

The role of climate in the dynamics of annual plants in a Chihuahuan Desert ecosystem

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ABSTRACT

Question: What is the role of temporal climate fluctuations in the dynamics of desert winter annual plants in the Portal Bajada, and in the sustained irruption of the non-native annual plant species, *Erodium cicutarium*?

Field site: Portal Bajada, San Simon Valley, Arizona, USA.

Methods: We counted plants at flowering over a 21-year period on twelve permanent plots and related these numbers to weather data collected at an on-site weather station, supplemented by observations from the National Climate Data Center. Specific summary climate variables considered most relevant to annual plant biology were developed as candidate predictors of plant response variables.

Statistical techniques: We removed trends in the data associated with the irruption of *E. cicutarium*, removed temporal autocorrelation, and applied a technique that sought the strongest climatic predictors of vegetation response variables by testing climate variables against each other in bivariate regression analyses. The validity of this technique was demonstrated by simulation. We supplemented our analysis with multivariate regression for simultaneous tests on multiple response variables.

Conclusions: Winter rainfall was the strongest predictor of total annual plant abundance, but number of species was more strongly predicted by average temperature over the total growing season (fall and winter), with cooler weather favouring more species. Average size of a rainfall event, although often thought important in desert plant biology, did not emerge as a significant predictor of the community-level variables, total abundance and number of species, but winter event size did emerge as a significant predictor of differences between the abundances of native species. Our analyses do not support a role for climate in the sustained irruption of *E. cicutarium*.

Keywords: Chihuahuan Desert, climate change, *Erodium cicutarium*, global warming, non-native invasives, seasonal precipitation, species diversity.

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INTRODUCTION

Can we predict vegetation dynamics from climate dynamics? Does climate change leave vegetation vulnerable to invasion by alien species? These questions are critical across the globe, given the challenges of human-caused climate change and the introduction of non-native species (Mooney and Hobbs, 2000; IPCC, 2014). Climate change and introduced species each have the potential to cause community reassembly (Chesson, 2011; Ignace and Chesson, 2014) through increases in the densities and diversities of non-native species and range shifts of native species (Dukes and Mooney, 1999; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Parmesan, 2006; Ignace and Chesson, 2014). Moreover, it has been proposed that climate change and non-native species do not act independently, as changes in climate can enhance the establishment and impact of non-native species by rendering local conditions less suitable for their native inhabitants (Dukes and Mooney, 1999; Sher and Hyatt, 1999; Shea and Chesson, 2002; Knapp *et al.*, 2008; Bradley *et al.*, 2010; Diez *et al.*, 2012; Ibanez *et al.*, 2014; Merow *et al.*, 2017). It is common to find spatial correlations between climate and vegetation processes, such as productivity and community dynamics, especially across large scales (Knapp and Smith, 2001; Gornish and Tylanakis, 2013). However, it has proved difficult to show how temporal changes in vegetation are linked to temporal changes in climate at any one locality (Gornish and Tylanakis, 2013). The challenge is to develop understanding of how changing climate affects vegetation dynamics on local scales.

The biological processes of arid and semi-arid ecosystems of the southwest USA are strongly affected by precipitation (Weltzin and Tissue, 2003) and are expected to be greatly affected by changes in temperature and precipitation patterns from global climate change. A general consensus of climate change models is that these regions will experience more frequent and more intense periods of drought (Easterling *et al.*, 2000; Seager *et al.*, 2007; IPCC, 2014; USGCRP, 2017) and increases in inter- and intra-annual variability of precipitation (Diffenbaugh *et al.*, 2005; IPCC, 2014; USGCRP, 2017). These ecosystems are already changing in terms of plant community species diversity and composition, likely due to rapid and extensive shifts in climate (Parmesan, 2006; Anderson *et al.*, 2012; Scheffers *et al.*, 2016) and are increasingly challenged by non-native species (Brooks, 2003; Barrows *et al.*, 2009; Olsson *et al.*, 2012; Huxman *et al.*, 2013; Ignace and Chesson, 2014; Li and Chesson, 2018).

Laboratory, mesocosm, and short-term field studies imply strong linkages between plant physiological processes and patterns of precipitation in semi-arid and arid ecosystems (Knapp *et al.*, 2002; Huxman *et al.*, 2004; Schwinning and Sala, 2004; Angert *et al.*, 2007; Ignace *et al.*, 2007; Kimball *et al.*, 2010). In addition, linkages are well established between weather events and ecosystem-level processes that promote plant growth, such as decomposition and nitrogen mineralization (Austin *et al.*, 2004; Rao and Allen, 2010; Concilio *et al.*, 2016). Laboratory and short-term field studies find species-specific responses to weather events through germination, physiology, and plant growth, suggesting that specific climatic factors should cause changes in vegetation (Went and Westergaard, 1949; Juhren *et al.*, 1956; Beatley, 1974; Went, 1979; Baskin *et al.*, 1993; Facelli *et al.*, 2005; Angert *et al.*, 2007; Kimball *et al.*, 2010; Walck *et al.*, 2011; Chesson *et al.*, 2013). Improved methods are needed to better link specific climatic detail believed to be biologically important with vegetation dynamics. The relative abundances of desert annual plant species vary greatly in time, assumed due to variation in weather and climate, but linking the detail of those fluctuations to specific details of the observed weather in the field is only now beginning to be successful (Kimball *et al.*, 2010; Huxman *et al.*, 2013). Species-specific responses to climate change provide the potential that an invader might be favoured by new conditions that are less favourable to native species (Dukes and Mooney, 1999; Sher and Hyatt, 1999; Shea and Chesson, 2002; Knapp *et al.*, 2008; Bradley *et al.*, 2010; Sorte *et al.*, 2013; Parmesan and Hanley, 2015).

