

Contemporary climate change in the Sonoran Desert favors cold-adapted species

SARAH KIMBALL*, AMY L. ANGERT†, TRAVIS E. HUXMAN*‡ and D. LAWRENCE VENABLE*

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA, †Department of Biology, Colorado State University, Fort Collins, CO 80523, USA, ‡B2 Earthscience, University of Arizona, Tucson, AZ 85721, USA

Abstract

Impacts of long-term climate shifts on the dynamics of intact communities within species ranges are not well understood. Here, we show that warming and drying of the Southwestern United States over the last 25 years has corresponded to a shift in the species composition of Sonoran Desert winter annuals, paradoxically favoring species that germinate and grow best in cold temperatures. Winter rains have been arriving later in the season, during December rather than October, leading to the unexpected result that plants are germinating under colder temperatures, shifting community composition to favor slow growing, water-use efficient, cold-adapted species. Our results demonstrate how detailed ecophysiological knowledge of individual species, combined with long-term demographic data, can reveal complex and sometimes unexpected shifts in community composition in response to climate change. Further, these results highlight the potentially overwhelming impact of changes in phenology on the response of biota to a changing climate.

Keywords: annual plant, climate change, ecophysiology, germination, long-term demographic data, phenology

Received 24 April 2009; revised version received 27 August 2009 and accepted 12 September 2009

Introduction

Climate change can have surprising effects on biological communities. Many studies have documented shifts in the geographic ranges and phenology of organisms in response to global climate change (Walther *et al.*, 2002; Parmesan & Yohe, 2003). Previous approaches focus on directional range shifts to higher latitudes and elevations in response to temperature increase (Kullman, 2001; Sturm *et al.*, 2001; Parmesan, 2006; Kelly & Goulde, 2008; Lenoir *et al.*, 2008). Phenological studies document earlier spring green-up and flowering due to warming (Zhou *et al.*, 2001; Wolfe *et al.*, 2005; Parmesan, 2007). However, it is clear that, due to individualistic responses of different species, complex ecological systems do not always respond in such straightforward ways (Hirsteinsson & Macdonald, 1992; Loya *et al.*, 2001; Suttle *et al.*, 2007). Genomic studies are increasingly showing that simple one-to-one mapping of genotypes and phenotypes may be clouded by complex interactions among genes and between genes and their environment. Likewise, species interactions and environmental feedbacks may lead to unexpected changes of plant communities in

response to variation in climate. Detailed data on demographic vital rates of species within their ranges allows for analysis of such complexity.

Community-level studies often indicate changes to community composition when species' ranges shift individually (Pauli *et al.*, 2007; Wilson *et al.*, 2007; Chen *et al.*, 2009; Wilson & Nilsson, 2009). Similarly, individual responses of organisms sometimes lead to mismatches in phenology of interacting species (Miller-Rushing *et al.*, 2007; Gordo & Sanz, 2009; Saino *et al.*, 2009). While most studies have focused on temperature increases, additional climate components, such as the timing and amount of precipitation, have also been identified as important determinants of phenological response to climate change (Penuelas *et al.*, 2004; Cleland *et al.*, 2006; Franks *et al.*, 2007; Levine *et al.*, 2008). Changes in precipitation can impact community composition by altering germination, seedling establishment, growth, and survival (Brown *et al.*, 1997; Weltzin *et al.*, 2003; Lloret *et al.*, 2009; Miranda *et al.*, 2009). Interestingly, changes in the timing, rather than amounts, of rainfall had a greater influence on community composition in some studies (Fay *et al.*, 2002; Levine *et al.*, 2008).

In arid regions, where water is already a limiting resource, changes in temperature and precipitation,

Correspondence: Sarah Kimball, tel. + 520 621 4022, fax + 520 621 9190, e-mail: kimballs@email.arizona.edu

including extreme events, are likely to have particularly strong effects on biotic communities (Thibault & Brown, 2008; Miranda *et al.*, 2009). Recent combinations of several climate models identified the Southwestern United States as an area where climate is expected to change more than other parts of North America, becoming significantly warmer and drier (Seager *et al.*, 2007; Diffenbaugh *et al.*, 2008; Wise, 2009). We analyzed a 25-year data set on germination, survival, and fecundity for a guild of Sonoran Desert winter annual plants to explore changes in demographic patterns over time (Venable, 2007) and to relate those changes to growth and ecophysiological patterns among species (Angert *et al.*, 2007; Huxman *et al.*, 2008) and to recent climate dynamics. Over the last 25 years, there has been a general warming of the Southwestern United States (Weiss & Overpeck, 2005). Additionally, there have been poleward shifts of stormtracks associated with recent high values of the January, February, and March index of the Northern Annular Mode. Stormtrack shifts have caused fall and spring rainstorms to travel north of the Sonoran Desert, decreasing precipitation and increasing temperatures in this region (McAfee & Russell, 2008). This decrease in precipitation should particularly influence winter annual plants that depend on fall and winter rain events to trigger germination and on winter and spring rainfall for successful reproduction.

The few climate change studies on annuals indicate complex community-level responses. For example, in a 5-year water manipulation experiment in a California grassland, increased water resulted in an increase in nitrogen-fixing forbs 1 year, which lead to an increase in annual grass cover the next year, which in turn lead to decreased germination of forbs the following year (Suttle *et al.*, 2007). Higher temperatures altered seed bank dynamics by increasing germination rates of some species and decreasing seed viability of others in an arid Australian shrubland (Ooi *et al.*, 2009). In Spain, a rainfall manipulation experiment indicated that large reductions in precipitation decreased germination, decreasing diversity as well as annual plant cover (Miranda *et al.*, 2009). The timing of germination is critical for the success of all annual species, and complex dormancy requirements have evolved in response to variable rainfall in deserts (Beatley, 1974; Gutterman, 1994; Adondakis & Venable, 2004). Selection is expected to favor plants that germinate following environmental cues that predict favorable future conditions for growth and reproduction (Cohen, 1967; Pake & Venable, 1996). For this reason, germination and vegetative physiology may be correlated.

