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Forecasting climate change impacts to plant community composition in the Sonoran Desert region

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Abstract

Hotter and drier conditions projected for the southwestern United States can have a large impact on the abundance and composition of long-lived desert plant species. We used long-term vegetation monitoring results from 39 large plots across four protected sites in the Sonoran Desert region to determine how plant species have responded to past climate variability. This cross-site analysis identified the plant species and functional types susceptible to climate change, the magnitude of their responses, and potential climate thresholds. In the relatively mesic mesquite savanna communities, perennial grasses declined with a decrease in annual precipitation, cacti increased, and there was a reversal of the *Prosopis velutina* expansion experienced in the 20th century in response to increasing mean annual temperature (MAT). In the more xeric Arizona Upland communities, the dominant leguminous tree, *Cercidium microphyllum*, declined on hillslopes, and the shrub *Fouquieria splendens* decreased, especially on south- and west-facing slopes in response to increasing MAT. In the most xeric shrublands, the codominant species *Larrea tridentata* and its hemiparasite *Krameria grayi* decreased with a decrease in cool season precipitation and increased aridity, respectively. This regional-scale assessment of plant species response to recent climate variability is critical for forecasting future shifts in plant community composition, structure, and productivity.

Keywords: arid, drought, long-term change, plant cover, southwestern United States

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Introduction

Predicting plant responses to climate change is essential for understanding the future structure and function of ecosystems. Accurate forecasts of climate-induced shifts in plant community composition can be enhanced by understanding past relationships between climate and plant species abundance through time and space. The long-term monitoring of plant community composition reveals a record of trends and fluctuations in species dynamics as environmental conditions, including climate, change through time (Bakker *et al.*, 1996). Because climate change affects vegetation over entire regions, it is necessary to integrate plant compositional shifts across multiple sites.

The climate in arid and semiarid regions of the southwestern United States can generally be characterized as having low and variable precipitation, high temperatures, and high evaporative demand. These conditions produce extensive periods of drought and limit water availability for plant growth (Noy-Meir, 1973). The Sonoran Desert, which has its northern limit in the southwestern United States, receives <400 mm of annual precipitation (AP) in a bimodal pattern: winter precipitation (WP) mostly originates from the Pacific Ocean as large frontal systems, whereas convective air masses and the North American monsoon produce localized summer precipitation (SP) (MacMahon & Wagner, 1985). SP generally produces shallow soil moisture utilized by plant species with shallow roots, whereas WP percolates deep into the soil profile and can be utilized by deeply rooted vegetation (Walter, 1971). Temporal variability in precipitation is high at daily to multiyear time-scales due to complex regional circulation influenced by different modes of Pacific sea surface temperature (e.g., El Niño-Southern Oscillation, Pacific Decadal Oscillation) (Kiladis & Diaz, 1989). High temperatures in the Sonoran Desert can directly limit plant growth and survival or indirectly limit plant water availability by increasing evaporative demand (Smith *et al.*, 1997). Low temperatures limit the distribution and productivity of many warm desert plants, including succulents (Shreve, 1911).

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The Sonoran Desert and other regions of the southwestern United States are expected to warm faster than the rest of the country and experience reduced AP, resulting in declines in soil moisture in an already water-limited environment (Seager *et al.*, 2007). Regional temperature records show increases in the intensity of heat waves, decreases in the frequency of freezing temperatures, and lengthening of the freeze-free season (Weiss & Overpeck, 2005). Climate models and long-term trends predict increased variability in precipitation seasonality, with fewer, larger, and more intense precipitation events (Easterling *et al.*, 2008).

Climate change is likely to have a large effect on the abundance and distribution of plant species in the Sonoran Desert, which is situated at the boundary between the southernmost distribution of temperate species and northernmost distribution of cold-sensitive subtropical species (Shreve & Wiggins, 1964; Turner *et al.*, 1995). Plant species that are able to tolerate or avoid drought may show no change or increase in abundance as conditions dry across the southwestern United States, whereas species lacking drought survival mechanisms may decrease or experience high mortality. Increases in temperature will have direct effects on plant growth and indirect effects by limiting soil moisture through increased rates of evapotranspiration. An increase in frost-free days is likely to result in many cold-intolerant plant species moving northward and upward in elevation, while cool- or mesic-adapted species with limited dispersal capability might be eliminated during a drought or hot period. A decrease in precipitation will have a negative effect on plant performance, but changes in the duration, timing, and amount of precipitation could differentially affect plant species by influencing the vertical distribution of water in the soil profile (Reynolds *et al.*, 2004). The performance of long-lived Sonoran Desert plants will depend on their root system architecture, ability to utilize SP vs. WP, tolerance to water stress, and photosynthetic pathways (Turner *et al.*, 1995; Schwinning & Ehleringer, 2001).