In this paper, we investigate climatic correlations with the dramatic compositional changes that have occurred over the last few decades in the guild of winter annual plants in the San Simon Valley (Chihuahuan Desert) near Portal, Arizona. The absolute and relative abundances of native species here characteristically show strong fluctuations over time (Guo *et al.*, 2002; Chesson *et al.*, 2013). Recently, the non-native Eurasian species, *Erodium cicutarium*, which previously had a minor presence in the San Simon Valley, irrupted over a wide area and has since remained at high abundance. *Erodium cicutarium* established in the southwest USA 250 years ago (Mensing and Byrne, 1998) and was reported as widespread in southern Arizona by at least 100 years ago (Burgess, 1991). *Erodium cicutarium* has been shown to reduce both the abundance and number of species of native annual plants in the southwest USA (Inouye, 1980; Brooks, 2000, 2003), including in the San Simon Valley (Schutzenhofer and Valone, 2006; Sears and Chesson, 2007). A recent study suggests that a change in the rodent community, combined with favourable weather conditions, facilitated the irruption of *E. cicutarium* (Allington *et al.*, 2013).

Up to 50% of the species in desert flora are annual plants, representing a significant portion of the primary productivity and a major food source for animals (Venable and Pake, 1999). Annuals are ephemerals that germinate and grow in response to the short-term availability of water and nutrients, and their patterns of germination and growth are sensitive to temperature at the time of rainfall (Gutierrez and Whitford, 1987; Whitford and Gutierrez, 1989; Pake and Venable, 1995; Brooks and Matchett, 2003; Adonakis and Venable, 2004; Facelli *et al.*, 2005; Rao and Allen, 2010). They are thus highly susceptible to changes in climate. We characterized the recent patterns of variation in climate parameters that are biologically likely to influence plant germination and growth. Using this information, we asked how well climate variables predict (1) the abundance and diversity of the annual plant guild, (2) the native diversity and the abundances of the major species that have characterized the vegetation over two decades, and (3) the recent shift in species composition to sustained domination by the non-native species *E. cicutarium*.

We characterized climate by total precipitation, mean precipitation event size, and mean temperature in three periods: the total growing season, fall, and winter. These categories were based on climate characteristics most relevant to desert annuals and on a general consensus of climate models that predicts the Southwestern United States will experience an increase in extreme precipitation events (Diffenbaugh *et al.*, 2005), while becoming hotter and more arid in the twenty-first century (Hoerling and Eischeid, 2007; Seager *et al.*, 2007; USGCRP, 2017).

In arid and semi-arid ecosystems of the western USA, precipitation occurs in sporadic and distinct events (Noy-Meir, 1973), and precipitation has most commonly occurred in events of 2 to 5 mm (Loik *et al.*, 2004; Schwinning and Sala, 2004). Precipitation events of this size can elicit a response from soil microbial communities (Austin *et al.*, 2004), stimulate root growth, and increase carbon fixation in some plants (Sala and Lauenroth, 1982; Schwinning *et al.*, 2003). It has been suggested that the size of a precipitation event is critically important to plant dynamics (Knapp *et al.*, 2008; Holt and Chesson, 2014; Liu *et al.*, 2017). The characterization of rainfall and temperature into fall and winter recognizes two phases in the seasonal development of the winter annual vegetation, with germination and early establishment prominent in the fall and major biomass growth occurring in the winter. Species-specific temperature sensitivity for germination and growth imply species-specific variations on this average pattern (Baskin *et al.*, 1993; Chesson *et al.*, 2013).

Our approach was to focus on a relatively small set of potential climate predictors based on their demonstrated or predicted relevance to biology of the species under study. We

provide a new statistical approach designed to determine which of these variables are robust predictors when multiple predictors are considered in a small dataset. Our approach also adjusts for non-stationarity due to the sustained irruption of *E. cicutarium* during the course of the study and for temporal autocorrelation.

MATERIALS AND METHODS

Study system

The study site (31.93 N, 109.08 W) is a Chihuahuan Desert ecosystem located in the San Simon Valley, approximately 6 km east of Portal, Arizona, and near the base of the Chiricahua Mountains, at an elevation of 1644 m (hereafter, we refer to the site as the Portal bajada). Open-range cattle grazing has occurred at this site since the late 1800s (Schutzenhofer and Valone, 2006). A fence was erected in 1977 to exclude livestock and encloses an area of 19.5 ha. Common shrub genera in this area include *Acacia*, *Ephedra*, *Flourensia*, and *Prosopis* (Guo *et al.*, 2002). The soil at the site is characterized as clay and gravel-rich, with much spatial variation in particle size (Sears and Chesson, 2007). *Erodium cicutarium* is currently abundant over many areas of the valley, with relative abundance ranging from 80% to 96% of the total annual plant community in recent years on permanent plots at the study site.

Climate data

A meteorological station in close proximity to our study site has been in operation since 1980, and meteorological data were provided by S.K. Morgan Ernest (University of Florida). Gaps in the data were filled by climate data from the San Simon weather station at the National Climate Data Center online (www.ncdc.noaa.gov/oa/ncdc.html). The regional climate has bimodal precipitation that is primarily concentrated in two seasons: summer rains (May–September) average 156 mm and winter rains (October–April) average 115 mm. The meteorological station collected daily precipitation (mm) and temperature (°C). We obtained monthly, total season (October–April), fall (October–December), and winter (January–April) precipitation totals (evolutionary-ecology.com/data/3143Appendix.pdf, Fig. S1) by summing daily precipitation amounts.