In a previous study, we measured ecophysiological traits related to vegetative growth for the dominant species in our system (Angert *et al.*, 2007; Huxman

et al., 2008). These traits were condensed into a single physiological principal component that characterizes species according to their position along a tradeoff between relative growth rate (RGR) and intrinsic water-use efficiency (WUE, Huxman *et al.*, 2008). Species with high WUE seem to be better able to grow during cool periods due to their photosynthetic and water-use patterns (Huxman *et al.*, 2008). This suggests that temperatures during vegetative growth may influence which species will be successful.

In this study, we relate long-term demographic patterns of a community of desert annual plants to climate variation and reveal how complex interactions with the environment lead to unexpected outcomes. We addressed the following questions: (1) How have weather patterns at our study site changed? (2) How has the winter annual plant community changed? (3) What critical life history stage (germination, survival, and/or fecundity) has driven any change in community composition? (4) Have species with specific vegetative physiology been favored?

Materials and methods

Long-term censuses

Since 1982, 72 permanent plots have been set up along a 250 m transect at the Desert Laboratory in Tucson, Arizona, through a creosote shrub flat that has been protected from grazing since 1906. Twenty-four of the plots are 0.05 m², and the rest are 0.10 m². Germination, survival, and fecundity of desert winter annuals have been recorded annually (Venable, 2007). Each year, the plots were visited after every autumn and winter rain event to record germination. Plots then were visited monthly or following subsequent rain events. Individuals were mapped and survival and reproduction were recorded until all plants died at the end of the growing season. In this study, we focused on nine abundant species for which we have both long-term demographic data and physiological data (Table 1). These species are abundant enough to permit reliable long-term demographic analysis and represent 74% of all individuals enumerated in the long-term data set.

Shift in community composition

To describe changes in community structure, we analyzed seedling density data from the 1982 to 1983 growing season through 2006–2007 for nine dominant species using two different methods, principal component analysis (PCA) and ordination. Throughout the rest of this paper, we will refer to each September through May growing season by the year in which the

Table 1 The relative importance of germination, survivorship, and fecundity as determinants of the interannual fluctuations in the abundance of each species

Species and family	Life history stage	Slope	R ²	P	Independent effects
<i>Erodium cicutarium</i> (erci) Geraniaceae	Germination	0.503	0.143	0.134	0.353
	Survivorship	0.371	0.261	0.036	0.470
	Fecundity	0.126	0.029	0.514	
<i>Eriophyllum lanosum</i> (erla) Asteraceae	Germination	1.086	0.634	0.000	
	Survivorship	-0.102	0.062	0.353	
	Fecundity	0.016	0.001	0.921	
<i>Erodium texanum</i> (erte) Geraniaceae	Germination	1.438	0.521	0.002	0.525
	Survivorship	0.140	0.065	0.339	
	Fecundity	-0.577	0.198	0.084	0.202
<i>Evax multicaulis</i> (evmu) Asteraceae	Germination	1.214	0.706	0.000	
	Survivorship	-0.095	0.048	0.450	
	Fecundity	-0.119	0.047	0.456	
<i>Pectocarya recurvata</i> (pere) Boraginaceae	Germination	0.269	0.042	0.430	
	Survivorship	0.270	0.132	0.153	0.067
	Fecundity	0.469	0.261	0.025	0.204
<i>Plantago insularis</i> (plin) Plantaginaceae	Germination	0.679	0.372	0.007	0.448
	Survivorship	0.206	0.227	0.046	0.303
	fecundity	0.115	0.029	0.500	
<i>Plantago patagonica</i> (plpa) Plantaginaceae	Germination	0.652	0.338	0.014	0.622
	Survivorship	0.157	0.154	0.119	0.169
	Fecundity	0.226	0.103	0.194	0.209
<i>Schismus barbatus</i> (scba) Poaceae	Germination	0.947	0.351	0.008	
	Survivorship	-0.032	0.004	0.804	
	Fecundity	0.125	0.022	0.530	
<i>Stylocline micropoides</i> (stmi) Asteraceae	Germination	1.122	0.730	0.000	
	Survivorship	-0.051	0.016	0.670	
	Fecundity	-0.016	0.001	0.919	

The results reported are the regression of total k on individual life stage k 's where k is the logarithmic or proportional change in abundance (see text for details). Significant factors are in bold. The final column gives the independent effect (determined by hierarchical partitioning; see 'Materials and methods') for each life stage. First, variables with zero-order correlations near zero were eliminated following recommendation in Murray & Conner (2009). Next, hierarchical partitioning was applied to models for species with more than one variable remaining.

season ends (i.e., the 1982–1983 through 2006–2007 seasons will be labeled 1983–2007). We used PCA to collapse community structure onto few axes, to simplify representation of any directional changes over time. For the PCA, we took the natural log of the number of seedlings per m² for each of the nine focal species for each year. The resulting data were approximately normally distributed. The first PC accounted for 60% of the variation (supporting information Table S1). We also used nonmetric multidimensional scaling (NMDS) to ordinate all years based on dissimilarity in the abundance of each of the nine focal species that germinated using the software PC-ORD (McCune & Mefford, 1999). The dissimilarity measure used was Sorenson (Bray–Curtis) distance. Mean annual temperature, total season precipitation, the date of the first germination event, temperature during first germination, and year were all included in the secondary matrix of the ordination to

allow for correlations with ordination space. Correlations of the species with position in ordination space were also calculated.

