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ARTICLE

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One hundred and six years of change in a Sonoran Desert plant community: Impact of climate anomalies and trends in species sensitivities

Charlotte Brown[1,2] | **Susana Rodriguez Buritica**[3] | **Deborah E. Goldberg**[4,5] | **Frank Reichenbacher**[1] | **D. Lawrence Venable**[4] | **Robert H. Webb**[6] | **Benjamin T. Wilder**[7]

[1]Desert Laboratory on Tumamoc Hill, University of Arizona, Tucson, Arizona, USA

[2]Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

[3]Biological Resources Research Institute Alexander von Humboldt, Bogota, Columbia, USA

[4]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

[5]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

[6]School of Natural Resources and Environment, University of Arizona, Tucson, Arizona, USA

[7]Next Generation Sonoran Desert Researchers (N-Gen), Tucson, Arizona, USA

Correspondence
Charlotte Brown
Email: charlotte.brown@usherbrooke.ca

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Abstract

A major restriction in predicting plant community response to future climate change is a lack of long-term data needed to properly assess species and community response to climate and identify a baseline to detect climate anomalies. Here, we use a 106-year dataset on a Sonoran Desert plant community to test the role of extreme temperature and precipitation anomalies on community dynamics at the decadal scale and over time. Additionally, we tested the climate sensitivity of 39 desert plant species and whether sensitivity was associated with growth form, longevity, geographic range, or local dominance. We found that desert plant communities had shifted directionally over the 106 years, but the climate had little influence on this directional change primarily due to nonlinear shifts in precipitation anomalies. Decadal-scale climate had the largest impact on species richness, species relative density, and total plant cover, explaining up to 26%, 45%, and 55% of the variance in each, respectively. Drought and the interaction between the frequency of freeze events and above-average summer precipitation were among the most influential climate factors. Increased drought frequency and wetter periods with frequent freeze events led to larger reductions in total plant cover, species richness, and the relative densities of dominant subshrubs *Ambrosia deltoidea* and *Encelia farinosa*. More than 80% of the tested species were sensitive to climate, but sensitivity was not associated with a species' local dominance, longevity, geographic range, or growth form. Some species appear to exhibit demographic buffering, where when they have a higher sensitivity to drought, they also tend to have a higher sensitivity to favorable (i.e., wetter and hotter) conditions. Overall, our results suggest that, while decadal-scale climate variation substantially impacts these desert plant communities, directional change in temperature over the last century has had little impact due to the relative

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importance of precipitation and drought. With projections of increased drought in this region, we may see reductions in total vegetation cover and species richness due to the loss of species, possibly through a breakdown in their ability to demographically buffer climatic variation, potentially changing community dynamics through a change in facilitative and competitive processes.

KEYWORDS

arid lands, climate anomaly, community structure, dominance, drought, extreme temperature, geographic range, growth form, longevity, long-term change, seasonal precipitation, species-specific response

INTRODUCTION

Anthropogenic climate change has large-scale impacts on plant communities by altering species distributions and abundance (Parmesan & Yohe, 2003; Root et al., 2003; Wiens, 2016). However, regions differ considerably in the degree to which climate is changing (IPCC, 2022) and in the vulnerability of plant communities to a given amount of change (Cleland et al., 2012; Gonzalez et al., 2010). Deserts have been flagged as climatically sensitive (Diffenbaugh et al., 2008; Diffenbaugh & Giorgi, 2012; Seager et al., 2007; Turco et al., 2015) as they are expected to have some of the highest amounts of warming and drying compared with other terrestrial regions (IPCC, 2022; Sala et al., 2000). Of particular importance are projections of higher frequencies of climatic extremes (Parmesan et al., 2022) and increases in interannual precipitation variability rather than changes in long-term means (Diffenbaugh et al., 2008; Overpeck et al., 2013).

Examinations of the impacts of climate on ecological systems to date have predominantly focused on responses to shifts in climatic means, for example, regional warming (Chapman et al., 2014), and such studies have ultimately improved the understanding of the impacts of climate change on species distributions, phenology, and productivity (Scheffers et al., 2016). However, this focus on climatic means has left us less prepared to understand and predict the impacts of climatic anomalies, which are projected to increase with climate change (IPCC, 2022) and are increasingly associated with population declines (Maxwell et al., 2019). Climatic anomalies represent short-term deviations from long-term means and are potentially so impactful because they can trigger threshold effects, where even small changes in a climate variable lead to disproportionately large impacts. For example, a prior study in the Sonoran Desert found that, while plants differed in their response to mean annual temperature and precipitation, there were particular climatic thresholds that changed cover gains to losses (Munson et al., 2012), suggesting that climatic anomalies may be more influential than climatic means for desert plant communities.

Desert plant communities are typically water limited as precipitation levels often do not match evapotranspiration demands due to high solar radiation and temperatures (Thornthwaite, 1948). Consequently, total productivity and proxies such as vegetation cover in these systems tend to be highly responsive to interannual precipitation fluxes (Goldberg & Turner, 1986; Munson et al., 2013; Noy-Meir, 1973; Ogle & Reynolds, 2004; Turner, 1990; Vidiella et al., 1999), with the negative impacts of low rainfall exacerbated by high temperatures (Hantson et al., 2021) but mitigated by freezing temperatures (Abella et al., 2019). However, despite these linkages between the total amount of vegetation and climate, evidence is less consistent for climate-driven community composition shifts (Cody, 2000; Goldberg & Turner, 1986; Martin & Turner, 1977; Shreve, 1929; Turner, 1990), potentially due to delayed responses (Cody, 2000) or the long lifespan of desert species (Abella et al., 2019; Shreve, 1929).

Desert vegetation could be relatively resistant to climate-change-driven community shifts (Gonzalez et al., 2010) due to adaptations to deal with already extreme temperatures and variable water availability (Stahlschmidt et al., 2011), such as modified photosynthetic pathways (Pereira et al., 2021), deep roots (Canadell et al., 1996), and high water-use efficiency (Ehleringer & Cooper, 1988). However, if increases in temperature or rainfall anomalies with future climate change push species past their physiological limits or alter water-use strategies, the efficacy of these adaptations may diminish, making deserts particularly vulnerable to change. For example, increasing temperatures resulted in 37% of Sonoran Desert plant species having higher transpiration rates without a change to carbon gain, reflecting either heat avoidance, where increased transpiration is used to cool leaves, or heat failure, where plants are no longer able to control transpiration rates (Aparecido et al., 2020).

Furthermore, species specificity in climate sensitivities (Foden et al., 2013; Munson et al., 2015; Pacifici et al., 2015) may result in a differential influence of climate on various aspects of community dynamics. For example, we may expect a temperature-induced shift in species composition due to species-specific differences in thermal tolerance. However, depending on the rate or degree of species replacement in desert communities, these composition shifts may or may not correspond to changes in total plant abundance. For example, we may see a stronger climate signal on compositional shifts than total abundance changes if high thermal tolerance species replace low thermal tolerance species. Conversely, if temperature increases are so severe that they surpass the physiological tolerances of all species in a consistent way, we would expect large declines in plant abundance without changes in species composition. Similarly, different aspects of species composition may respond differently to climate change because of, for example, differential responses of plant growth versus survival resulting in different responses of species relative cover and density, respectively.

An additional challenge to predicting climate's impact on plant communities is that climatic factors do not act in isolation, and species can differ in their response to various aspects of climate (Munson et al., 2012). For example, with a high degree of succulence, cacti may be more sensitive to the frequency of cold temperatures than the amount of precipitation. Consequently, species growth forms contain information about traits that may alter their sensitivity to climate changes, including this degree of succulence or woodiness (Munson et al., 2015). Other specific attributes of plants, including their relative dominance, longevity, and geographic range size may also provide insight into how a species will respond to changing climate (Pacifici et al., 2015). Dominant desert plant species seem among the most responsive to climate (Munson et al., 2012), potentially due to stronger trait–environment linkages (Umaña et al., 2017). Conversely, rare species have an inherent vulnerability to catastrophic events and a reduced capacity to recover after local extinction events (Foden et al., 2013), making them potentially more vulnerable to changes in climate. A species' geographic range can reflect the breadth of its physiological tolerances (Bozinovic et al., 2011; Pither, 2003; Stevens, 1989). As such, species with larger range sizes are exposed to more variable climates and should be less vulnerable to changes in climate. Last, species longevity can act as a buffer for populations, as long-lived species rely less on frequently favorable conditions for establishment to maintain their population (Morris et al., 2008). Determining which aspects of plants impact their climate sensitivities may help to narrow down what species will be most affected by future changes in climate.