Additionally, daily precipitation was summed for November–February, as this was the period that predicted years of zero plant survival ('guild failure'). We searched for various time windows to determine if they provided a threshold value that corresponded to guild failure. This was systematized by considering all windows, with a monthly resolution, and choosing a threshold that maximized the number of failures predicted successfully. We calculated average daily temperature for the total season, fall, and winter periods (Fig. S1). We calculated event size as the mean daily precipitation for all days during which some precipitation was measured for total season, fall, and winter periods (Fig. S2).

Plant measurements

We established 12 (80 × 50 cm) permanent plots in fall 1987. A census of flowering/fruitlet plants was completed at the end of each growing season (April–May, when most of the winter annual plants were maturing seeds), from 1988 through 2008. Each growing season (October–April) is labelled with the year of the final census; for example, the 1988–1989

growing season is labelled 1989. We analysed total plant abundance, native plant abundance, mean number of species, and the abundances of *Erodium cicutarium* and the three most consistently abundant native species – *Eriastrum diffusum*, *Spermolepis echinata*, and *Plantago purshii* – on these permanent plots as evident from Ignace and Chesson (2014, Figure 1).

Statistical analysis

Several analytical challenges arise in relating climate and vegetation community dynamics with field data. First, the abundances of a biological population are naturally temporally correlated, given that the individuals present in any given year are derived by survival and reproduction from those present earlier. Additionally, native plant abundance at the Portal bajada has declined dramatically as *Erodium cicutarium* abundance has increased, creating a native plant abundance trend that may mask their response to climate. Thus, we took steps to correct for temporal autocorrelation of all species abundances and to correct native plant abundance in the presence of *E. cicutarium*. Correcting the data for temporal autocorrelation and adjusting the native plant abundances by removing the trend allowed us to uncover relationships between the plant community and climate characteristics.

Decorrelating: Adjusting for first-order temporal autocorrelation

The kind of autocorrelation to be expected in population size when fluctuations are driven by environmental factors that vary independently from year to year is Markovian, i.e. first-order autocorrelation (Madsen, 2007), which seems an adequate assumption for our data. We followed an effective method to adjust time-series plant data for a first-order temporal autocorrelation (Ramsey and Schafer, 2012). Implementing this method, we regressed the response variable on the explanatory variables and obtained the residuals. The correlation coefficient r_1 ,

$$r_1 = \frac{c_1}{c_0},$$

is calculated from the autocovariance estimates,

$$c_1 = \frac{1}{n-1} \sum_{t=2}^n res_t \times res_{t-1}$$

$$c_0 = \frac{1}{n-1} \sum_{t=1}^n res_t^2,$$

where res_t is the deviation of observation t from its estimated mean. The coefficient r_1 is the correlation between adjacent residuals from a single time series. The coefficient r_1 is an estimate of the first-order autocorrelation and is used to filter the response and explanatory variables by:

$$V_t = Y_t - r_1 Y_{t-1} \text{ and } U_t = X_t - r_1 X_{t-1}.$$

Standard methods were then used to regress V_t against U_t . These new variables V_t and U_t are related with the same slope as Y_t and X_t , but the errors are not autocorrelated. This technique works with both the univariate and multivariate X_t .

*Detrending: Adjusting for relative abundance of *Erodium cicutarium**

Significant numbers of *E. cicutarium* did not occur in the dataset until 1997, after which *E. cicutarium* followed an increasing trend over time as a proportion of total plant abundance. To study climate effects, rather than the effects of this time trend, we fitted a sigmoid curve to the relative native plant abundance (total density of natives/[total native plus total *E. cicutarium*]) data using the following equation:

$$f(x) = \min + \frac{\max - \min}{1 + \left(\frac{x}{\text{mid}}\right)^{-\text{slope}}},$$

where *min* is the bottom and *max* is the top of the curve, *mid* is the midway point between *min* and *max*, the *slope* is from the curve at its midpoint, and *x* is time, with drought years omitted. To detrend native plant abundance, we divided the actual native plant abundance by $f(x)$. We detrended the *E. cicutarium* by dividing by $1 - f(x)$. Without detrending, the density of natives and *E. cicutarium* in any given year strongly depends on the abundance in the previous non-drought year, obscuring the effects of weather and rendering standard statistical analyses invalid.

Linear regression analyses

Multiple linear regression was used with the decorrelated, detrended variables V_t against U_t to test for the effects of total season, fall, and winter (1) precipitation and mean temperature, (2) mean event size and mean temperature, and (3) precipitation and mean event size on total and native plant densities and number of species. Plant densities and number of species were ln-transformed for all analyses. Simple linear regression was used to test for changes in all climate variables across years (1988–2008). These statistical analyses were performed with JMP statistical software (JMP v.10; SAS, Cary, NC).

Dealing with multiple independent variables in small datasets

Challenges arise in analyses that attempt to test the influence of climate on vegetation dynamics, because numerous climate variables are correlated with each other over time, an issue referred to as multicollinearity in the regression literature (Draper and Smith, 1998). Thus, one variable may appear to have a strong causative relationship for a given dependent variable, when in fact it is merely correlated with another variable that is the true cause. Multiple regression and various approaches to multi-model inference are often assumed to solve this problem (Burnham and Anderson, 2002), but are seriously limited by the amount and quality of the data. Moreover, if none of the putative causative factors is in fact experimentally manipulated in a controlled manner, causation is impossible to establish, no matter how fancy the model. Spurious results are common from incautious application of such techniques in these kinds of circumstances (Burnham and Anderson, 2002).