There is a long (>100 years) tradition of vegetation monitoring at sites across the Sonoran Desert (Hastings & Turner, 1965; Goldberg & Turner, 1986; McClaran & Angell, 2006; Anderson *et al.*, 2010; Webb & Turner, 2010). The monitoring sites are within national parks and research facilities that are protected from human disturbance, but were influenced by historic land uses. Although long-term monitoring has revealed vegetation dynamics at a particular site, there have been few attempts to look for patterns of plant species and functional type responses to climate across multiple sites. A regional assessment can be used to provide a robust prediction of the impact of future climate change to plant community composition. Particularly useful, but rarely identified, are thresholds in climate that have caused a reduction in plant abundance. The overall goal of our cross-site analysis was to identify regional trends in plant species and functional type responses to climate. Our specific objectives were to: (1) determine which plant species and functional types in the Sonoran Desert region are most sensitive to climate change; (2) identify climate thresholds that are indicative of changes in plant abundance; and (3) document the magnitude of plant responses that have occurred over a regional climate gradient.

Methods

Study sites

We used long-term vegetation data from four sites in the Sonoran Desert of southern Arizona (Fig. 1): (1) Organ Pipe Cactus National Monument (OPCNM), which includes mountain ranges, bajadas, and valley floors 220 km west of Tucson, Arizona (31°57′N, 112°48′W); (2) the Rincon District of Saguaro National Park (SNP), which is on the western slope of the Rincon Mountains on the east side of Tucson (32°12′N, 110°41′W); (3) the Desert Laboratory (DL), a research facility centered on the volcanic outcrop of Tumamoc Hill on the west side of Tucson (32°13′N, 111°00′W); and (4) the Santa Rita Experimental Range (SRER), another research facility located 55 km south of Tucson on the northwest slope of the Santa Rita Mountains (31°54′N, 110°53′W).

Vegetation data

The vegetation data from each of the four sites consisted of repeat measurements of perennial plant species canopy cover using two methods: (1) mapped census – plotting the canopy edge of all individual perennial plants in large permanent plots (100–1000 m^2) (Goldberg & Turner, 1986; Webb & Turner, 2010), or (2) line-intercept – determining linear distance intercepted by a plant, measured by a perpendicular projection of its foliage to the transect line (Canfield, 1941)

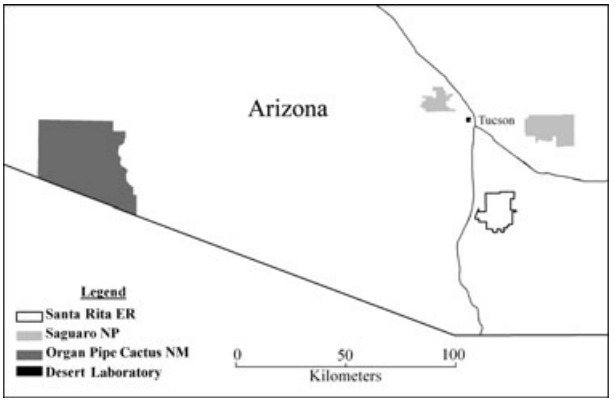

Fig. 1 Map of the long-term vegetation monitoring sites in the Sonoran Desert.

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along multiple transects (20–50 m in length). The monitoring of vegetation in large plots or multiple transects is suitable for arid and semiarid regions because it captures changes through time in a high number of plant species, locally rare species, and sparsely distributed species.