Analysis of life stages determining shifts of abundance

Any long-term shift in community composition could be due to changes in patterns of germination, survival, and/or fecundity. To determine the relative importance of each of these critical life history stages, we performed analyses using 25 years of long-term data on the ratio of seeds germinating in the current year divided by seeds produced the previous year, the proportion of seedlings that survived to reproduce, and per capita seed production (Morris, 1959; Varley & Gradwell, 1970). We calculated ' k ,' the logarithmic or proportional change in abundance, for each life stage, then an overall k for the entire year from germination to germination,

analyzing each species separately. In life-table analyses, k is known as the 'killing power,' or the intensity of mortality at any life stage, is calculated as $\log(a_x/a_{x+1})$, and may be summed to compare total mortality from generation to generation (Haldane, 1992). The change in abundance for each species each year, 'total k ,' was defined as $\ln(\text{seedlings in previous year}/\text{seedlings in current year})$. 'Survivorship k ' was calculated as $\ln(1/\text{per capita survivorship in previous year})$ and 'fecundity k ' was $\ln(1/\text{per capita fecundity in previous year})$. 'Germination k ' was calculated as $\ln(\text{number of seeds produced in the previous year}/\text{seedlings in current year})$. Number of seeds produced in the previous year was calculated as the number of seedlings per m^2 in the previous year times per germinant fecundity. We used linear regression to determine the importance of each of these k values to total k (Morris, 1959; Varley & Gradwell, 1970; Haldane, 1992). This method is similar to a 'key factor analysis,' in which census data for multiple years are used to construct a life-table, and the critical phase that determines interannual fluctuations in population size can be determined by calculating the regression coefficient of each individual k value on the total generation k value (Podoler & Rogers, 1975). One potential problem with k analysis is that life stage k values may be correlated. For this reason, after performing our linear regressions, we used hierarchical partitioning to calculate the independent effect of variables that did not have zero-order correlations near zero (Murray & Conner, 2009). In this method, the effect of each life stage k on total k was calculated as the contribution of the life stage k to the variance in total k averaged over all possible models with that life stage k present (Murray & Conner, 2009).

Germination niche

After we determined that germination was primarily responsible for the shifts in relative abundance and community composition (see 'Results'), we investigated the germination niches of the species and related niche dimensions to abundance patterns. We investigated the rainfall and temperature components of the germination niches of each of the nine focal species. We calculated the total precipitation in the rainfall event that triggered each germination cohort and the average daily temperature during and for 5 days following the rainfall event for all cohorts in the 25-year data set. Maximum, mean, and minimum daily temperatures between September 1 and May 25 for 1982–2007 were all highly correlated ($r > 0.86$ for all variables for all years), so we report the average temperature. For some individuals it was difficult to determine the exact rainfall event that triggered germination, so we only

included seedlings in cohorts larger than 100 individuals, which constituted 97% of all germinated individuals. The average temperature and precipitation conditions for germination were calculated for each species and the relationships between these germination niche variables and seedling abundance and physiological PC score were explored with regression. Niche topographies were constructed for each species demonstrating the number of individuals that germinated under different temperature and rainfall regimes.

To further define the germination niches of the nine focal species, we again used NMMDS. In this case, we ordinated all germination cohorts, rather than years as in the earlier ordination, based on dissimilarity in the abundance of each species that germinated with the software PC-ORD (McCune & Mefford, 1999). Correlations of the species with position in ordination space were calculated. The average vegetative physiology of each cohort was calculated by weighting the physiological PC score of each species by its abundance in that cohort (see 'Physiological traits' for more details or Huxman *et al.*, 2008). The resulting cohort physiological PC value was included in the secondary matrix to calculate the correlations with ordination space. The total precipitation in the rainfall event that triggered germination, cumulative precipitation that season before the germination event, average temperature during and for 5 days following the rain event, and calendar date of the year were also included in the secondary matrix and correlated with ordination space.

Physiological traits

We used previously collected data on vegetative physiology to determine whether abundance patterns were related to plant growth physiology. In the 2004–2005 growing season, a large study was conducted to measure traits of nine focal species for which there are long-term records from the censuses and that differ in their degree of interannual demographic variability (Angert *et al.*, 2007; Huxman *et al.*, 2008). In this previously conducted study, thirty plots were established along a 250 m transect. Every 2 weeks throughout the growing season (from germination through senescence) one or two randomly selected individuals of each of nine species were harvested from each plot to determine biomass production and allocation characteristics. In the lab, harvested plants were separated into root, leaf, stem, and reproductive biomass. Buds, flowers, and fruits were all considered reproductive biomass (Angert *et al.*, 2007; Huxman *et al.*, 2008).

During February and March of 2005, carbon assimilation (A) and internal CO_2 concentration (C_i) response curves were measured with a Li-Cor 6400 portable

photosynthesis system (Li-Cor, Lincoln, NE, USA). The CO_2 concentration in the cuvette was varied to construct $A-C_i$ curves from which $V_{C_{\max}}$ (maximum rate of carboxylation by Rubisco) and J_{\max} (light-saturated rate of electron transport) were calculated. Leaves were analyzed for their carbon isotope ratios to determine intrinsic WUE. Physiological traits were combined by PCA into a single variable, physiological PC [a combination of integrated SLA (area under the curve of SLA vs. time), integrated LMR, RGR responsiveness [(relative change in RGR surrounding the mid-season rain event), J_{\max} : $V_{C_{\max}}$, and leaf N]. These traits underlie the construction of growth rate and WUE and were selected purposefully to understand variation among strategies in these species. More details regarding measurements of physiological traits and PC can be found in Angert *et al.* (2007) and Huxman *et al.* (2008).

In this study, we used the previously collected data described above to calculate a community average physiological PC score for each year or cohort by averaging the physiological PC score of the nine species weighted by their abundances in each year or cohort. We summarized the trajectory of community vegetative physiology by the directional trend in annual community average physiological PC score over time.

Results

Weather patterns and germination

At our field site over the last 25 years, there was an average 6.6 mm yr^{-1} decrease in precipitation during the winter annual growing season (September 1–May 5) and a corresponding $0.05 \text{ }^\circ\text{C yr}^{-1}$ increase in average temperature (Fig. 1a and b; precipitation $R^2 = 0.224$, $P = 0.020$; temperature $R^2 = 0.212$, $P = 0.020$). Most of this decline in precipitation and increase in temperature occurred early in the growing season (supporting information Fig. S1). During the critical germination season (October–December), total precipitation decreased 4.4 mm yr^{-1} ($R^2 = 0.273$, $P = 0.009$) and mean temperature increased $0.05 \text{ }^\circ\text{C yr}^{-1}$ ($R^2 = 0.131$, $P = 0.083$). Along with the overall decrease in precipitation, there was a reduction in number and a delay in timing of germination-triggering rain events. Rain events were defined as triggering germination when new seedlings were present 10–14 days following the rain event (previous experience has shown that virtually all germination occurs within 14 days after a storm). Germination often began in October in the 1980s, but shifted to primarily December by the current decade. The date of first germination receded $2.67 \text{ days yr}^{-1}$ on average during our study (Fig. 1c, $R^2 = 0.303$, $P = 0.005$; cf. supporting information Fig. S2 for timing

and relative size of all germination cohorts). The change in timing has resulted in a dramatic decrease ($0.4 \text{ }^\circ\text{C yr}^{-1}$) in the average temperature at which first germination occurred (Fig. 1d; $R^2 = 0.334$, $P = 0.003$).