Given these challenges, we make no pretence of uncovering specific causative relationships between plants and climate but argue instead that there is much merit in the more limited aim of demonstrating the existence of a strong link between climate and vegetation dynamics, along with good indications of which aspects of climate are most important. We achieve this outcome by choosing climate variables known or hypothesized to be important in the biology of the species, restricting these variables by season corresponding to key processes in the life-cycles of the plants, as discussed above. Multiple regression is then used

with these climate variables in pairs within a season. This procedure allows understanding of which member of a pair retains predictive power in the presence of the other and also has the larger R^2 value for predicting a response when present alone (see [Appendix](#)). While this procedure might at first sight appear unorthodox and statistically problematic, we show by simulation that it is in fact robust ([Appendix](#)) and overcomes problems that arise from merely choosing the best fitting of a set of complex models when limited data are available (Burnham and Anderson, 2002).

Multivariate analyses

To understand how climate differentially affects species and potentially leads to changes in species composition, we used multivariate profile analysis on carefully chosen dependent and independent variables predicted to discriminate between species. To discriminate between individual native species' responses to climate, we used multivariate multiple regression to test whether the species had the same regression coefficients on climate variables.

RESULTS

Climate characteristics

Weather fluctuated greatly from year to year at the Portal bajada, but also showed trends ([Appendix](#) Figs. S1 and S2). Total season and winter mean event size have decreased significantly since 1988 (Fig. S2; total season $R^2 = 0.24$, $P = 0.02$; winter $R^2 = 0.22$, $P = 0.03$). Total season, fall, and winter precipitation over 1988–2008 (Figs. S1 and S2) had decreasing trends, but these were not significant given high year-to-year variation. Similarly, temperature for total season, fall, and winter had non-significant increasing trends (Fig. S3). Climate records indicate a double El Niño in 1991–1992 and 1992–1993 and a single, very strong El Niño in 1997–1998 (Brown and Ernest, 2002). Although these periods correspond to higher than average rainfall, they are not the only high rainfall periods at the study site (Figs. S1 and S2).

Guild failure

Winter annual plants showed pronounced year-to-year fluctuations over 1988–2008 (Fig. 1a). No plant survived to reproduce at the end of the growing season in six of these years (1990, 1996, 1999, 2000, 2002, and 2006), an outcome that we refer to as 'guild failure'. Inspection of the data suggested that precipitation during November through February was strongly associated with 'guild success' (Fig. 2). Moreover, the range in precipitation of 35–42 mm during November through February separated guild failure from guild success, i.e. guild failure years had no more than 35 mm, while guild success years had at least 42 mm. Precipitation during this critical period has declined significantly since 1988 ($R^2 = 0.20$, $P = 0.04$; Fig. 2).

Irruption of *Erodium cicutarium*

Our data capture the dramatic sustained irruption of the non-native species, *Erodium cicutarium*. Prior to 1996, *E. cicutarium* was present in the soil seed bank, but few plants grew and reproduced in that period. Starting in 1996, *E. cicutarium* began a period of strong

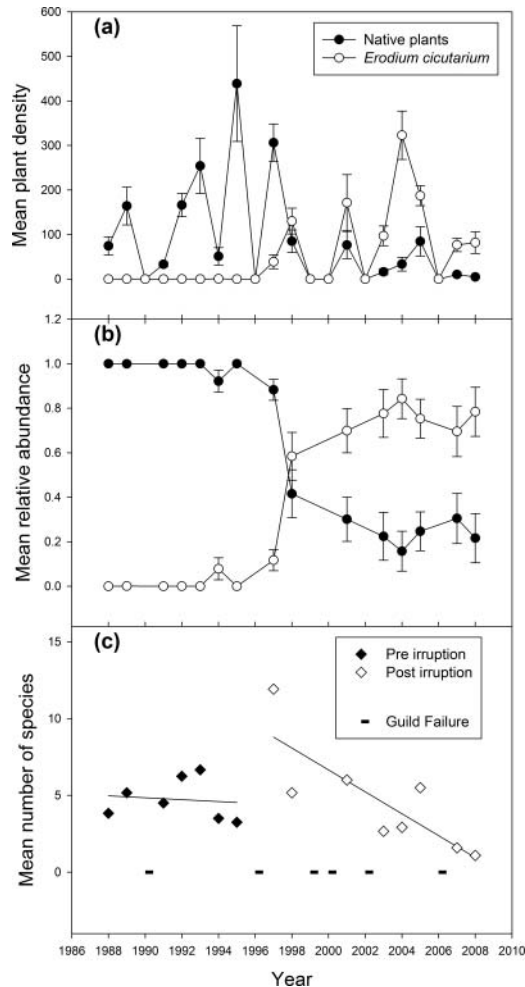


Fig. 1. (a) Mean density (individuals per m²) of native plants and *Erodium cicutarium*, 1988–2008. (b) Mean relative abundance of native plants and *E. cicutarium*, 1988–2008. (c) Mean number of species per plot, 1988–2008. Solid circles (●) represent all native species taken together and open circles (○) represent *E. cicutarium*. Solid diamonds (◆) represent pre-irruption (1988–1996) of *E. cicutarium*; open diamonds (◇) represent post-irruption (1997–2008) of *E. cicutarium*; dashes (■) represent years with no plants ('guild failure'). Error bars are ± 1 standard error.