Vegetation plots at OPCNM were 20 × 50 m (1000 m^2) and located at 348–820 m elevation (Table 1). Most plots were on level terrain ($\leq 1°$ slope), with the exception of LO1 and 3S4, and had high variability in soil texture (ranging from silt loam to loamy sand). Ten of the plots were from the Ecological Monitoring Program (EMP; OPCNM, 2006) and were read twice from 1988 to 1997 and eight of the plots were from an investigation of the status of four dominant plant communities in the monument from 1975 to 1988 (Steenbergh & Warren, 1977). For the latter, we only used plots that occurred >1 km from areas that experienced heavy historic grazing, which ceased in 1968. Plant species canopy cover in the EMP plots was estimated using the line-intercept method on six transects in a box-cross orientation (two transects along the lengths, two along the widths, and two along the diagonals of the plot; OPCNM, 2006) and was estimated in the Steenbergh and Warren plots on 11 evenly spaced 20 m transects parallel to the plot width.

Vegetation plots at SNP occurred at 905–1140 m elevation on N, NW, W, and S facing slopes (<1–14°) of the Rincon Mountains on soils with loam, sandy loam, and loamy sand textures. Four of the plots were ungrazed or lightly grazed control plots designed to study the impact of livestock grazing (which ended in 1979) (Steenbergh, 1976), and another four plots were used to study the establishment of *Carniegia gigantea* (saguaro) along an elevation gradient (Turner *et al.*, 1969). The Steenbergh plots were 20 × 50 m, and plant species canopy cover was read using the line-intercept method on 21 evenly spaced 20 m transects parallel to the plot width in 1976 and 2007. The Turner plots were 15 × 15 m and plant species canopy cover was assessed using the mapped census method in 1965 and 2005.

Vegetation plots at DL were 10 × 10 m (100 m^2; Area B consists of eight contiguous plots) and occurred at 723–813 m elevation on the hillslope and piedmont of Tumamoc Hill, as well as on alluvium deposits to the west of the hill. The plots were located on NW, NE, SW, and SE aspects that had a 4–25° slope and were protected from grazing, since 1907. Plant species canopy cover was measured using the mapped census method at approximately decadal intervals from 1910 to 2001.

We used vegetation measurements from three areas at SRER that experienced light to moderate grazing during the study period and experienced no other human alterations. Measurements at each area were taken on ten 30 m transects, which spanned 950–1190 m elevation on NW facing gentle slopes (0–5°). Soil textures in the monitored areas were deep sandy loams and loamy sands.

Climate data

Climate data were obtained from weather stations with long-term records nearest to the vegetation plots and transects, including OPCNM Headquarters (31°56′N, 112°47′W), Tucson Magnetic Observatory (32°15′N, 110°50′W), University of Arizona (32°14′N, 110°57′W), and SRER (31°46′N, 110°51′W). Climate variables included AP, monsoonal (summer) precipitation (July–September), WP (October–March), mean annual temperature (MAT), and mean minimum and maximum annual temperature (based on mean monthly mean, minimum, and maximum temperatures).

Statistical analyses

Canopy cover of each species was calculated for the mapped census method by taking the total area occupied by all canopy cover polygons of a plant species and dividing it by the total area of the plot. Canopy cover of each species was calculated for the line-intercept method by totaling the intercept measurements for all individuals of a plant species along the transect and dividing it by the total transect length. Nonmetric multidimensional scaling and cluster analysis was performed to designate plant communities using the cover of all plant species in plots or transects (vegan package in R; Oksanen *et al.*, 2008). All years were included in the scaling to account for shifts in plant community composition through time. Plant species were aggregated into plant functional types based on expected similarities in their response to environmental conditions.

The relatively long vegetation sampling intervals did not allow us to examine the effects of short-term climate events (e.g., a heat wave, frost) on the performance of plant species. It is entirely possible that plant populations, in the course of the typical sampling interval of 10 years, went through both gains and losses of cover in response to specific climate events. Our analysis focused instead on long-term trends in plant species cover that may have been the response to a climate regime change (e.g., a change in the frequency of heat waves or frost conditions). Consequently, we related the change in canopy cover to the means of climate variables over the vegetation sampling interval, which characterized the average climate regime. If the time between sampling events exceeded 10 years, we used the 10-year mean of the climate variable prior to the end of the sampling interval. The AP anomaly was calculated by the difference between AP and the long-term mean AP. An additional aridity index was calculated using the ratio of AP to MAT.