Long-term data are essential for documenting vegetation change and response to climate (Hughes et al., 2017; Magurran et al., 2010) by allowing enough time points to quantify climatic anomalies and providing enough time for plants to respond. Yet, relatively few datasets extend past the last few decades, especially in desert plant communities (Tielbörger & Salguero-Gómez, 2014). Here, we take advantage of a 106-year dataset based on permanent plots established in 1906 in a Sonoran Desert plant community at the Desert Laboratory on Tumamoc Hill. We determined the influence of decadal-scale climate on community structure and composition changes and followed these communities for an additional 30+ years from prior analyses (Goldberg & Turner, 1986; Shreve, 1929; Shreve & Hinckley, 1937) that found large fluxes in total plant cover and density, but little change in the relative contribution of species. Specifically, we asked:

> **Q1.** Have climate, the total amount of vegetation, and/or species composition changed directionally between 1906 and 2012?
>
> **Q2.** How do decadal-scale climate anomalies influence total vegetation amount and species composition? Which climatic variables are particularly influential and which aspects of vegetation are most responsive?
>
> **Q3.** How variable are species' sensitivities to decadal-scale climate variation, and to what degree are species climate sensitivities associated with their growth form, range size, longevity, or relative dominance?

As is inevitable for such a long-term data set, some limitations exist, most notably, irregular and sometimes extended intervals between censuses (Appendix S1: Table S1) as oversight of the plots shifted among entities and individuals and there were some inconsistencies in methodologies (see Rodriguez-Buritica et al., 2013 for a history of the plots and potential inconsistencies). We elaborate on the possible implications of these limitations in the *Discussion*. Nevertheless, the unparalleled length of the data set allowed us to gather important insights that would have been unobtainable in any other way.

MATERIALS AND METHODS

Study site

We used long-term community data on desert perennial plants from the Desert Laboratory on Tumamoc

Hill (32.219722°, −111.003746°) in Tucson, Arizona (Rodriguez-Buritica et al., 2013). Tumamoc Hill is a 325-ha preserve of mostly undisturbed vegetation typical of the Arizona Upland subdivision of the Sonoran Desert. Domestic, but not natural, grazers have been excluded since 1907, and grasses and several highly palatable shrubs have increased since then, at least through 1978 (Bowers & Turner, 1985; Goldberg & Turner, 1986; Shreve & Hinckley, 1937; Webb & Turner, 2010). Two dominant plant community types correspond to the two main substrate types and geographic features on Tumamoc Hill: the rocky, basaltic slopes dominated by little-leaved paloverde (*Parkinsonia microphyllum*), brittlebush (*Encelia farinosa*), and saguaro cactus (*Carnegiea gigantea*), and the alluvial fan communities dominated by creosote *(Larrea tridentata*), triangle-leaf bursage *(Ambrosia deltoidea*), and white ratany (*Krameria bicolor*) (Bowers & Turner, 1985; Goldberg & Turner, 1986). The mean annual rainfall between the study years 1906 and 2012 was ~364 mm/year, with ~60% of the rain falling between May and September. Maximum temperatures were often exceeded 38°C in the summer and could drop below 0°C in the winter (Bowers & Turner, 1985).

Community and species data

We used data from 10 plots of ~100 m^2 each and one plot of 800 m^2, where individual perennial plants have been mapped approximately every 10 years since 1906 (see below). Plot sampling methods are detailed in Rodriguez-Buritica et al. (2013). Briefly, the stem locations of all perennial plants were mapped during each census, with canopy cover also mapped starting in 1910. In 2001 and 2010, the census maps were digitized, and individuals were tracked through successive mappings by matching stem location coordinates (see Rodriguez-Buritica et al. (2013) for more details on digitization, individual tracking, and error). Data from Rodriguez-Buritica et al. (2013) are the most up-to-date and utilize additional quality control procedures. We focused our analyses on nonseedling, semi-woody-to-woody perennial plants to increase consistency between censuses, as woody plant seedlings and perennial grasses and forbs were not consistently recorded.

Using the database from Rodriguez-Buritica et al. (2013), we extracted each species' total density and cover in each plot at each census. Density was measured as the number of rooted crowns per plot area (in stems per square meter). Cover was measured as the sum of canopy areas of all individuals per plot area (in square meters per square meter). In instances where individuals overlapped, the cover of all individuals was included. Total density and cover per plot were calculated as the sum of species-level densities and covers so that, in principle, total cover could exceed 100%. For plants rooted outside a plot, their canopy was included in species-level and total cover but not in species-level and total density (Rodriguez-Buritica et al., 2013). Species richness was calculated as the number of unique species rooted in a plot.

Community composition was measured in three ways: species presence–absence, relative density, and relative cover. Species presence–absence was measured using species density data, where any species with a density greater than zero was recorded as present. Relative density and cover were calculated by dividing a species' density or cover by the total plot density or cover. Three nonmetric multidimensional scaling (NMDS) ordinations were used to reduce species presence–absence, relative density, and relative cover to two axes. The Jaccard dissimilarity was used as the distance metric for the presence–absence data, and the Ruzicka dissimilarity for the relative density and cover data as described in Legendre and Legendre (2012).

Climate data

Climate data were primarily obtained from weather stations located at the Desert Laboratory. However, when there were gaps in the weather record or errors with weather station data, we filled holes by averaging available records from National Oceanic and Atmospheric Administration (NOAA) weather stations surrounding the hill. Weather replacements primarily came from three NOAA stations: Tucson Weather Forecast Office (32.22917°, −110.9536°), Tucson University of Arizona no. 1 station (32.25800°, −111.0052°), and USDA Campbell Ave Experimental Farm (32.28160°, −110.9441°), although we used up to 45 weather stations that fell within a 13 km radius around Tucson. Weather station data were used to measure changes in the number of anomalously hot days (≥38°C, 1SD from the 106-year mean) and freeze days (≤0°C) as well as the cold season (November–April, hereafter "winter") and warm season (May–October, hereafter "summer") precipitation (in millimeters) over time. Temperature thresholds were chosen to represent anomalies or extremes rather than focusing on mean annual temperature and have previously been found to have biological importance in this desert system (Bowers, 1981; Rodríguez-Buriticá et al., 2019; Turnage & Hinckley, 1938). Extremes or anomalies are defined as values at least one standard deviation away from the 106-year mean. To measure drought conditions over time, we extracted Tucson's 1-month Standard Precipitation–Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) from the Global SPEI database (Beguería et al., 2010) at a 0.5° spatial resolution. Values less than −1 represent a month that experienced moderate to severe drought (Wang et al., 2014). We characterized the number of drought months per year as the total number of months with a SPEI ≤ -1. Due to April being the median month in which censuses were conducted, the annual climate was measured from 1 April to 31 March.

Q1. Long-term directional change in community structure and composition and climate

To test for directional shifts in climate from 1906 to 2012, we used five separate linear models with the annual number of hot days or freeze days, summer or winter precipitation, and drought frequency as response variables and year as a predictor.