growth similar in character to logistic growth. The difference between ln-transformed native plant density and *E. cicutarium* density (native – *E. cicutarium* density) changed significantly over time ($R^2 = 0.71$, $P = 0.0002$), with native annuals decreasing in abundance and *E. cicutarium* increasing. By 1998, *E. cicutarium* had reached higher mean density than all native plants combined. Since 1998, the relative abundance of *E. cicutarium* has remained higher than that of all native plants, reaching mean relative abundances as high as 84% (Fig. 1b). Excluding years with guild failure, there is a significant decline in the number of species over the years 1988–2008 ($P = 0.05$). Number of species was high before the

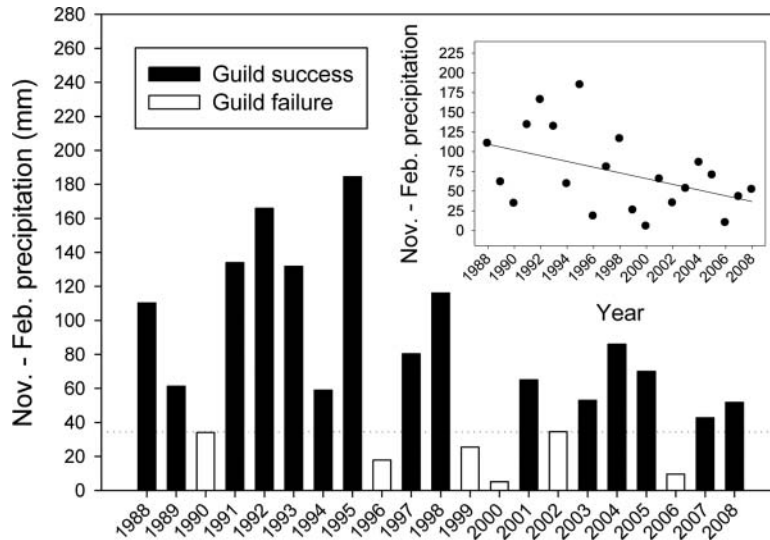


Fig. 2. Precipitation (mm) summed from November through February. Guild success (solid bars, ■) and guild failure (clear bars, □) correspond to disjunct ranges of rainfall in this dataset. The inset graph shows the significantly declining trend of this precipitation over time ($R^2 = 0.20$, $P = 0.04$).

beginning of the *E. cicutarium* irruption in 1996, but decreased significantly below pre-irruption levels over 1997–2008 (Fig. 1c, $P = 0.007$). Native plant abundance and number of species were strongly correlated (Fig. S4; $R^2 = 0.52$, $P = 0.002$).

Plant community response to climate

Hypotheses on how annual plants respond to climate were based on multiple regression of plant abundance and number of species variables on climate variables in pairs as defined in the Methods. This technique identifies climate variables that remain significant predictors when paired with other variables, as justified in the [Appendix](#).

Overall abundances

Total plant abundance and native abundance showed similar patterns ([Appendix](#) Tables S1 and S2). The analysis is on the detrended-decorrelated natural logs of both of these variables. For both total and native abundance, precipitation, whether total season precipitation, fall precipitation, or winter precipitation, is always significant – and often highly significant – regardless of the variable that it is paired with (Fig. 3; Tables S1 and S2). In contrast, mean event size is never significant when paired with these total precipitation variables, suggesting that mean event size contains no further information of value. Only when paired with total season temperature is mean event size a significant predictor of total plant (Table S1, $P = 0.03$) or native abundance (Table S2, $P = 0.01$), although on removal of outliers, winter mean event size becomes a significant predictor for native abundance when paired with winter temperature (Table S2, $P = 0.015$).