Life stage determining shifts in community composition

Corresponding to the shift in climate, there was an overall decline in the abundance of all winter annual plants during our study (Fig. 2a). This decline affected species unequally, shifting community composition (Fig. 2b, supporting information Fig. S3, supporting information Tables S1 and S2). Calculations of k followed by simple regression and hierarchical partitioning analysis revealed that germination, rather than survivorship or fecundity, was the primary factor driving abundance changes for seven of our nine study species (Table 1, supporting information Fig. S4). The other two species, *Erodium cicutarium* and *Pectocarya recurvata*, had abundance patterns primarily influenced by survivorship and fecundity, respectively. Hierarchical partitioning confirmed these results and provided additional information, clarifying the importance of germination in addition to survivorship for *E. cicutarium*.

Germination niches and vegetative physiology

Some species tended to germinate earlier in the season under warmer temperatures, while others germinated later in the season under colder conditions (Fig. 3, supporting information Fig. S5). Patterns of change in abundance corresponded with these differences in germination niches, even for those species whose abundance patterns were influenced more by later life history stages (Figs. 2d, e and 3). For example, *E. cicutarium*, a species that was best able to germinate in cool temperatures, increased over time, while *Plantago insularis*, a species that germinated best in warmer temperatures, decreased (Fig. 3a: this pattern was still significant when the one outlier was removed).

The first axis for the germination cohort ordination was positively correlated with year and average cohort physiological PC score, and was negatively correlated with cumulative growing season precipitation before germination and temperature during germination (Fig. 4). In other words, cohorts with species that germinated following larger precipitation events with higher temperatures are located on the left side of the ordination graph, while cohorts with species with high physiological PC scores (low RGR and high WUE) that germinated following smaller precipitation events and lower temperatures are on the right side of the figure. This

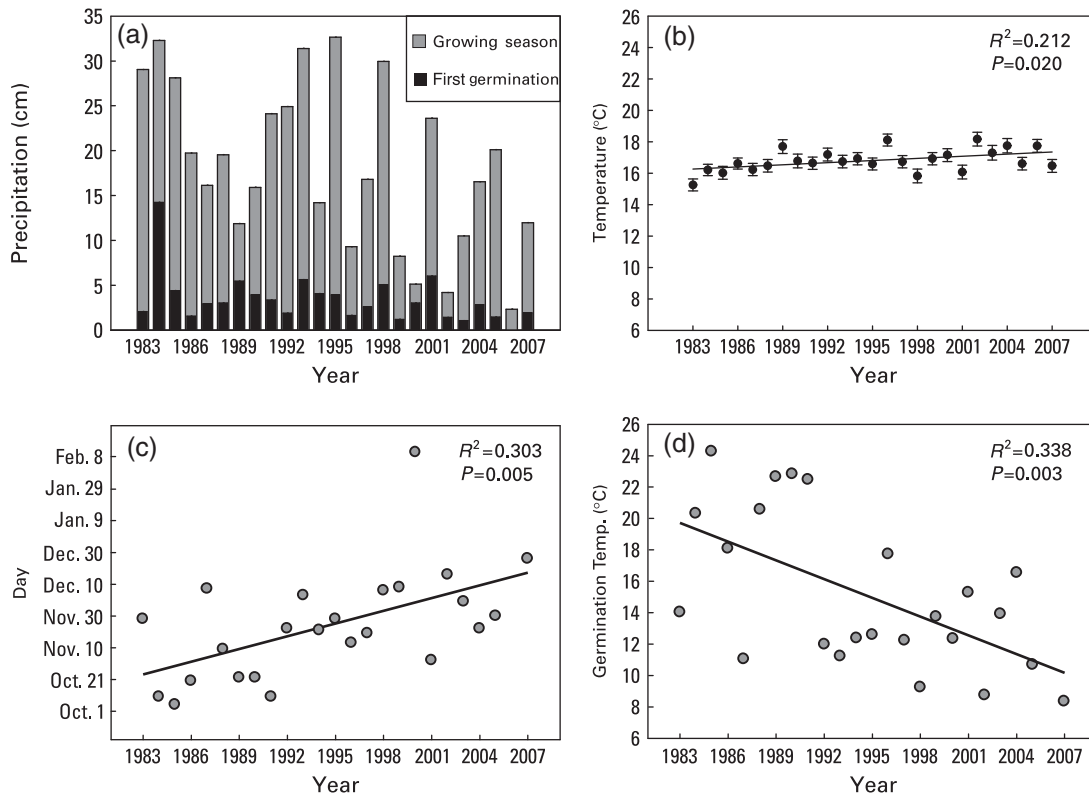


Fig. 1 Climatic and germination trends for 1982–1983 to 2006–2007 winter annual seasons. Each growing season is labeled with the year in which the season ended (i.e., 1983–2007). (a) Bars indicate total precipitation during the desert annual season (September 1–May 5, in gray) and the amount of precipitation that triggered the first germination event (in black). (b) Mean growing season temperature. Error bars indicate SE of the means. (c) The date that the first germination event occurred. The regression is still significant when the year 2000 outlier is removed ($P = 0.002$). (d) Mean temperature during the first rain event and for 5 days following that rain event.

suggests that temperature and precipitation constitute important germination niche axes for desert winter annuals and that germination niche is correlated with postgermination functional traits. Year was strongly correlated with axis 1, reflecting the temporal trend in species composition and community average physiological PC score. The second axis indicates the abundance of all species, which decreased with decreasing total growing season precipitation (Fig. 4).