To assess change in vegetation over time, we used the six metrics of community structure defined in the *Community and species data* section. For species composition metrics, we focused our analyses of change over time on NMDS axis two plot scores, which correspond more closely with time than NMDS axis one (see Appendix S1: Figure S1). We tested for directional change in vegetation between 1906 and 2012 using six linear mixed models with each community structure metric as a response variable, census year as a continuous predictor variable, and plot as a random factor. We also tested for directional changes in total density and cover and species richness of each of the dominant growth forms at our site using a separate mixed model for each growth form: cactus, suffrutescent herb (woody base, maximum height (MH) ≤1 m tall), subshrub (MH ≤1.5 m tall), shrub (MH 1.5-6 m tall), and tree (MH ≥6 m tall). Growth forms were assigned primarily based on Felger (2001) and SEINet Portal Network (http//:swbiodiversity.org/seinet/index.php, 21 June 2022); however, when discrepancies existed between sources, we used our best judgment based on our study site. Pseudo-R^2 values for all mixed models were calculated using the methods outlined in Nakagawa et al. (2017).

Q2. Effects of climate on community dynamics

To determine the influence of climate on vegetation change, we first quantified changes in the six metrics of community structure described in the *Community and species data* section. Changes in total density, cover, and richness between censuses were measured by subtracting total density, cover, or richness at one census from that at the prior census (hereafter, intercensus interval). Changes in community composition between censuses were measured as directional shifts along NMDS axis two, calculated by subtracting the NMDS axis two value for one census from the prior census. For analysis, we restricted intercensus intervals to be greater than 3 years to allow for climate variation between censuses and removed intercensus intervals greater than 60 years, which is longer than the estimated longevity of many of the surveyed species (median longevity of all species: 57 years). This helped ensure that observed changes in species composition were less influenced by species lifespans and reduced the chance of missed establishment and mortality events occurring between censuses. As a result, intercensus intervals ranged from 3 to 23 years in length (median length: 9 years; see Appendix S1: Table S1 for census schedule). To account for varying time intervals between censuses, we measured changes in community structure and composition per unit of time by dividing each measure of change by the number of years between a census and its prior census. Importantly, the length of intercensus intervals used in these analyses was not associated with the values of our defined climate variables (variance inflation factor [VIF] < 2).

To assess vegetation response to climate anomalies, we used the annual climate variables described in the *Climate data* section to characterize the degree of extreme events during each intercensus interval. For temperature, we calculated the average number of annual anomalously hot and freeze days per year over the interval. For precipitation, we calculated the proportion of anomalous years for winter and summer precipitation during the interval (Table 1; Hansen et al., 2012). We measured drought frequency as the proportion of years with an above-average number of drought months (Table 1).

We recognize that there are many ways to characterize climate, and our focus on and definition of extreme climates may impact our results. Therefore, we also characterized climate in two additional ways, neither of which improved the explanatory power of climate on community change (Appendix S1: Table S2) and therefore are not presented in the main text. First, recognizing that desert plants may be most sensitive to recent climate events, we characterized climate as the climate in the year prior to each census. This approach consistently led to lower explanatory power for all aspects of community change except for changes in species relative cover (Appendix S1: Table S2). Second, rather than focusing on the frequency of extremes during an intercensus interval, we calculated the average magnitude of the extreme

TABLE 1 Descriptions of climate summaries used to determine overall community and species-level responses to climate.

Climate variable	Description	Measurement per year	Intercensus measurement	Range
Hot days	Average no. annual anomalously hot days (≥38°C)	Total no. days above 38°C	Mean	23.8–87.50
Freeze days	Average no. annual freeze days (≤0°C)	Total no. days below 0°C	Mean	5.57–32.75
Wetter winters	Proportion of years with above-average cold-season precipitation (November–April) anomalies	*z*-score from the 106-year mean of cold-season precipitation	$\frac{\sum_{Y \in \text{Year}}^{N} [z_Y \geq 1]}{N}$	0–0.44
Wetter summers	Proportion of years with above-average warm-season precipitation (May–October) anomalies	*z*-score from the 106-year mean of warm-season precipitation	$\frac{\sum_{Y \in \text{Year}}^{N} [z_Y \geq 1]}{N}$	0–0.50
Drier winters	Proportion of years with below-average cold-season precipitation (November–April) anomalies	*z*-score from the 106-year mean of cold-season precipitation	$\frac{\sum_{Y \in \text{Year}}^{N} [z_Y \leq 1]}{N}$	0–0.33
Drier summers	Proportion of years with below-average warm-season precipitation (May–October) anomalies	*z*-score from the 106-year mean of warm-season precipitation	$\frac{\sum_{Y \in \text{Year}}^{N} [z_Y \leq 1]}{N}$	0–0.44
Drought frequency	Proportion of years with an above-average no. drought months anomalies	*z*-score from the 106-year mean of annual drought month frequency	$\frac{\sum_{Y \in \text{Year}}^{N} [z_Y \geq 1]}{N}$	0–0.50

Note: Climate summaries were calculated for 32 intercensus intervals ranging from 3 to 23 years (median = 9 years) from 1906 to 2012. Units for one standard deviation for cold-season and warm-season precipitation and drought months per year corresponds to 66.69, 62.07 mm, and 1.64 months, respectively. Brackets in equations represent the Iverson brackets, where 1 indicates the condition is true and 0 indicates it is false. *N* represents the no. years within an intercensus interval, and z_y represents the *z*-score of a particular climate variable in a particular year (*Y*).

(i.e., average above-average and below-average *z*-scores) rather than the proportion of extreme years. This approach had very similar explanatory power to proportion (Appendix S1: Table S2).

Multimodel inference was used to test intercensus climate regimes' impact on community structure changes. Due to the 9-year median time interval between censuses, these analyses test the response of plant communities to roughly decadal-scale climate anomalies. First, six linear mixed models were used to fit a global model for change in each of the six community structure metrics, as described above. Global models included all the climate variables except wet winters in Table 1 and the interactions between extreme temperatures and seasonal precipitation anomalies. The frequency of wet winters was removed from the analysis due to its high multicollinearity (VIF = 5.013) to allow for a more reliable interpretation from the multimodel inference. This variable was negatively correlated with dry summers ($r = -0.678$) and dry winters ($r = -0.597$). All other climate predictors had a VIF of less than two and were standardized to have a mean of zero and a standard deviation of one prior to analysis to permit comparisons between climate variables. Plot was included as a random factor. Next, we performed model selection using the dredge function in R's *MUMIN* package (Barton, 2009). It constructs all possible submodels nested within the global model and ranks them according to the corrected Akaike information criterion (AIC_c). We report the top model here and include the averaged regression coefficients from models with delta AIC ≤2 from the top model in Appendix S1: Table S3, which showed similar results.

Q3. Trends in species-level sensitivities to climate

Species-level sensitivity to climate was calculated as the regression coefficient from a linear mixed model of proportional cover or density change between censuses and all singular climate variables, except wet winters, and interactions between the temperature and precipitation variables. Plot was included as a random effect for all species-level linear mixed models. To be included in the species-specific analyses, species had to be present in more than one census period and have at least nine observations of cover/density change over time. This criterion resulted in 39 species for analysis.

To test whether climate sensitivity based on proportional cover changes varies as a function of species growth form, dominance, longevity, and New World geographic range, we first quantified these four attributes for each of our 39 species (Appendix S1: Table S4). Species growth form was determined, as explained above. Species dominance was calculated as the average relative cover in plots in which it was present from 1910 to 2012. Longevity was measured as the maximum age over all individuals of a species observed in the plots. The age of each individual was determined by tracking its stem location through successive mappings, where age was estimated as the difference between years when it was first and last found. Due to the time between censuses, we buffered this age estimation by adding either the median age or the time between censuses, whichever was shorter. Consequently, we may have overestimated the age of all species, but this would not alter the relative age differences between species. New World geographic range was calculated using observance data from the Global Biodiversity Information Facility (GBIF) using the *rgbif* package (Chamberlain et al., 2022). Observance data were then projected into a Lambert azimuthal equal-area coordinate system and range size in a kilometer square was calculated by fitting a convex hull around the projected points. Next, we ran four weighted least-squares regressions for each climate variable with species sensitivity (i.e., proportional cover change-climate regression coefficient) as the response variable and one of the four species attributes as a predictor. Data were weighted by the inverse of the standard error from each species-specific proportional cover-climate linear mixed model. Consequently, species with less variable cover-climate relationships had a larger weight. Given the high number of species tested, we focused our interpretation on effect sizes rather than significance.