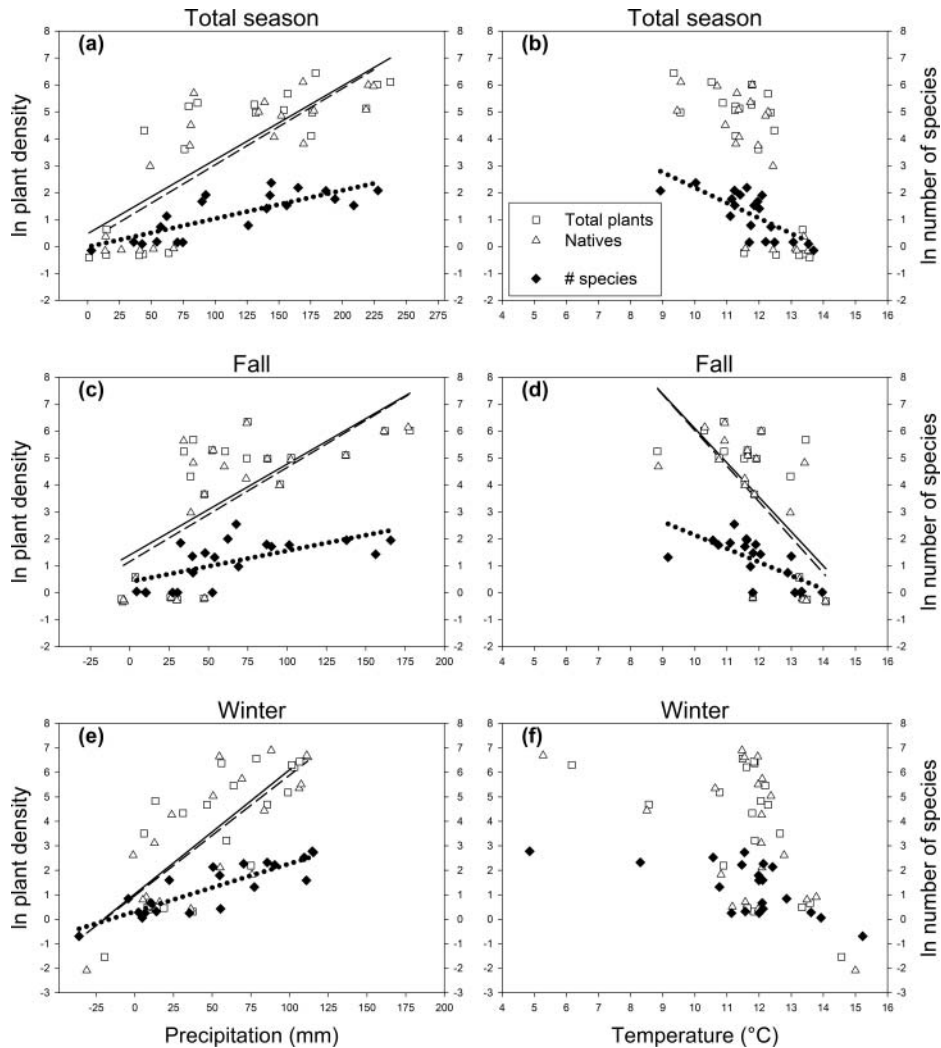


Fig. 3. Multiple regression results for ln total plant density ($\square$, solid line), ln native plant density (Δ , dashed line), and ln number of species ($\blacklozenge$, dotted line). Multiple regressions include total season precipitation (mm) (a) and total season mean temperature ($^{\circ}\text{C}$) (b), fall (October–December) precipitation (c), mean fall temperature (d), winter (January–April) precipitation (e), and mean winter temperature (f).

Total season and fall temperatures are significant predictors of both total and native abundances when paired with mean event size (Tables S1 and S2). Winter temperature is marginally non-significant when paired with event size, for both total and native abundances. When paired with precipitation, temperature was only a significant predictor for total plant density and native plant density in the total-season analysis after removal of an outlier (Tables S1 and S2, $P < 0.05$). Thus, precipitation emerges as the most important climate variable for both all plants and all native plants, with other variables only having

predictive value when precipitation is not considered in the analysis. To see if fall and winter precipitation differ in their explanatory power in the presence of each other, we included them in the same multiple regression. Winter precipitation was the stronger explanatory variable (Tables S1 and S2, $P < 0.001$), with fall marginally non-significant or marginally significant on removal of an outlier (Tables S1 and S2).

Number of species

As number of species was related to native species abundance (Fig. S4, $P = 0.002$), number of species was detrended, adjusting for the decline in native species using the fitted trend in native species abundance and the fitted relationship between number of species and native species abundance. Guild failure years were excluded, as number of species is meaningless in the absence of plants. In these analyses, only temperature variables had any detectable effects (Table S3), and number of species declined with temperature. Total season temperature was a clear predictor and was significant whether paired with precipitation (Table S3, $P = 0.03$) or mean event size (Table S3, $P = 0.04$). Winter temperature became significant on removal of outliers (Table S3, $P = 0.032$ with precipitation). There is a suggestion of an effect of fall temperature, but it was never significant (Table S3, $P = 0.13$ with precipitation, $P = 0.08$ with mean event size).

Comparisons between species

To determine whether the responses of species reflect those of the total community, four species were considered individually: *E. cicutarium* and the three most consistently abundant native species (Tables S4–S7). Although precipitation was a significant predictor for all species, it was not the most important predictor for all. Individual species differed markedly in which other variables were important. Documenting different patterns of significant predictor variables for different species is not a reliable way of understanding whether species are truly different, however. For this, we used multivariate multiple regression to compare species responses to climate. We compared native species collectively with *E. cicutarium* before comparing them with each other.

Natives versus *Erodium cicutarium*

We tried to relate the difference between $\ln$ total native and $\ln$ *E. cicutarium* abundances to the three climate variables (fall and winter precipitation and fall temperature) that seemed most likely to separate species, using detrended-decorrelated data. To further sharpen possible species differences, guild failure years were omitted. However, no significant effect of climate was observed for this difference ($P = 0.3$), suggesting similar responses to climate by natives and *E. cicutarium*. To further explore this possibility, we asked whether the abundances of the now dominant *E. cicutarium* would predict the native species abundances and whether climate variables had additional predictive value once *E. cicutarium* abundance was accounted for. Indeed, *E. cicutarium* abundance strongly predicted the abundance of native species in guild non-failure years (Fig. S5). The effect of *E. cicutarium* was always a significant predictor of native species abundance ($P < 0.02$) except when paired with winter precipitation, where it was marginally non-significant ($P = 0.08$), likely because of the strong effect of winter precipitation on all species, including *E. cicutarium* and natives

considered separately. However, winter precipitation was not a significant predictor ($P = 0.76$) when paired with *E. cicutarium* abundance, despite its typically strong showing when paired with other climate variables.