Germination niches were related to vegetative physiology, as described by physiological PC score. *Evax multicaulis*, the species with the lowest PC score (high RGR and low WUE), decreased in abundance over time and tended to germinate under warmer temperatures and with more precipitation. *P. recurvata*, the species with the highest PC score (low RGR and high WUE), increased in abundance over time and had a broader germination niche that included cooler temperatures with less precipitation (Fig. 3b). This strong linkage between germination and vegetative physiology resulted in a striking shift in the community physiology. Relative abundance of species with high physiological

PC scores (low RGR and high WUE) increased, and species with low PC scores (high RGR and low WUE) decreased (Fig. 2c).

Discussion

We have shown that warming and drying of the Sonoran Desert over the last 25 years is associated with changes in the composition of the winter annual plant community. Delayed onset of germination-triggering winter rains resulted in lower temperatures during germination, leading to an increase in cold-adapted species despite warmer winter temperatures. We have demonstrated how this system's response to changes in climate is determined less by the temperature during the growing season than by the timing of germination-triggering rain events, a factor that has been important in other systems as well (Fay *et al.*, 2002; Levine *et al.*, 2008). Our study demonstrates how phenology (in this case, the timing of germination), can constrain the ability of organisms to respond to changes in climate drivers, leading to unexpected results. Other examples

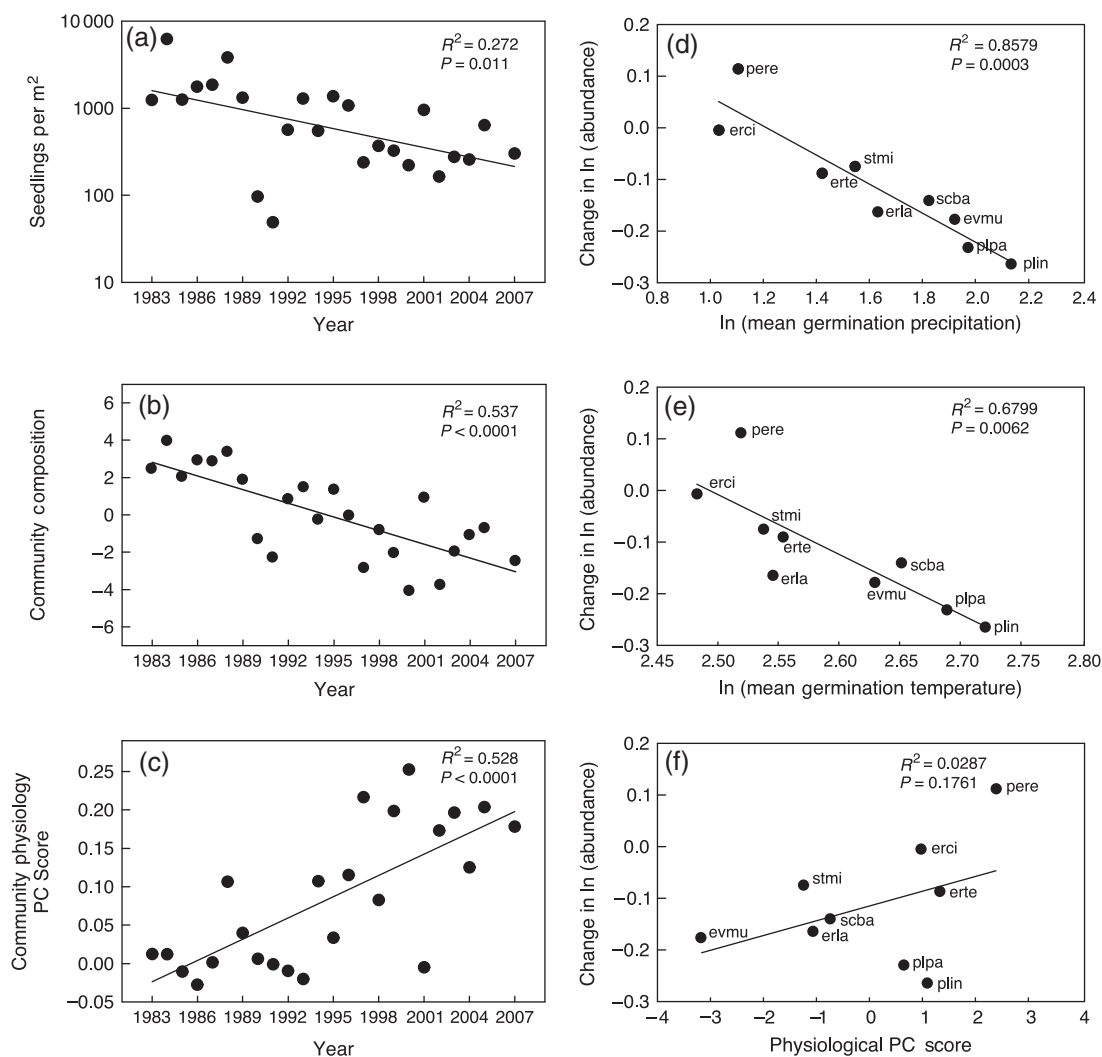


Fig. 2 Linear regressions between temporal changes in the annual plant community and potential environmental and physiological drivers from 1983 to 2007. Each growing season is labeled as the year in which the season ended. (a) Total annual seedling density of all nine species. Each dot represents 1 year. (b) Community composition over time. Each dot represents 1 year. The y -axis indicates the first principal component score from the analysis of the yearly abundance of the nine focal species. Other methods, like the ordination in supporting information Fig. S3, gave similar results. (c) The average physiological PC scores of seedlings (species PC scores weighted by abundance) over time. (d) Proportional change in abundance vs. the average amount of precipitation that triggered germination for each species. (e) Change in abundance and the average germination temperature (the temperature during the rain event that triggered germination and for 5 days following the event) for each species. (f) Change in abundance vs. the physiological PC score for each species. Full species names are given in Table 1.

of paradoxical responses to climate change due to phenological constraints include a study on buzzards, which found that increased temperatures in spring lead to early egg hatching, but summer temperatures were unchanged, resulting in lower temperatures experienced by hatchlings and higher mortality (Lehikoinen *et al.*, 2009). Similarly, earlier snowmelt in the Rocky Mountains resulted in advanced flowering phenology for *Delphinium barbeyi*, *Erigeron speciosus*, and *Helianthella quinqueensis*, and more frost damage to flower buds

of those species despite warming trends in the growing season (Inouye, 2008).