To determine if plant species canopy cover was related to the suite of climate variables and time, we used a hierarchical partitioning (HP) approach (Chevan & Sutherland, 1991; hier.part package in R; Walsh & Mac Nally, 2009). HP is an analytical method of multiple regression that quantifies the relative importance of each explanatory variable to the total explained variance of the regression model, both independently and together with the other explanatory variables, calculated for all possible candidate models. The advantage of HP for determining the amount of variance in plant species/functional type cover explained by climate variables and time is that it overcomes the problem of multicollinearity among temperature, precipitation, and time in the model. We only analyzed plant species and functional types that had a sufficient sample size for model fitting. To normalize estimates of cover, we used the change in cover of plant species per unit time:

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Table 1 Characteristics of plots at Sonoran Desert monitoring sites

Monitoring site	Plot	Plot size	Method	Elevation (m)	Slope (°)	Aspect	Soil characteristics	Years measured	Plant community‡
OPCNM	SE1	1000 m^2	Line-intercept	508	1	Level	Sandy loam, 40% rock	1990, 1995	Upland-Hill
OPCNM	LO1	1000 m^2	Line-intercept	487	15	S	Sandy loam, 60% rock	1990, 1995	Upland-Hill
OPCNM	EA2	1000 m^2	Line-intercept	524	1	Level	Sandy loam	1988, 1994	Creosote bush
OPCNM	GR1	1000 m^2	Line-intercept	418	1	Level	Sandy loam	1990, 1997	Creosote bush
OPCNM	GR2	1000 m^2	Line-intercept	418	1	Level	Silty clay loam	1990, 1997	Mesquite
OPCNM	AG1	1000 m^2	Line-intercept	348	1	Level	Loamy sand	1989, 1994	Mesquite
OPCNM	AG3	1000 m^2	Line-intercept	348	1	Level	Silt loam, saline	1989, 1994	Saltbush
OPCNM	AR2	1000 m^2	Line-intercept	477	< 1	Level	Silt loam	1990, 1996	Mesquite
OPCNM	DO1	1000 m^2	Line-intercept	427	< 1	Level	Loam, saline	1989, 1994	Saltbush
OPCNM	DO2	1000 m^2	Line-intercept	427	< 1	Level	Silt loam, saline	1989, 1994	Saltbush
OPCNM	3S4	1000 m^2	Line-intercept	820	3	NE	Loam, 50% rock	1975, 1988	Upland-Piedmont
OPCNM	4W2	1000 m^2	Line-intercept	508	< 1	Level	Sandy loam, 30% rock	1975, 1988	Upland-Piedmont
OPCNM	1SE1	1000 m^2	Line-intercept	418	< 1	Level	Fine sandy loam, caliche at 30 cm	1975, 1988	Creosote bush
OPCNM	1SE2	1000 m^2	Line-intercept	418	< 1	Level	Fine sandy loam	1975, 1988	Creosote bush
OPCNM	1SE3	1000 m^2	Line-intercept	418	< 1	Level	Fine sandy loam	1975, 1988	Creosote bush
OPCNM	2E1	1000 m^2	Line-intercept	348	< 1	Level	Sandy loam, 30–60% rock	1975, 1984, 1988	Saltbush
OPCNM	2E2	1000 m^2	Line-intercept	348	< 1	Level	Loam, 80% rock	1975, 1984, 1988	Saltbush
OPCNM	2E3	1000 m^2	Line-intercept	348	< 1	Level	Sandy loam, 50% rock	1975, 1984, 1988	Saltbush
SNP	1	1000 m^2	Line-intercept	980	< 1	Level	Sandy loam – loam	1976, 2007	Mesquite
SNP	4	1000 m^2	Line-intercept	1010	6	NW	Sandy loam – loam	1976, 2007	Mesquite
SNP	6	1000 m^2	Line-intercept	1140	6	N	Sandy loam – loam	1976, 2007	Mesquite
SNP	8	1000 m^2	Line-intercept	1070	6	S	Sandy loam – loam	1976, 2007	Upland-Piedmont
SNP	12	225 m^2	Mapped census	905	14	W	Sandy loam	1965, 2005	Upland-Piedmont
SNP	22	225 m^2	Mapped census	905	14	W	Sandy loam	1965, 2005	Upland-Piedmont
SNP	13	225 m^2	Mapped census	1000	14	W	Sandy loam	1965, 2005	Upland-Hill
SNP	23	225 m^2	Mapped census	1000	14	W	Sandy loam	1965, 2005	Upland-Hill
DL	B	100 m^2 (N = 8)	Mapped census	740	8	NW	Gravelly loamy sand (alluvium)	1928, 1936, 1948, 1957, 1968, 1978, 1984, 2001	Creosote bush
DL	4	100 m^2	Mapped census	723	8	NW	Gravelly sandy loam (alluvium)	1968, 1978, 1985, 2001	Creosote bush
DL	7	100 m^2	Mapped census	753	9	NE	Coarse sandy loam (basaltic and andesitic colluvium)	1968, 1978, 1985, 2001	Upland-Piedmont
DL	9	100 m^2	Mapped census	769	9	NE	Coarse sandy loam (weathered basaltic andesite)	1968, 1978, 1985, 2001	Upland-Piedmont