Natives versus natives

We used multivariate multiple regression to test whether the native species had different regression coefficients on climate variables, restricting attention to the four variables expected to be most likely to discriminate between species based on the individual species analyses. These were fall and winter precipitation, fall temperature, and winter event size, which jointly significantly distinguished the three focal native species ($P < 0.05$). When climate variables were considered separately or in pairs, however, only winter event size significantly distinguished species ($P < 0.05$), and this was the case regardless of which of the other climate variables was paired with winter event size.

DISCUSSION

Climate and plants interact strongly. In arid ecosystems, where water influences biological processes, it is not surprising that precipitation should emerge as a key predictive variable for vegetation dynamics. However, the high variability and complexity of processes in desert environments have often led to equivocal results (Ernest *et al.*, 2000; Guo *et al.*, 2002; Kimball *et al.*, 2010). Discrete pulses of precipitation have been expected to have an important role (Knapp *et al.*, 2008), and various studies imply that responses of plants to the environment should be species-specific (Silvertown *et al.*, 1999; Chesson *et al.*, 2004, 2013; Ogle and Reynolds, 2004; Levine *et al.*, 2008; Angert *et al.*, 2009; Kimball *et al.*, 2010; Chesson, 2011; Huxman *et al.*, 2013). These issues have the potential to complicate the relationship between the amount of precipitation and plant abundance. Despite these complications, however, we found a clear association between the amount of precipitation and the overall abundance of winter annual plants at flowering. This relationship held for native species and for the entire assemblage of winter annual plants, which includes the now-dominant invasive species, *E. cicutarium*. Precipitation was a strong predictor of plant abundance whether we considered the total for the growing season or divided it into the fall and winter seasons. However, when fall and winter precipitation were compared in the same multiple regression, winter precipitation emerged as more important than fall precipitation. Thus, although fall is an important season for germination in this plant community, the main period for growth of the plants, the winter season, was the stronger determinant of the number of plants at flowering, with at best a small additional contribution from the fall season. Our results replicate the finding that total seasonal rainfall has a positive effect on plant abundance at the Portal bajada (Thibault *et al.*, 2010), but refine it by revealing the greater importance of the winter season and the relative lack of importance of other variables.

In contrast, temperature and mean size of a precipitation event did not appear to be important to total annual plant or native plant abundance. When compared with precipitation, these climate variables did not have high predictive value. This result suggests strong overriding resource limitation by precipitation, which sets the size of the annual plant community in any year. Much has been made in the literature of the packaging of precipitation events into discrete events, especially for arid ecosystems (Loik *et al.*, 2004; Ogle and Reynolds, 2004; Reynolds *et al.*, 2004; Knapp *et al.*, 2008). Indeed, it is reasonable to expect that rainfall events

below a certain size may not be effective in promoting germination or growth. Nevertheless, our analysis implies that once the total precipitation for a period has been set, there is little additional information in the average sizes of the precipitation events contributing to this total at the whole-community level. Thus, several small events may have a roughly similar effect to a large event with the same total. We found that temperature also had little effect at the community level of analysis, despite the fact that temperature can limit plant growth. To the extent that productivity is determined by actual evapotranspiration (Rosenzweig, 1968), it appears that most precipitation becomes actual evapotranspiration in this desert ecosystem, severely limiting a role for temperature in productivity.

Although temperature and mean event size were not strongly associated with total plant abundance, they were associated with individual species abundances. That temperature is associated is perhaps not surprising, given the known species-specific responses of desert annual plants to temperature, especially germination at the time of rainfall (Baskin *et al.*, 1993; Chesson *et al.*, 2013). However, the temperature variable used here is simply average temperature over several months, which is likely to be too coarse to capture species differences and, indeed, there is no evidence that it significantly discriminates between species. A species-specific response to mean event size was not expected, although it is consistent with laboratory studies of germination showing strong interactions between species and the amount of moisture (Holt and Chesson, 2014). Mean event size was strongly predictive for only one species, *Spermolepis echinata*, but was the only climate variable that consistently distinguished the three native species.

Species-specific effects are consistent with whole-community abundances that depend strongly only on the supply of one resource, water. The species differences mean that different species contribute most to total community abundances and ecosystem functioning in different years. Potentially, as has been found in grassland ecosystems (Tilman *et al.*, 2006) and in model plant communities (Chesson *et al.*, 2001), high species diversity is important to the maintenance of ecosystem functioning in the presence of environmental fluctuations that favour different species in different years. The fact that different species are favoured in different years (species-specific responses to the environment) can contribute to diversity maintenance by the storage effect (Chesson *et al.*, 2004), and for which evidence is provided in another study of the Portal bajada (Chesson *et al.*, 2013).

The results here are consistent with the idea that the annual plants of the Portal bajada species compete with one another, yet are positively correlated in abundance over time. Although it has been suggested that competing species ought to be negatively correlated on average over time (Houlahan *et al.*, 2007), there is no necessity of that. A strong effect of total abundance on precipitation, which fluctuates greatly over time, can easily lead to positive average correlations between species (Chesson, 2011), although there is evidence of competition (Sears and Chesson, 2007). In fact, one would expect to find a high degree of correlation in abundances of plants in a water-limited desert environment, where all potentially realize the benefits of higher water years, while at the same time varying greatly in relative abundances owing to the species-specific responses to the environment.

A related issue is the extent to which species diversity reflects the weather in any year. Strong associations between climate variables and number of species would suggest that some years favour many species, implying common responses to climate variables, and a diminished tendency for responses to climate to distinguish species. Interestingly, total season temperature was the clearest predictor of number of species, suggesting that cooler conditions favour a larger number of species, yet total abundance is more strongly

associated with precipitation. Thus, there is an important distinction between conditions that allow more individuals to germinate and survive and those that benefit more species.

