.57***	1.69***	1.07	↓ _{Pop1} 3.92 ³ ***

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 one indicating slower germination for the treatment in the numerator of the comparison. For total germination, F-statistics for ANOVAs are shown, with degrees of freedom indicated as follows: ¹F_(1,118), ²F_(3,116), ³F_(2,117), and ⁴F_(1,78)

Significance levels are indicated as follows: ¹ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

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, with population numbers as described in Table 1

A “–” indicates no differences among treatments or populations

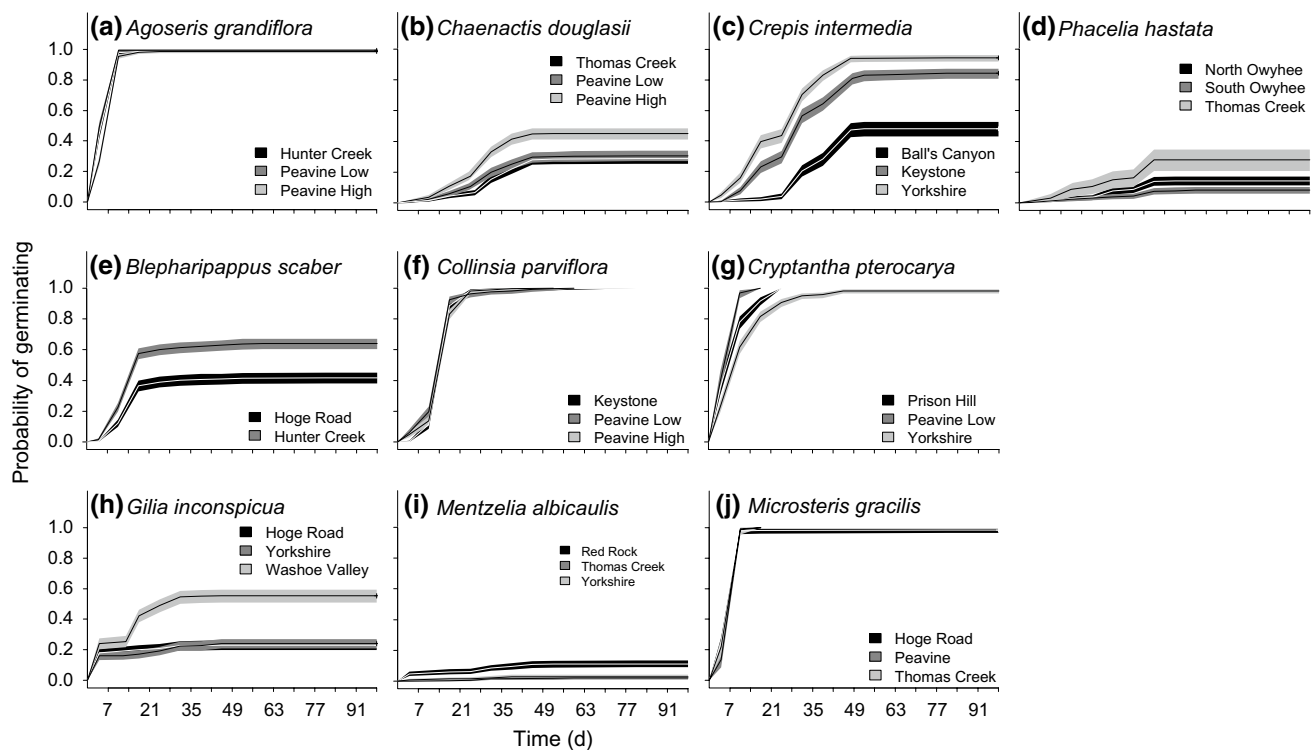


Fig. 3 Time-to-event plots of seed germination for each population of (a–d) perennial and (e–j) annual species across all treatments. Ninety-five percent confidence intervals are indicated by the colored area around the curves for each population

selectivity (Question 3a) and population-level differences in germination (Question 3b) (Table 4a), 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 3a).

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 4b), 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 the 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 3b).

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

Models did not indicate a significant relationship between the degree of spatial or temporal (inter-annual) variation in 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 4).