Table 1 (continued)

Monitoring site	Plot	Plot size	Method	Elevation (m)	Slope (°)	Aspect	Soil characteristics	Years measured	Plant community‡
DL	10	100 m^2	Mapped census	795	8	NE	Coarse sandy loam (weathered basaltic andesite)	1968, 1978, 2001	Upland-Piedmont
DL	11	100 m^2	Mapped census	802	17	SW	Coarse sandy loam (weathered basaltic andesite)	1910, 1928, 1936, 1948, 1960, 1968, 1975, 1978, 1984, 2001	Upland-Hill
DL	12	100 m^2	Mapped census	813	12	NE	Coarse sandy loam (weathered basaltic andesite)	1929, 1936, 1948, 1960, 1968, 1975, 1978, 1984, 2001	Upland-Hill
DL	14	100 m^2	Mapped census	812	25	NW	Coarse sandy loam (weathered basaltic andesite)	1969, 1978, 1985, 2001	Upland-Hill
DL	15	100 m^2	Mapped census	733	4	SW	Coarse sandy loam (weathered basaltic andesite)	1910, 1928, 1936, 1948, 1959, 1968, 1975, 1978, 1984, 2001	Upland-Hill
DL	16	100 m^2	Mapped census	734	4	SE	Gravelly loamy sand (alluvium, rhyolite with calcrete rubble)	1928, 1936, 1948, 1957, 1959, 1967, 1968, 1974, 1978, 1984, 2001	Creosote bush
SRER	12B	10 × 30 m transects	Line-intercept	970–990	0–2	NW	Sandy loam	1957–2009	Mesquite
SRER	2N	10 × 30 m transects	Line-intercept	1070–1190	1–5	NW	Sandy loam – loamy sand	1957–2009	Mesquite
SRER	3	10 × 30 m transects	Line-intercept	950–1030	0–5	NW	Sandy loam	1957–2009	Mesquite

‡derived from nonmetric multidimensional scaling.
DL, Desert Laboratory; OPCNM, Organ Pipe Cactus National Monument; SNP, Saguaro National Park; SRER, Santa Rita Experimental Range.

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$$\text{Change in cover} = \frac{\ln(\text{cover}_{t2}/\text{cover}_{t2})}{t2 - t1} \times 10, \qquad (1)$$

where cover_{t2} is plant cover in year $t2$ and cover_{t1} is plant cover in the previous sampling year, $t1$.

A positive value of this index indicated that a plant species gained cover over the observation interval, whereas a negative value indicated that it lost cover. We removed cover values that were significant outliers in the multiple regression, which were identified using a Bonferroni Outlier Test (Companion to Applied Regression package in R; Fox, 2009). We report the independent effect of each variable to explain variability in the full model adjusted according to the number of explanatory variables (% of adjusted R^2). The statistical significances of the independent effects of variables were determined by the upper 95% confidence level of Z-scores generated by a randomization routine (Walsh & Mac Nally, 2009).

When the independent effect of a climate variable was significant in a HP model, we performed a simple linear regression between the change in cover index and the climate variable. A significant slope between the index and a particular climate variable indicated that the rate of cover change was sensitive to that aspect of climate, and suggests that the climate variable (or a close correlate) was a driver of the observed change in plant cover. Furthermore, the point where the regression slope intersects the x-axis (the x-intercept) indicates a transition between gains and losses of cover, which we define as a climate threshold for change.

Results

Mean annual temperature had high interannual variability and generally increased over the last century at the DL (0.03 °C yr^{-1}; $r^2 = 0.74$, $P < 0.0001$), SNP (0.01 °C yr^{-1}; $r^2 = 0.18$, $P = 0.0007$), and OPCNM (0.03 °C yr^{-1}; $r^2 = 0.42$, $P < 0.0001$), but did not change at SRER (Fig. 2a). The AP anomaly across sites indicated two distinct wet periods (1910–1925, 1975–2000) and two distinct dry periods (1940–1965, 2000–present) (Fig. 2b), which are similar to previous accounts (Turner *et al.*, 2003).