All analyses were run in R (v.4.2.0, R Core Team, 2022) using the *lmerTest* (Kuznetsova et al., 2017), *lme4* (Bates et al., 2015), *MuMIn* (Barton, 2009), and *vegan* (Oksanen et al., 2020) packages.

RESULTS

Q1. Long-term directional change in climate and community structure

From 1906 to 2012, the annual number of hot days increased while the annual number of freeze days decreased; however, the amount of seasonal precipitation and the number of drought months per year showed no long-term directional trends (Figure 1). The number of days per year above 38°C almost doubled while the number of days below 0°C had decreased since 1906 (Figure 1A). Despite this overall trend, the days below 0°C spiked in approximately 2005 (Figure 1C). Two prolonged drought periods occurred between the mid-1940s and early 1960s, and the mid-1980s and 1990s, as represented by a continual high proportion of drought months (Figure 1D).

Over the 106 years, total density and cover, and species richness increased in these plant communities, with a slight decrease in plant density and richness since ~1975 (Figure 2A). Variations in community composition over time were largely associated with variation along NMDS axis 2 (see Appendix S1: Figure S1 for plot trajectories through time). NMDS axis one was mostly associated with composition differences between the two habitat types of the site, the alluvial fans and basaltic andesite slopes (Figure 3A); however, there was little significant interaction between substrate type and time on directional trends (Appendix S1: Table S5). Shifts in relative density and cover between censuses were associated with changes in the dominance of two subshrubs, *A. deltoidea* and *E. farinosa*. In contrast, shifts in presence and absence were associated with a higher presence of cacti (Figure 3A). Overall, the most responsive growth form was cacti, with a shift toward higher absolute cover, density, and richness (Figure 2B), as well as a higher presence of species in a plot (Figure 3A). Subshrubs have also significantly shifted over time, with increases in absolute density and species richness (Figure 2B) and relative density (Figure 3A). Overall, species composition showed very weak trends over time (Figure 3B), which were largely driven by large shifts in a few plots between 1906 and 1968 rather than an overall trend.

Although the site was grazed by domesticated grazers until 1907, 1 year after the first census, it is unlikely that the observed directional shifts over time resulted from vegetation recovery from grazing. Due to the topography of the site, there would probably be little to no grazing on the rocky, steep, basaltic andesite slope compared with heavy grazing on the alluvial fan; however, there was essentially no difference in the magnitude or direction of shifts between the two substrate types for each metric of community structure (Appendix S1: Table S5). There was a slight difference between trends in species relative density between substrate types, where composition on the alluvial fans showed a slightly stronger change over time (slope: -0.011 ± 0.003) compared with the basaltic andesite slopes (slope: -0.002 ± 0.001). However, the stronger trend in the alluvial fans was largely driven by the establishment of an unpalatable species, *A. deltoidea* (Marshall, 1994), in one plot between 1906 and 1968.

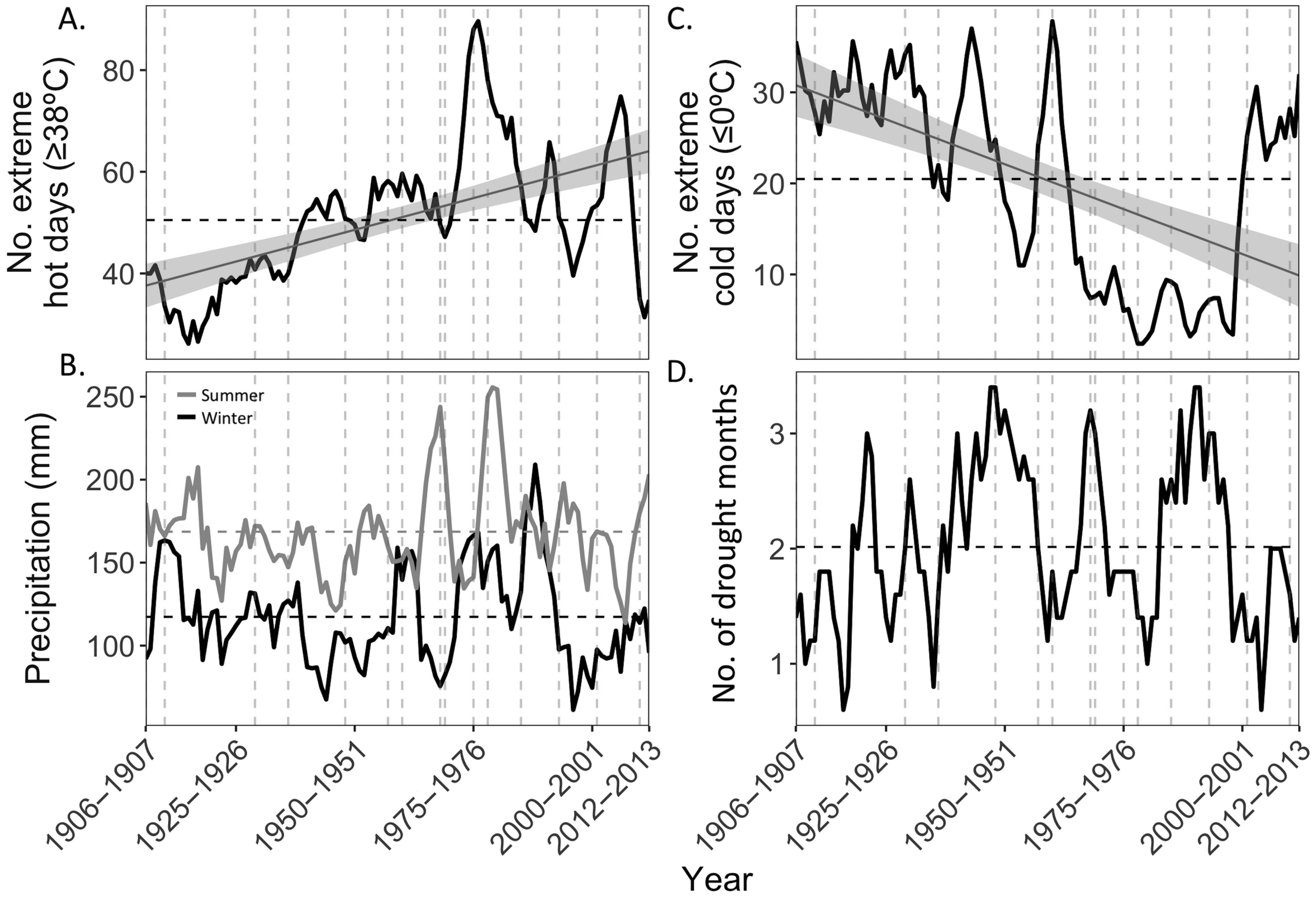

FIGURE 1 Temporal trends in temperature (A, C), precipitation (B), and moderate to severe drought months (D) from 1906 to 2012 on Tumamoc Hill in the Sonoran Desert. "Years" were measured from 1 April to 31 March. Black and gray solid lines represent a five-year moving average. Regression lines are trendlines from linear models and were included when there was a significant trend (α = 0.05) over time. Horizontal dashed lines represent the 106-year averages. Vertical dashed lines represent years where a census occurred. Temperature and precipitation data were collected from weather stations on or within 12 km of Tumamoc Hill. Moderate to severe drought months were classified as 1-month SPEI values less than −1 (Wang et al., 2014).

This lack of general trend among plots within the alluvial flats and the trend toward a higher density of unpalatable species in both the alluvial fans and basaltic andesite slopes, suggests that evidence of grazing impacts is weak.

Q2. Effects of decadal-scale climate on change in community structure

Collectively, climate variables explained 0%–56.4% of the variance in changes to community structure on a roughly decadal scale (Table 2). Climate had the largest impact on changes in total cover and composition based on species' relative density and, to a lesser extent, species richness (Table 2). Interestingly, the total cover was more responsive to climate than relative cover, suggesting nondifferential cover responses to climate between species. In contrast, total density was less responsive to climate than relative density (Table 2), suggesting species-specific density responses to climate with some compensation among species. Similar to total cover changes, climate had a relatively large influence on species richness changes (i.e., the balance of species gain and loss) but not in changes to species presence–absence (Table 2), suggesting climate seems to have inconsistent effects on which species are gained and lost.