The decrease in rainfall and increase in temperatures for January through April were not as strong as changes in weather patterns earlier in the growing season (supporting information Fig. S1). If the weak later season trends continue, then they may also favor species with low physiological PC scores, because their high WUE may provide increased survivorship and fecundity later in the season (Huxman *et al.*, 2008). However, the

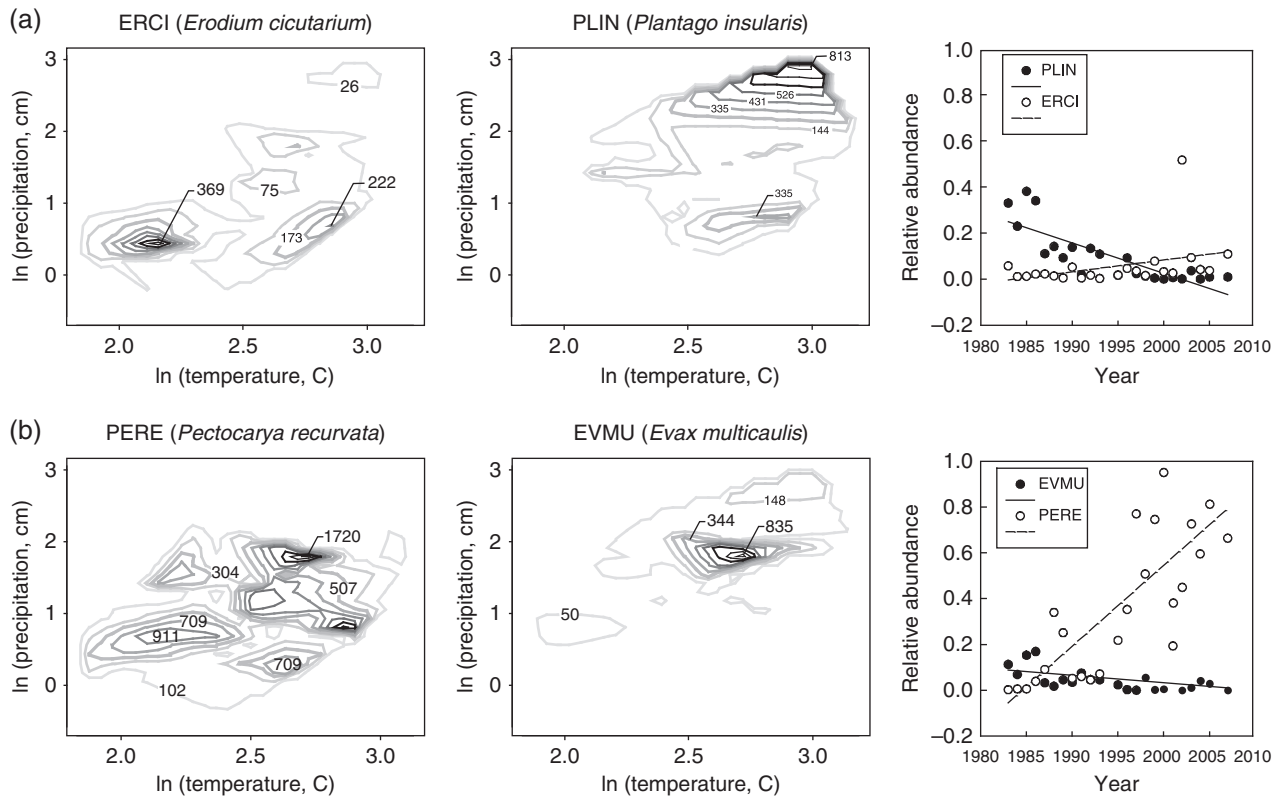


Fig. 3 Germination niches and relative abundance for four species. (a) Contour plots indicating the germination niches of *Plantago insularis* (PLIN, a species that germinates under warm temperatures and high precipitation) and *Erodium cicutarium* (ERCI, a species that germinates under cool temperatures and low precipitation). Precipitation is the total precipitation in the rain event that triggered germination. Temperature is the average temperature during and for 5 days following the rain event. The z-axis is the number of individuals that germinated. The third panel illustrates the relative abundance of the two species (based on the abundance of all nine focal species) from 1983 to 2007. (b) Contour plots for *Evax multicaulis* (EVMU, the species with the lowest physiological PC score, -3.163) and *Pectocarya recurvata* (PERE, the species with the highest physiological PC score, 2.381) indicating germination niches of the two species. The third panel indicates change in relative abundance over time.

change in the community postgermination growth physiology seems to have had a minor role in the community changes that this group of plants has undergone during the last 25 years. Our long-term demographic dataset allowed us to compare the relative importance of germination, survival, and fecundity in changing community composition, and our k analysis indicated that the primary life stage determining multi-decadal community shift in this system was germination (Table 1).

Germination phenology, rather than vegetative growth, may be the most important driver of community shifts in response to climate change, while shifts in survivorship and fecundity correlated with physiology are secondary modifiers that act as a filter following the strong driver of the altered germination climate. These results are reinforced by the tight relationship between the mean temperature and precipitation experienced by each species at germination and the 25-year change of

abundance (Fig. 2d and e). The correspondence of species' physiological PC scores and their long-term change in abundance was much weaker (Fig. 2f). This supports other recent studies predicting the importance of seasonal timing rather than conditions at the height of the growing season in determining changes in community composition with warming (Bradshaw & Holzapfel, 2008; Levine *et al.*, 2008).