The annual vegetation of the Portal bajada is dynamic, changing with a strong trend due to the sustained irruption of the alien species *E. cicutarium* and subsequent decline of native species documented here. We asked whether climate could explain the sustained irruption of *E. cicutarium*, which rose from a small but persistent population to dominate the study area. The irruption of *E. cicutarium* is not a case of a recent arrival of an invasive species, but of a sudden change in success of a species long present. *Erodium cicutarium* appears to have been sustained at the Portal bajada prior to the mid-1990s by dense populations that could be observed along the verges of roads, with a minor presence on plots away from these roads. This simultaneous increase of *E. cicutarium* over a broad area, coupled with the decline of native species and no evident invasion front, is suggestive of an environmental change that rendered it better adapted to the conditions at our study site than the native species (Sher and Hyatt, 1999; Shea and Chesson, 2002). Indeed, Allington *et al.* (2013) have implicated a change in the rodent community that lessened seed predation as a primary factor leading to the sustained irruption of *E. cicutarium*. By way of contrast, in other parts of the arid southwest, nitrogen deposition has been implicated in the current dominance of *E. cicutarium* (Brooks, 2003; Steers *et al.*, 2011; Concilio *et al.*, 2016). Experimental manipulations of *E. cicutarium* at the Portal bajada show that it has strong competitive effects on other species (Schutzenhofer and Valone, 2006; Sears and Chesson, 2007; Ignace and Chesson, 2014). Such strong competitive effects might result from higher water-use efficiency than native species, if results elsewhere are a reliable guide (Kimball *et al.*, 2014).

Our data indicate some changes in the climate over the study period (Figs. S2 and S3). Although only mean event size showed statistically significant change over the 21-year period under study, statistical non-significance means only that the observed changes are consistent with a stationary stochastic process, not that the changes did not occur. Since the changes did occur, they might have contributed to changes in the plant community, given its sensitivity to climate. However, we found no significant differences between *E. cicutarium* and the native species collectively in response to climate variables. Moreover, abundance of *E. cicutarium* strongly predicted total abundances of native species, and no other climate variables were significant predictors of total native species when paired with *E. cicutarium*.

Exploring the linkages between weather and plants involved several statistical challenges. Both trends and autocorrelation had to be removed before analyses could proceed. We argue here that biologically sensible climate statistics should be developed for use as independent variables. Use of less biologically appropriate variables could hamper the detection of even strong effects of climate. Finally, despite having a long time series of observations by ecological standards, the limited number of observations together with the large number of weather variables leads to serious challenges. Fitting models with large numbers of independent variables in such circumstances is fraught with difficulties (Burnham and Anderson, 2002), especially when these variables are correlated with each other. The outcome can be models that fit the data, but do not explain it, and have no predictive power. Rather than trying to find a best model for the data, we have sought the best individual climate predictors from the data by pitting pairs of independent variables against each other in multiple regressions on two variables. This was highly effective in ranking the roles of the climate variables, and has yielded linear predictive models with small numbers of independent variables. Our simulations of this method show that it is statistically valid (Appendix).

CONCLUSION

In this study, the yearly total abundance of a desert annual plant community was strongly associated with precipitation, especially winter precipitation, with little association with other climate variables. Packaging of water into precipitation events of different sizes seemed not to matter. Only the total amount of water during the winter season was predictive, despite hypotheses to the contrary for arid ecosystems (Knapp *et al.*, 2008). The yearly number of species provided a different perspective, with temperature important but no appreciable association with precipitation. Moreover, although winter precipitation was generally important for individual species, other variables were also important for them. These differences between total plant abundance, diversity, and abundances of species are consistent with precipitation controlling overall abundance and the division of this abundance between species being governed by species-specific responses to further details of the climate. Cooler temperatures led to parcelling of this abundance between more species, with other sorts of weather being more species selective.

The sustained irruption of *E. cicutarium* is one of the most striking features of the trajectory of the winter annual plant community over the period captured by our data, but these data do not implicate climate in the irruption of *E. cicutarium*. Indeed, the climate changes that have occurred at the Portal bajada do not discriminate between *E. cicutarium* and the native species collectively. Nevertheless, climate controls on this community are clear. Predictions for future climate change imply strong climate effects in the Southwestern United States. Although total precipitation may control overall plant abundances in the area we studied, differential responses of species to climate variables may drive dramatic changes in species composition.

Valid conclusions about the role of climate in community dynamics based on time series face serious challenges because analyses that fail to account for autocorrelation and non-stationarity or that use large numbers of predictor variables can easily give misleading results. Our methods here show how relatively simple procedures tailored to the specific issues of the data allow some of these challenges to be met. We recognized that fitting a complex model to the data was neither appropriate nor useful in this case. Instead, our simple procedures allowed those variables with the most predictive power to be identified, which is often all that is sought, even though a complex model might be fitted.

ACKNOWLEDGEMENTS

We thank Morgan Ernest for providing long-term climate data collected at an adjacent research site and acknowledge the Bureau of Land Management for permission to use the site for research. We thank Stephanie Hovatter and Krista Robinson for assistance in the field. This work was supported by the National Science Foundation (DEB 8615028, 9307658, 0816231, and 1119784). All opinions, findings, and conclusions or recommendations expressed in this article are those of the authors and do not necessarily reflect the views of the National Science Foundation.

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