The climate variables most influential in driving change depended on the specific aspect of community structure (Table 2). However, drought frequency, drier summers, and an interaction between freeze-day frequency and wetter summers were the most consistently significant variables for community dynamics. Increased drought frequency resulted in larger reductions in total cover and shifts in relative density toward higher values of NMDS axis 2 (Table 2), which correspond to the reduced relative density of the dominant subshrubs

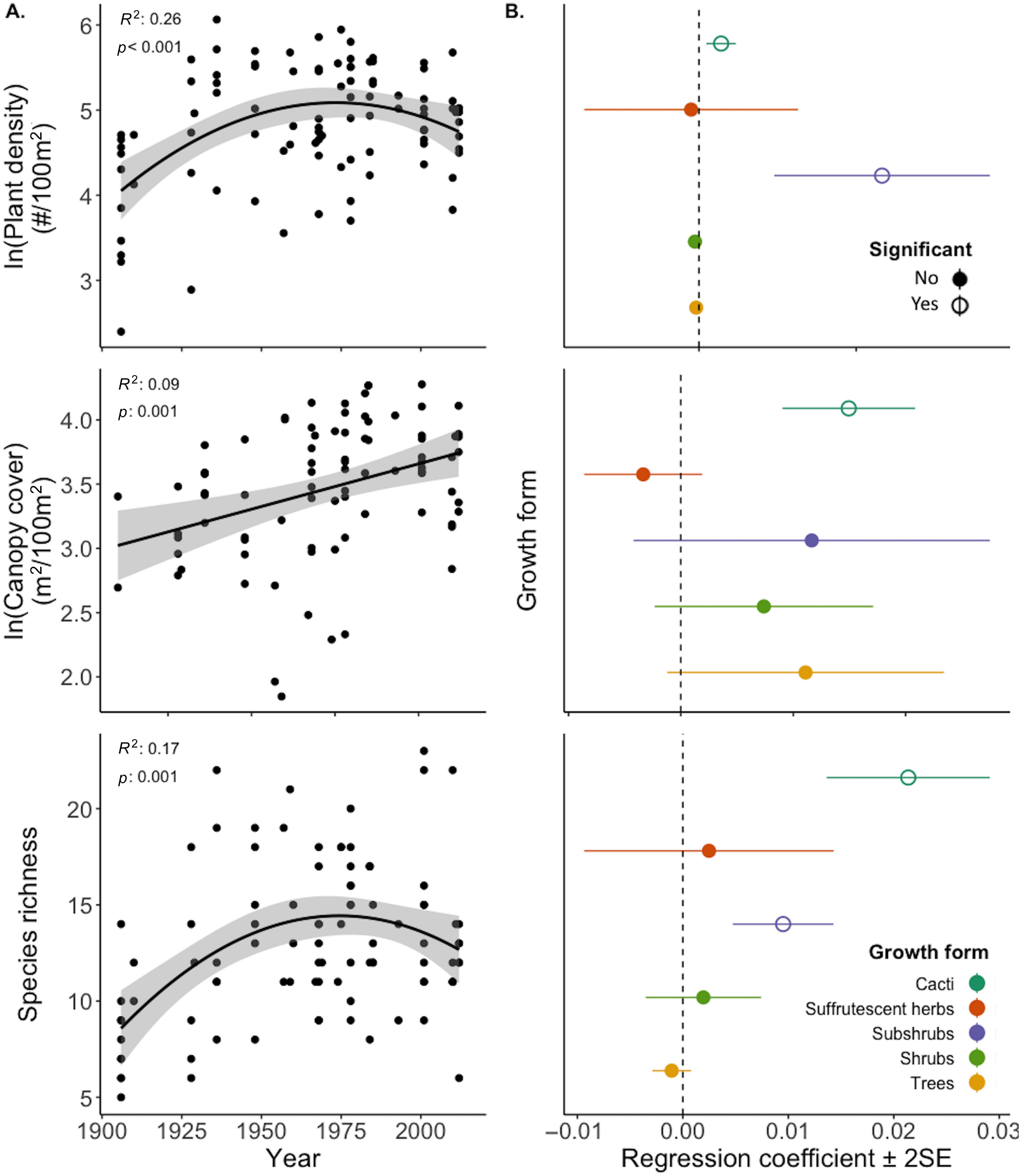

FIGURE 2 Temporal trends in community structure from 1906 to 2012 in a Sonoran Desert community. (A) Total density, cover, and species richness over time. Points represent one of 11 plots surveyed 3–10 times from 1906 to 2012. A trendline is included when a significant relationship ($\alpha = 0.05$) was found between the community measure and time based on linear mixed models or generalized linear mixed models with plot as a random factor. (B) Coefficients of regressions of absolute density, cover, and species richness per growth form over time from 1906 to 2012. Positive regression coefficients represent an increase in density, cover, or richness over time, while negative regression coefficients represent a decrease. Open circles represent significant shifts ($\alpha = 0.05$).