Our study raises questions about the future of the Sonoran Desert winter annual community. Will current weather trends continue or are our observations part of a longer-term cycle? There is some evidence that tropical cyclone activity was unusually high during the 1970s and 1980s, so the decline during our study may be a return to longer-term average conditions (see <http://www.cefa.dri.edu/Westmap/>, Daly *et al.*, 2008). If the Sonoran Desert does continue to get warmer and drier, as current climate models predict (Diffenbaugh *et al.*, 2008), will species with high RGR

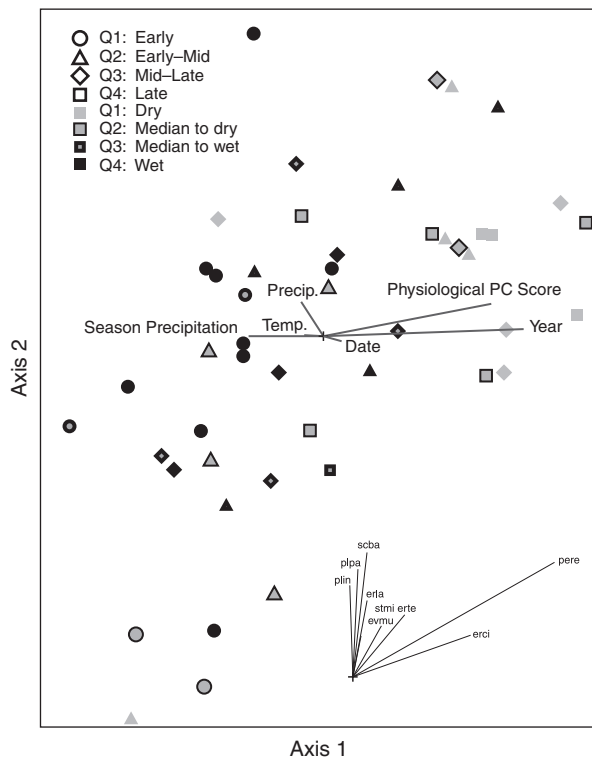


Fig. 4 Ordination of germination cohorts in species space. The marker shape for the cohorts indicates the timing of precipitation (early, early-mid, mid-late, or late), and marker shading indicates the total amount of precipitation that growing season (dry, dry-median, median-wet, or wet). The distance between the cohorts is proportional to their dissimilarity. The final stress for the ordination was 10.95. Central vectors indicate correlations of secondary matrix variables with ordination space (total precipitation so far that season, date, year, physiological PC score, amount of precipitation that triggered germination, and mean temperature during germination, supporting information Table S3). Additional vectors indicate the correlations of species with ordination space (supporting information Table S3). Full species names are given in Table 1.

and low WUE continue to decline in abundance? Finally, will germination phenology continue to be the driver altering community composition? Germination may have been the dominant factor in vegetation change because most of the climate change over our study period occurred during the germination season (supporting information Fig. S1). Perhaps, if later season growing conditions continue to become warmer and drier, and if later conditions change more relative to the weather during germination, survivorship and fecundity (and hence growth physiology) will become more important to shifts in community composition.

Previous studies have also documented unexpected biological responses to linear climatic trends (Inouye, 2008; Lehikoinen *et al.*, 2009). One study on germination

of annual plants indicated that temperature during germination was critical in determining the population growth rate for three rare species (Levine *et al.*, 2008). Our study is unique in using long-term data on vital rates to demonstrate which critical life history stage determines shifts in the dynamics of an entire, intact community. It is also unique in its focus on how germination phenology alters the way species experience environmental change, producing counter-intuitive results. In this case, the warming and drying of the southwestern US has increased the abundance of cold-adapted species.

Acknowledgements

Funding was provided by NSF grants BSR 9107324, DEB 9419905 (LTREB), DEB 0212782 (LTREB) DEB 0717466 (LTREB), 0817121 (LTREB) to D. L. V., DEB 0453781 to D. L. V. & T. E. H., and DEB 0717380 to A. L. A., D. L. V., & T. E. H. The Phileology Foundation of Fort Worth Texas provided additional support. Thanks to two anonymous reviewers for valuable suggestions and to Julio Betancourt for discussions of long-term weather patterns.

References

- Adonakis S, Venable DL (2004) Dormancy and germination in a guild of Sonoran Desert annuals. *Ecology*, **85**, 2582–2590.
- Angert AL, Huxman TE, Barron-Gafford GA, Gerst KL, Venable DL (2007) Linking growth strategies to long-term population dynamics in a guild of desert annuals. *Journal of Ecology*, **95**, 321–331.
- Beatty JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology*, **55**, 856–863.
- Bradshaw WE, Holzapfel CM (2008) Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology*, **17**, 157–166.
- Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 9729–9733.
- Chen IC, Shiu HJ, Benedick S *et al.* (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 1479–1483.
- Cleland EE, Chiariello NR, Loarie SR, Mooney HA, Field CB (2006) Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13740–13744.
- Cohen D (1967) Optimizing reproduction in a randomly varying environment when a correlation may exist between conditions at a time a choice has to be made and subsequent outcome. *Journal of Theoretical Biology*, **16**, 1–14.
- Daly C, Halbleib M, Smith JI *et al.* (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, **28**, 2031–2064.
- Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters*, **35**, L16709, doi: 10.1029/2008GL035075.
- Fay PA, Carlisle JD, Danner BT *et al.* (2002) Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences*, **163**, 549–557.

- Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 1278–1282.
- Gordo O, Sanz JJ (2009) Long-term temporal changes of plant phenology in the Western Mediterranean. *Global Change Biology*, **15**, 1930–1948.
- Guterman Y (1994) Strategies of seed dispersal and germination in plants inhabiting deserts. *Botanical Review*, **60**, 373–425.
- Haldane JBS (1992) Disease and evolution (reprinted from *La Ricerca Scientifica Supplemento*, Vol 19, pg. 1-11, 1949). *Current Science*, **63**, 599–604.
- Hersteinsson P, Macdonald DW (1992) Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*, **64**, 505–515.
- Huxman TE, Barron-Gafford G, Gerst KL, Angert AL, Tyler AP, Venable DL (2008) Photosynthetic resource-use efficiency and demographic variability in desert winter annual plants. *Ecology*, **89**, 1554–1563.
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823–11826.
- Kullman L (2001) 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio*, **30**, 72–80.
- Lehikoinen A, Byholm P, Ranta E *et al.* (2009) Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos*, **118**, 829–836.
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Levine JM, McEachern AK, Cowan C (2008) Rainfall effects on rare annual plants. *Journal of Ecology*, **96**, 795–806.
- Lloret F, Peñuelas J, Prieto P, Llorens L, Estiarte M (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 53–63.
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecology Letters*, **4**, 122–131.
- McAfee SA, Russell JL (2008) Northern annular mode impact on spring climate in the western United States. *Geophysical Research Letters*, **35**, L17701, doi: 10.1029/2008GL034828.
- McCune B, Mefford MJ (1999) *PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design*. Gleneden Beach, OR. Available at <http://people.oregonstate.edu/~mccune/pcord.htm>
- Miller-Rushing AJ, Katsuki T, Primack RB, Ishii Y, Lee SD, Higuchi H (2007) Impact of global warming on a group of related species and their hybrids: Cherry tree (Rosaceae) flowering at Mt. Takao, Japan. *American Journal of Botany*, **94**, 1470–1478.
- Miranda JD, Padilla FM, Lazaro R, Pugnaire FI (2009) Do changes in rainfall patterns affect semiarid annual plant communities? *Journal of Vegetation Science*, **20**, 269–276.
- Morris RF (1959) Single-factor analysis in population dynamics. *Ecology*, **40**, 580–588.
- Murray K, Conner MM (2009) Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology*, **90**, 348–355.
- Ooi MKJ, Auld TD, Denham AJ (2009) Climate change and bet-hedging: interactions between increased soil temperatures and seed bank persistence. *Global Change Biology*, **15**, 2375–2386.
- Pake CE, Venable DL (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**, 1427–1435.
- Parnesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860–1872.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pauli H, Gottfried M, Reier K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. *Global Change Biology*, **13**, 147–156.
- Peñuelas J, Filella I, Zhang XY *et al.* (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist*, **161**, 837–846.
- Podoler H, Rogers D (1975) A new method for the identification of key factors from life-table data. *Journal of Animal Ecology*, **44**, 85–114.
- Saino N, Rubolini D, Lehikoinen E *et al.* (2009) Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biology Letters*, **5**, 539–541.
- Seager R, Ting MF, Held I *et al.* (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181–1184.
- Sturm M, Racine C, Tape K (2001) Climate change – Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 3410–3415.
- Varley GC, Gradwell GR (1970) Key factors in population studies. *Journal of Animal Ecology*, **29**, 399–401.
- Venable DL (2007) Bet hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Weiss JL, Overpeck JT (2005) Is the Sonoran Desert losing its cool? *Global Change Biology*, **11**, 2065–2077.
- Weltzin JF, Loik ME, Schwinning S *et al.* (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, **53**, 941–952.
- Wilson RJ, Gutierrez D, Gutierrez J, Monserrat VJ (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, **13**, 1873–1887.
- Wilson SD, Nilsson C (2009) Arctic alpine vegetation change over 20 years. *Global Change Biology*, **15**, 1676–1684.
- Wise EK (2009) Climate-based sensitivity of air quality to climate change scenarios for the southwestern United States. *International Journal of Climatology*, **29**, 87–97.
- Wolfe DW, Schwartz MD, Lakso AN, Otsuki Y, Pool RM, Shaulis NJ (2005) Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International Journal of Biomechanics*, **49**, 303–309.
- Zhou DW, Wang TH, Valentine I (2005) Phenotypic plasticity of life-history characters in response to different germination timing in two annual weeds. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **83**, 28–36.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Total precipitation and mean temperature for different parts of the growing season from 1983 to 2007. September through December is on the left and January through April is on the right. Each growing season is labeled as the year in which the whole season ended.

Figure S2. Timing of all rain events that triggered a germination cohort during the 1983 to 2007 germination seasons (Oct.1 to April 15). Each growing season is labeled as the year in which the season ended. The amount of rainfall and the proportion of total germination for each year are given.

Figure S3. Ordination of growing seasons in species space. The seasons are colored according to the passage of time, from blue to green to yellow-green to orange. Each growing season is labeled as the year in which the season ended. The distance between the years is proportional to their dissimilarity in species composition. Note that species composition changed with time (along axis 1). The final stress for the ordination was 7.68. Vectors indicate correlations of secondary matrix variables with ordination space (supporting information Table S2).

Figure S4. Linear regressions of the life stage k values (germination, survivorship, and fecundity) on total k . Each species was analyzed separately. R^2 and P values are given in Table 1 of the manuscript.

Figure S5. Contour plots indicating the germination niches of *Eriophyllum lanosum*, *Erodium texanum*, *Plantago patagonica*, *Schismus barbatus*, and *Stylocline micropoides*. Circles in the graph on the lower right indicate conditions during all rain events that triggered germination. Precipitation is the total precipitation in the rain event that triggered germination. Temperature is the average temperature during and for five days following the rain event. The z-axis is the number of individuals that germinated. See Fig. 3 of the manuscript for contour plots of the other four focal species.

Table S1. Results of the principal component analysis on species composition from 1983–2007 (Fig. 2b). Correlations of species abundance with the first two PCs are given. The first PC accounted for 60% of the variation and the second accounted for 16% of the variation.

Table S2. r values indicating the relationship of species and secondary variables with community composition ordination space (supporting information Fig. S3). ‘Temperature’ is the average growing season temperature, ‘Precipitation’ is the total growing season precipitation, ‘Germination Date’ is the date of the first germination event that year, ‘Germination Temperature’ is the temperature during the first germination event, and ‘Year’ is the calendar year in which the growing season ended.

Table S3. r values indicating the relationship of species and secondary variables with germination ordination space (Fig. 4 of manuscript). ‘Temp’ is the average temperature during the rain event and for 5 days following the rain event that triggered germination. ‘Precipitation’ is the total precipitation in the rain event that triggered germination. ‘Seasonal precip’ is cumulative growing season rainfall prior to that particular germination event, ‘date’ is the date of germination, ‘PCA’ is the physiological PC score from high RGR and low WUE to low RGR and high WUE, and ‘year’ is the year of germination.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.