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 focal 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 species, all except for *C. parviflora*. Given that these

Table 3 Coefficient of variation (CV) of fraction of total germinated seeds for (a) perennial and (b) annual forbs, with population numbers as described in Table 1

(a)	<i>Agoseris grandiflora</i>	<i>Chaenactis douglasii</i>	<i>Crepis intermedia</i>	<i>Phacelia hastata</i>		
CV by species across treatments:	0.010	0.773	0.455	0.788		
CV by population across treatments:						
1	0.009	0.675	0.912	0.620		
2	0.010	1.056	0.281	0.705		
3	0.011	0.687	0.116	0.554		
Selectivity:	0.010	0.806	0.436	0.626		
Fraction germinated by population:						
1	0.989	0.273	0.480	0.143		
2	0.994	0.307	0.843	0.083		
3	0.986	0.450	0.944	0.281		
CV by species across populations:	0.004	0.296	0.350	0.652		
(b)	<i>Blepharipappus scaber</i>	<i>Collinsia parviflora</i>	<i>Cryptantha pterocarya</i>	<i>Gilia inconspicua</i>	<i>Mentzelia albicaulis</i>	<i>Microsteris gracilis</i>
CV by species across treatments:	0.349	0.000	0.017	0.957	1.147	0.013
CV by population across treatments:						
1	0.396	0.000	0.000	1.392	0.721	0.018
2	0.094	0.000	0.000	0.601	0.914	0.000
3		0.000	0.027	1.137	0.447	0.000
Selectivity:	0.245	0.000	0.009	1.044	0.694	0.006
Fraction germinated by population:						
1	0.371	1.000	1.000	0.231	0.113	0.983
2	0.639	1.000	1.000	0.239	0.020	1.000
3		1.000	0.983	0.526	0.030	1.000
CV by species across populations:	0.307	0.000	0.011	0.549	1.007	0.011

See text within the "Methods" section for details regarding calculating the values within this table. Higher CV values indicate higher variation in total seed germination among treatments or populations

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 focal 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, is generally more

Table 4 Effects of (a) local and (b) range-wide 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

	Selectivity			Population-level difference			
	NA	ZA	IMP	NA	ZA	IMP	
(a)							
Range size	3.38E−04	6.20E−05	0.18	3.40E−04	7.74E−05	0.23	
Fraction of AET from PPT	9.02E−01	4.18E−02	0.05	8.80E−01	4.02E−02	0.05	
Available water in the spring	9.69E − 01	1.38E−01	0.14	1.01E+00	3.29E−01	0.32	
SWB	−1.37E−01	−7.58E − 03	0.06	3.55E − 01	2.42E − 02	0.07	
Minimum temperature	9.70E+01	8.41E+00	0.09	−1.30E+02	−1.12E+01	0.09	
Summer PPT	1.71E+00	1.82E−01	0.11	3.03E−01	1.15E−02	0.04	
Annual PPT	−1.49E+00	−2.46E−01	0.17	−4.07E−01	−3.16E−02	0.08	
AET	−2.15E+00	−1.41E+00	0.66	−1.79E+00	−1.11E+00	0.62	
	Selectivity			Population-level difference			
	NA	ZA	IMP	NA	ZA	IMP	
(b)							
Range size	2.10E−04	1.32E−05	0.06	Range size	3.04E−04	3.71E−05	0.12
Fraction of AET from PPT	−1.62E + 00	−1.17−01	0.07	Fraction of AET from PPT	−2.43E−01	−1.58E−02	0.07
Available water in the spring	−3.61E+00	−2.38E+00	0.66	Available water in the spring	−8.38E−01	−5.61E−02	0.07
SWB	−8.68E−02	−4.38E−03	0.05	SWB	−1.80E−01	−1.90E−02	0.11
Minimum temperature	−3.72E+01	−2.63E+00	0.07	Minimum temperature	−1.77E+01	−1.33E+00	0.07
Summer PPT	−4.87E−01	−2.38E−02	0.05	log (summer PPT)	−6.21E−01	−4.36E−02	0.07
log (annual PPT)	−2.35E+00	−1.05E+00	0.45	Annual PPT	−1.37E+00	−2.63E−01	0.19
AET:CWD	−2.81E−02	−2.09E−03	0.07	AET:CWD	−2.29E−02	−2.02E−03	0.09
Relative drought	9.61E−01	5.05E−02	0.05	Relative drought	1.88E+00	4.63E−01	0.25

Standardized parameter estimates from the naturally averaged model (NA) and the zero-averaged model (ZA) are shown

See text for details regarding the relative parameter importance (IMP) and methods for measuring climate variability

Acronyms for climate variables are defined as follows: *AET* actual evapotranspiration, *SWB* soil water balance, *CWD* climate water deficit, *PPT* precipitationValues in bold indicate a significant relationship ($P < 0.05$)

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 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 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 treatments, 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 which we observed among these species.

Finally, we know that different germination strategies influence 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 and Bazzaz 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 and 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 was an important predictor 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).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement This article does not contain any studies with human participants or animals performed by any of the authors.

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