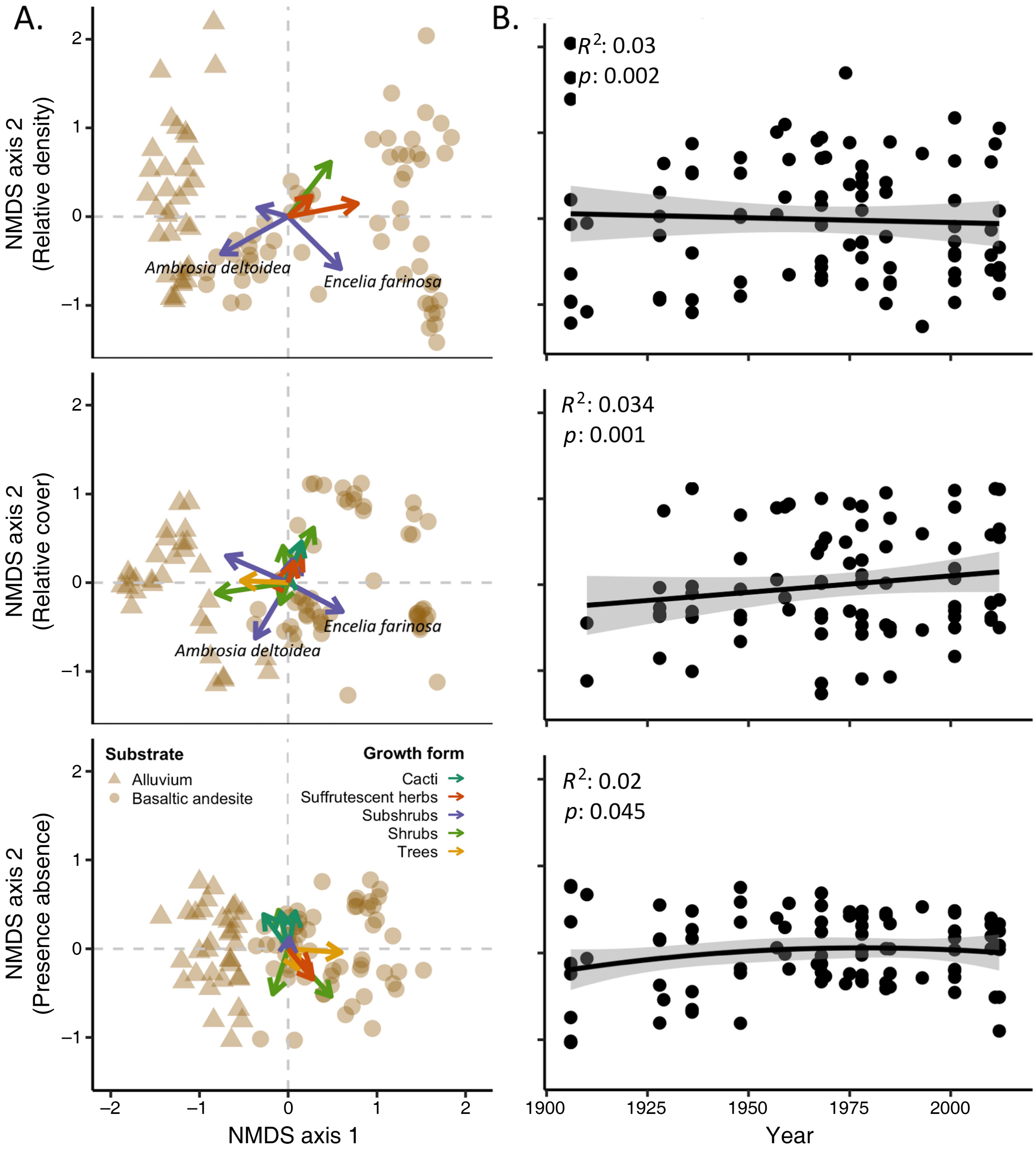

FIGURE 3 Community composition from 1906 to 2012 in a Sonoran Desert plant community. (A) Nonmetric multidimensional scaling of relative density, relative cover, and presence–absence over time. Shapes represent different substrate types within communities. Species vectors are weighted by their correlation to NMDS axes. Displayed species are color-coded by growth form and limited to those with a significant relationship as per a permutation test using the "envfit" function (Oksanen et al., 2020). Stress values for each NMDS were 0.143, 0.150, and 0.178 for relative density, relative cover, and presence–absence, respectively. To see plot trajectories over time, see Appendix S1: Figure S1. (B) Trends in relative density, relative abundance, and presence–absence based on NMDS axis two over time. A trendline is included when a significant relationship (α = 0.05) was found between a given community measure and time based on linear mixed models with plot as a random factor.

A. deltoidea and *E. farinosa* (Figure 3A). Increases in the frequency of drier summers led to similar responses in total cover and relative density as to drought and also reduced relative cover of the dominant subshrubs, *A. deltoidea* and *E. farinosa* (Table 2; Figure 3A). Interactions between temperature and seasonal precipitation also impacted community change. Frequent freezing and wet conditions together reduced total density and

TABLE 2 Regression coefficients from six models testing the impacts of decadal-scale climate on community structure and composition changes.

Model	Coefficient	Standard error	R^2
Total density			0.146
Intercept	−2.399	1.833	
Freeze days	2.928	1.92	
Wetter summers	2.353	2.035	
Cold days × wetter summers	**−4.257**	**1.949**	
Total cover			0.564
Intercept	**0.367**	**0.131**	
Drier summers	**−0.432**	**0.135**	
Drier winters	**−0.412**	**0.156**	
Drought frequency	**−0.748**	**0.152**	
Total richness			0.247
Intercept	**−0.101**	**0.043**	
Hot days	**−0.214**	**0.047**	
Freeze days	−0.155	0.057	
Wetter summers	**−0.046**	**0.045**	
Cold days × wetter summers	**−0.179**	**0.05**	
Composition—relative density			0.513
Intercept	**−0.024**	**0.007**	
Freeze days	0.009	0.009	
Wetter summers	**0.016**	**0.007**	
Drier summers	**0.020**	**0.006**	
Drought frequency	**0.023**	**0.005**	
Cold days × wetter summers	**−0.03**	**0.007**	
Cold days × drier summers	−0.017	0.009	
Composition: relative cover			0.082
Intercept	0.001	0.003	
Drier summers	**0.008**	**0.003**	
Composition: presence–absence			0.000
Intercept	−0.001	0.002	

Note: Models represent the results from multimodel inference using climate variables detailed in Table 1. The single best model based on the lowest AIC$_c$ is presented below. Model-averaged coefficients for models within two delta AIC$_c$ of the lowest AIC$_c$ are presented in Appendix S1: Table S3 and show similar results. Bolded coefficients represent significant predictors at alpha = 0.05. All climate variables were included in global models and standardized prior to analysis to allow comparisons in effect sizes among variables within a model.

richness and shifted composition to have a higher relative density of dominant subshrubs *A. deltoidea* and *E. farinosa* (Table 2).

Q3. Species-level sensitivities to climate

Thirty-two out of the 39 tested species (82.1%) responded significantly to one of the tested climate variables in either density or cover. Although species differed in the climate variables to which they were sensitive, species significantly influenced by climate typically had negative responses to drier climates (i.e., more frequent dry summers or drought years; Figure 4; Appendix S1: Figure S2). In addition, species responded more significantly to climate through changes in cover than density (Figure 4; Appendix S1: Figure S2).

The sensitivity of species' cover to climate was not related to species' local dominance, longevity, range size, or growth form (Figure 5). Overall, there was a significant negative association with a species sensitivity to drought and favorable conditions (i.e., wetter and hotter) ($F_{1,37} = 13.65$, $p < 0.001$, $R^2 = 0.25$). Species that had higher negative sensitivities to drought also had higher positive sensitivities to favorable conditions (Appendix S1: Figure S3). Although not statistically significant, more locally dominant species tended to be less responsive, either positively or negatively, to any climate variable compared with subdominant species. Conversely, rarer species exhibited highly variable responses to climate, both in magnitude and direction (Figure 5). Although growth forms did not differ overall in sensitivity to any climate variables, cacti and suffrutescent herbs tended to be the most sensitive to climate variables of the growth forms with a high variation in sensitivities (Figure 5).

DISCUSSION

Despite a slight directional change in some aspects of community structure and climate in this Sonoran Desert community over the 106-year study period, the aspects of community structure most strongly influenced by roughly decadal-scale climate variation did not show strong trends over the long term. This lack of long-term climate-driven directional shifts was likely to have been due to nondirectional shifts in seasonal precipitation and drought—the most important variables on a decadal scale—rather than the lack of importance of climate for community dynamics.

To observe directional shifts in communities due to climate, both of the following criteria must be met:

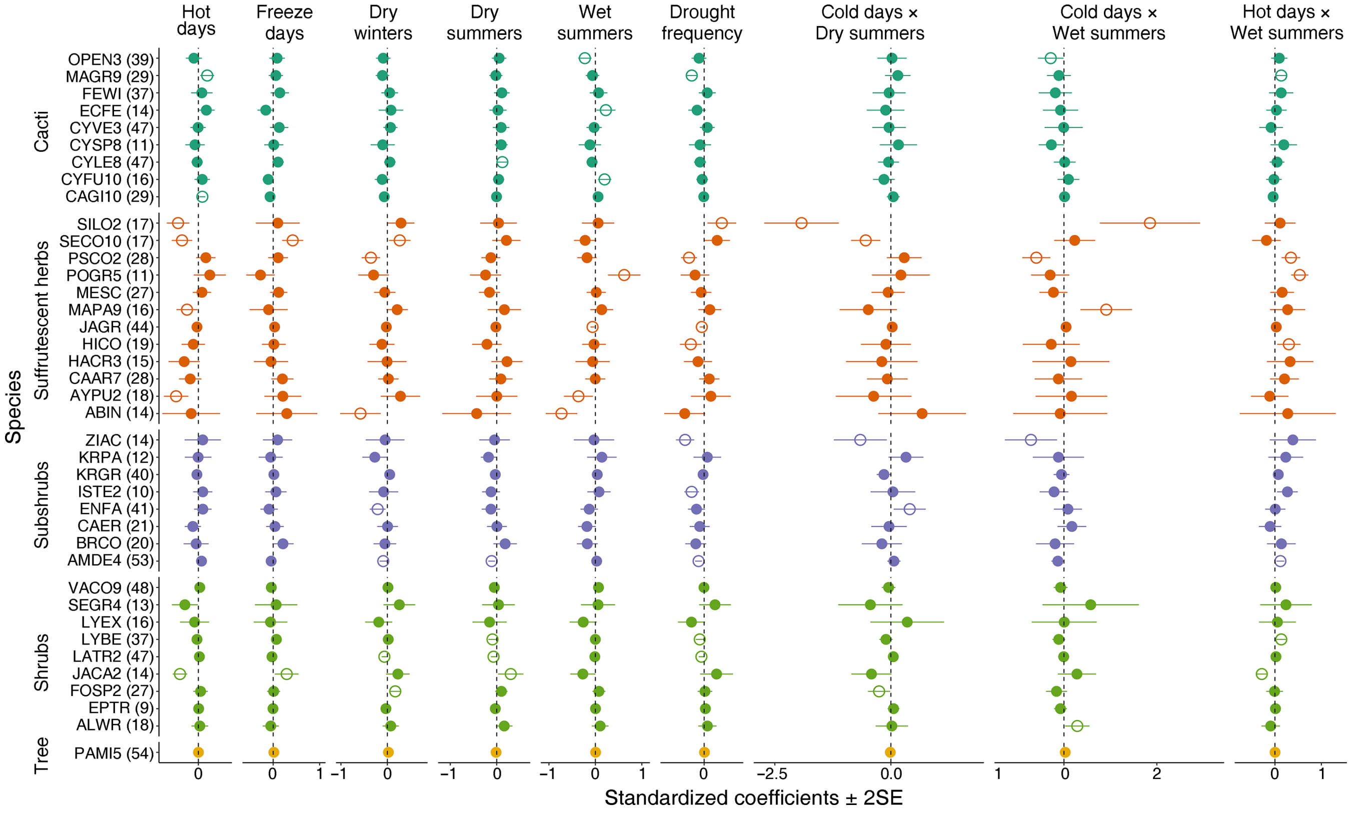

FIGURE 4 Species-specific sensitivities through cover changes to climate anomalies. Sensitivities are calculated as the regression coefficient of a linear mixed model examining the relationship between species cover changes and climate regimes between censuses based on 11 plots surveyed 3–10 times from 1906 to 2012. Significant shifts are represented by open circles for display purposes, but the interpretation is focused on effect size. Full species names are given in Appendix S1: Table S4. Numbers within parentheses represent sample size, or the number of unique plot-census combinations, for each species.

species respond to differences in climate and climate shifts directionally over time. We found that total cover and species relative density were highly responsive to climate, and 82.1% of species showed sensitivity to at least one aspect of climate. However, the aspects of climate most influential in driving these changes in community structure—namely seasonal precipitation and drought frequency—did not shift directionally over time. The temperature did shift directionally over time; however, its influence on community structure interacted in complex ways with seasonal precipitation. Overall, this suggests that nonclimatic mechanisms may be driving observed directional shifts in this Sonoran Desert community, and the lack of directional, long-term shifts in seasonal precipitation or drought between 1906 and 2012 may mask long-term climate signals, making predictions of what these communities will look like with future climate change difficult. Conversely, we found evidence for demographic buffering in species. Species that were more sensitive to drought also benefited more from favorable, hot-and-wet conditions, potentially explaining the relatively low observed compositional change in species over the last 106 years.

Like many long-term datasets with irregular and sometimes extended intervals between censuses, we recognize that some limitations may exist. To account for the variable interval lengths, we adjusted for time in our measures of community change. However, as intervals increase in length, the ability to capture all recruitment and short-term growth events becomes more challenging, where species may have recruited and died or grew or died back within an intercensus period. Consequently, we are limited in the conclusions we can make about more short-lived (<10 years) species. Therefore, we focus our interpretation below on species establishment rather than recruitment and the growth and survival of longer-lived (>10 years) species, which are better described by our dataset. Additionally, due to changes in oversight of the plots between the 1900s and 1960s, fewer plots were sampled than from the 1960s to 2012. Consequently, we may have been less able to capture variation in community change during earlier climatic periods due to the smaller number of sample plots. However, because these earlier periods were not typically at the outer range of climate values, especially for the more influential precipitation variables, we are confident

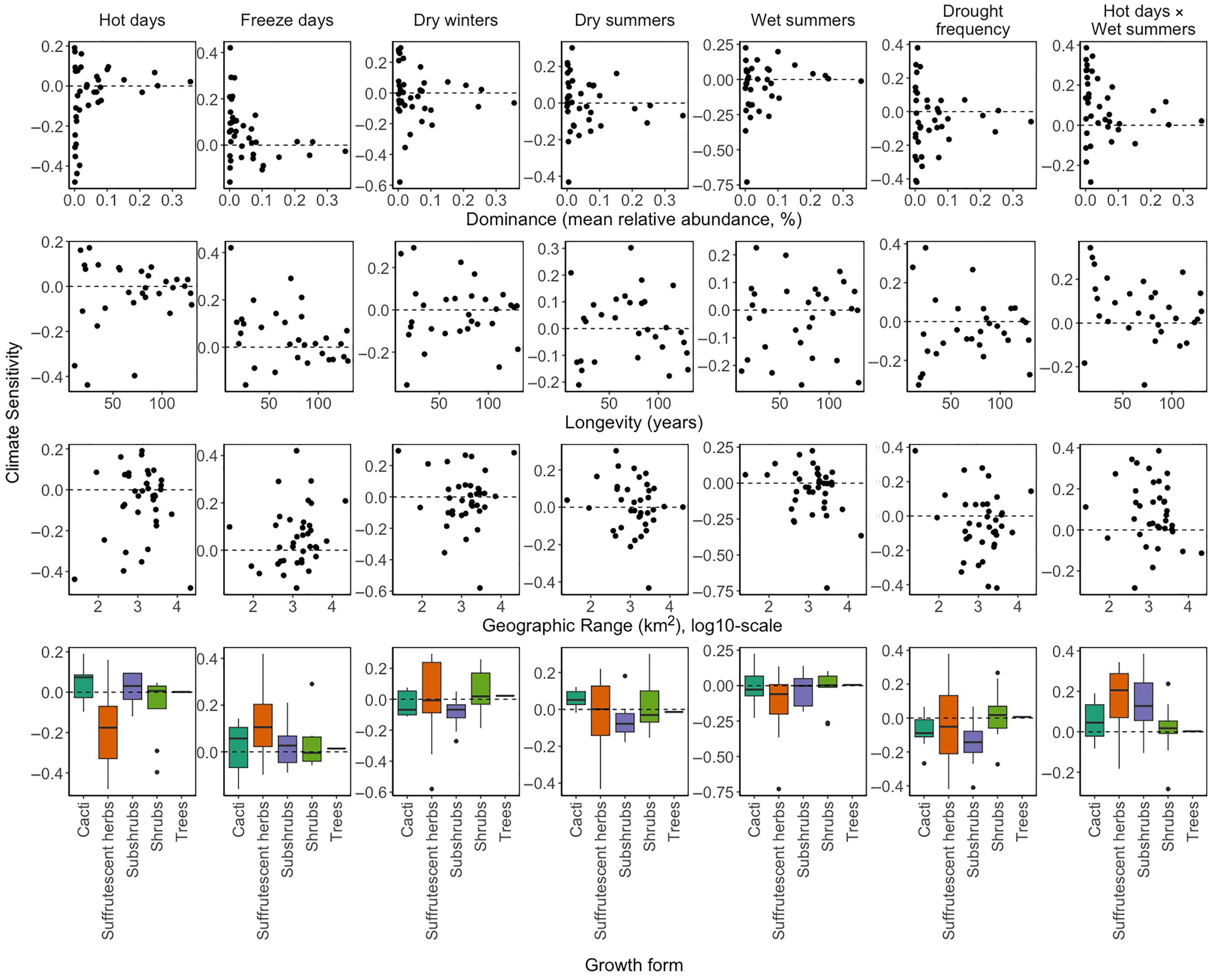

FIGURE 5 Species climate sensitivities in relation to species dominance, longevity, New World geographic range, and growth form for 39 desert plant species. Species sensitivities were calculated as the regression coefficient from a linear mixed model of proportional cover change between censuses and each climate variable. For visualization, scalings of climate sensitivities differ across climate variables. Trendlines were included when a significant relationship was found based on weighted least-squares regression, where species sensitivities were weighted by the inverse of the species-specific regression coefficient standard error. Consequently, species with less variable cover-climate relationships were weighted more heavily. We only had sensitivity data for one tree species, *Parkinsonia microphylla*, so we removed tree as a factor in the growth form analysis.

in the trends we found on how climate influences community change. Despite these potential limitations, we feel the unparalleled length of this data set provides important insights that could not be obtained with a shorter but maybe more regularly sampled data set.

Effects of decadal-scale climate on community dynamics

The decadal-scale climate was highly influential in explaining variance in total vegetation cover change, which agrees with prior studies that found a strong relationship between plant cover and other indices of productivity and climate in desert systems (Goldberg & Turner, 1986; Munson et al., 2013; Ogle & Reynolds, 2004; Turner, 1990; Vidiella et al., 1999). However, we did not find evidence for climate being as influential for changes in species composition based on species relative cover, with two to four times less of its variance explained by climate (Table 2). The lack of climate-driven compositional shifts in desert plant communities has been hypothesized to be the consequence of species longevity (Cody, 2000) or the overall nonresponsiveness of desert plant species to climate (Shreve, 1929). However, we found support for neither, as the majority of species exhibited sensitivity to at least one climatic factor (Figure 4), and this sensitivity was independent of species longevity (Figure 5). Interestingly, we see the opposite trend with composition in terms of relative density, where decadal-scale climate strongly influenced changes in relative density but not total density (Table 2), suggesting that climate may control species-specific establishment and mortality rates more than biomass growth rates.

Indeed, episodic establishment and mortality driven by favorable and unfavorable climates, respectively, have been observed for various desert plant species (Bobich et al., 2014; Bowers, 2005; Bowers & Turner, 2001; Miriti et al., 2007) and have been responsible for composition changes in desert communities, including the increased density and dominance of woody shrubs (Brown et al., 1997). However, climate does not seem to have consistent, repeatable effects on species gain and loss, as evidenced by climate explaining more variance in species richness change than in site-level presence and absence. Systematic loss of particular species may be limited due to stabilization processes in these long-lived communities such that high mortality rates are balanced by increased survival through reduced competition or future establishment through seedbanks, micro-climate shifts, and mutualistic or facilitative interactions (Lloret et al., 2012).

Drought frequency was among the most influential climatic factors driving changes in community structure in this Sonoran Desert community. Increased drought frequency led to reductions in total cover and reduced the relative density of locally dominant subshrubs, *A. deltoidea* and *E. farinosa* (Table 2; Figure 3B). This suggests that we are probably seeing two mechanisms by which drought impacts net primary productivity. First, through reduced photosynthesis and growth of all species. Next, through differential mortality as physiological tolerances are surpassed, species relative density within communities shifts. Compositional shifts can maintain community productivity under a high frequency of precipitation anomalies in semiarid grasslands (Felton et al., 2019). However, this does not appear to occur in this system, as compositional shifts coincided with declines in total cover. Furthermore, a simple buffering of drought followed by above-average precipitation anomalies, such that above-average precipitation counteracts the negative impacts of drought (Felton et al., 2019), appears to be lacking in this system due to interactions between temperature and precipitation.

Reductions in total density, species richness, and shifts in relative density also occurred over intercensus intervals with a high frequency of freeze days and wet summers (Table 2). These reductions in the face of high precipitation, suggest that species may have limitations to when they can take advantage of favorable (i.e., high precipitation) conditions or that wet summers may make plants more susceptible to frost damage and mortality, potentially through increased succulence. Freeze events limit the distribution of Sonoran Desert plant species (Turnage & Hinckley, 1938) and increase their mortality (Bowers, 1981; Turner et al., 2003). However, desert species differ in their vulnerability to frost damage (Lonard & Judd, 1985; Webb & Bowers, 1992), allowing for differential effects and, thus, community shifts. Overall, our results indicate that understanding how precipitation and temperature interact is essential for predicting future climate impacts on plant communities.

Attributes associated with species climate sensitivities

Certain species-level traits may promote differential climate responses, allowing for consistent and repeatable effects on species that lead to directional shifts in species composition. Longevity, in particular, has recently been highlighted as a key trait associated with species sensitivity to climate in plant (Compagnoni et al., 2021) and mammal species (Jackson et al., 2022). However, we found that long-lived species were not more resilient to climate changes (Figure 5). Both prior studies examined the impacts of climate 1-year preceding population surveys, while our study looks at the climate roughly 1-decade preceding surveys. The longer timescale may have allowed us to capture long-lived species being more vulnerable to perturbations (Gamelon et al., 2014), which is reflected in our climate variables that incorporate the accumulation of anomalies (e.g., the proportion of anomalous years) between surveys. Alternatively, it could reflect functional differences between biomes or herbaceous and woody species, as most species in Compagnoni et al. (2021) are herbaceous from temperate regions, while we examined semi-woody to woody species in a desert. For example, in desert systems, short-lived species have been found to have a high potential for demographic buffering (Salguero-Gómez et al., 2012), such that they maintain relatively constant vital rates in variable environments (Boyce et al., 2006), through changes in body size and persistence in the seed bank (Salguero-Gómez et al., 2012). However, it could also be due to our inability to capture more short-lived species (<10 years) due to the frequency of surveys. To understand what traits may dictate a species' sensitivity to climate, more examination is needed into whether the relationship between longevity and climate sensitivity is timescale-, biome-, or growth-form-specific.

Geographic range sizes can indicate physiological tolerance ranges (Bozinovic et al., 2011; Pither, 2003; Stevens, 1989), with larger ranges potentially indicating stronger tolerance to climate variation. However, we did not find a relationship between a species' geographic range and their climate sensitivity (Figure 5). This lack of relationship could be because desert species are already exposed to extreme temperatures and precipitation, which may constrain variation in species' physiological tolerances. Alternatively, the degree of deviation from a species' center range (Gerst et al., 2011) or optimal climatic conditions may be more important than range size (Lynn et al., 2021). Overall, our results suggest that we may not be able to use species' local dominance or rarity, longevity, geographic range, or growth to predict sensitivity.

Conclusions

Overall, we found a lack of long-term, climate-driven directional community shifts in this Sonoran Desert community despite long-term trends in temperature, presumably due to anthropogenic climate change. This lack of climate-driven shifts is probably due to nondirectional shifts in the precipitation anomalies that drive decadal-scale community dynamics. However, given the importance of drought frequency for community dynamics and future climate projections of a mean annual temperature of 24.8°C (a 4.3°C increase from the 1906–2012 mean) and mean annual precipitation of 332 mm (a 32 mm decrease from the 1906–2012 mean) by 2071–2100 at this site (Wang et al., 2016), we may see significant reductions to total cover, density, and richness, as well as relative density of dominant subshrub species in these systems in the future. Up to the most recent census in 2012, species' ability to take advantage of favorable conditions allowed them to maintain relative abundance despite their higher sensitivity to unfavorable conditions. However, with future changes, we may see a degradation in this buffered population growth necessary for storage effects to take place, ultimately impacting community dynamics through changes in facilitative and competitive processes.

AUTHOR CONTRIBUTIONS

Benjamin T. Wilder, Deborah E. Goldberg, and D. Lawrence Venable obtained support for Charlotte Brown to work on the long-term dataset. All authors contributed to the development of the main conceptual ideas. Charlotte Brown analyzed the data and wrote the manuscript with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sets from Rodriguez-Buritica et al. (2013), available as supporting information in their data paper in *Ecology* at https://doi.org/10.1890/12-1164.1, were utilized for this research. Additional climate data and data used to estimate species longevities are available in the University of Arizona Research Data Repository at https://doi.org/10.25422/azu.data.24185751.

ORCID

Charlotte Brown https://orcid.org/0000-0002-3989-6401
Susana Rodriguez Buritica https://orcid.org/0000-0001-8175-1057
Frank Reichenbacher https://orcid.org/0000-0002-3381-4313

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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