Nonmetric multidimensional scaling indicated five plant communities: (1) savannas dominated by *Prosopis velutina* (mesquite); (2) Arizona Uplands (Sonoran desertscrubs) on hillslope and, (3) piedmont/bajada landscape positions, and two shrublands dominated by (4) *Larrea tridentata* (creosote bush) and, (5) *Atriplex* species (*Atriplex polycarpa* and *Atriplex canescens* subsp. *linearis*; saltbushes; Fig. 3). These plant communities spanned a gradient in elevation, soil texture, and potential water availability (Table 1). Savannas dominated by *P. velutina* were the most mesic plant communities and occurred at relatively high elevation (950–1190 m) or near intermittently flowing streams. Although there was variability in soil texture among mesquite savannas, most had fine-textured soil relative to other plant communities. The increasingly more xeric Arizona Upland communities occurred at lower elevation (487–1070 m) and had weathered bedrock-rocky sandy loam soils on hillslopes and coarse sandy loam soils on piedmonts/bajadas. Creosote bush and saltbush shrublands were the driest communities at the lowest elevation (418–740 m and 348–427 m, respectively). Creosote bush shrublands occurred on gravelly to fine sandy loam-loamy sand soils in alluvial and valley bottom settings. Saltbush shrublands occurred on alluvial/playa surfaces with mostly fine-textured, saline soils.

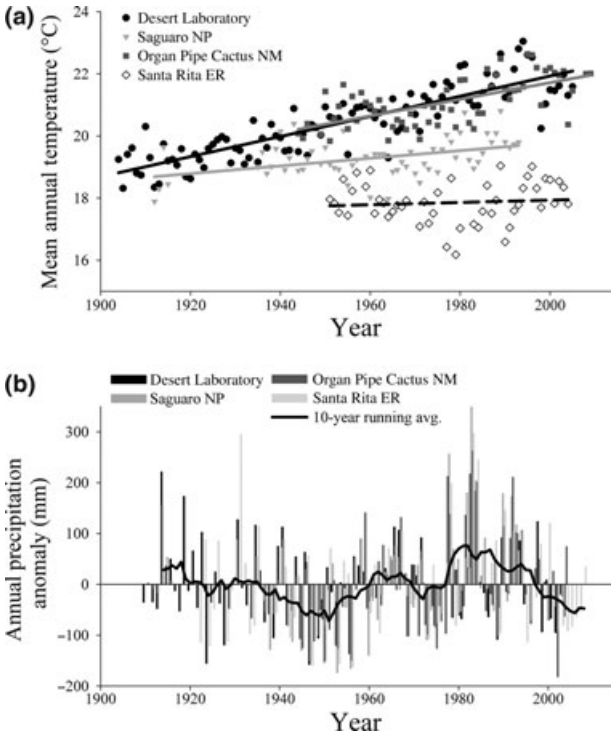

Fig. 2 (a) Mean annual temperature (°C) and (b) annual precipitation anomaly (mm) from 1904 to 2009 for all weather stations ($N = 4$) in or near the four vegetation monitoring sites. Trends in mean annual temperature shown by fitted linear regressions: Desert Laboratory (slope = 0.03 °C yr^{-1}; $r^2 = 0.74$, $P < 0.0001$), Saguaro National Park (slope = 0.01 °C yr^{-1}; $r^2 = 0.18$, $P = 0.0007$), Organ Pipe Cactus National Monument (slope = 0.03 °C yr^{-1}; $r^2 = 0.42$, $P < 0.0001$), Santa Rita Experimental Range (slope = 0.00, $r^2 = 0.01$, $P = 0.54$). Ten-year running average of the annual precipitation anomaly is shown by the black line.

Climate variables and time explained 7–84% of the variation in the change of plant species and functional type canopy cover between sampling years. In mesquite savannas, the change in cover of *P. velutina*, the dominant tree, decreased with increasing MAT (slope = −0.30, $r^2 = 0.17$, $P < 0.01$; Fig. 4a) and was negative above a threshold of 18.2 °C. The change in

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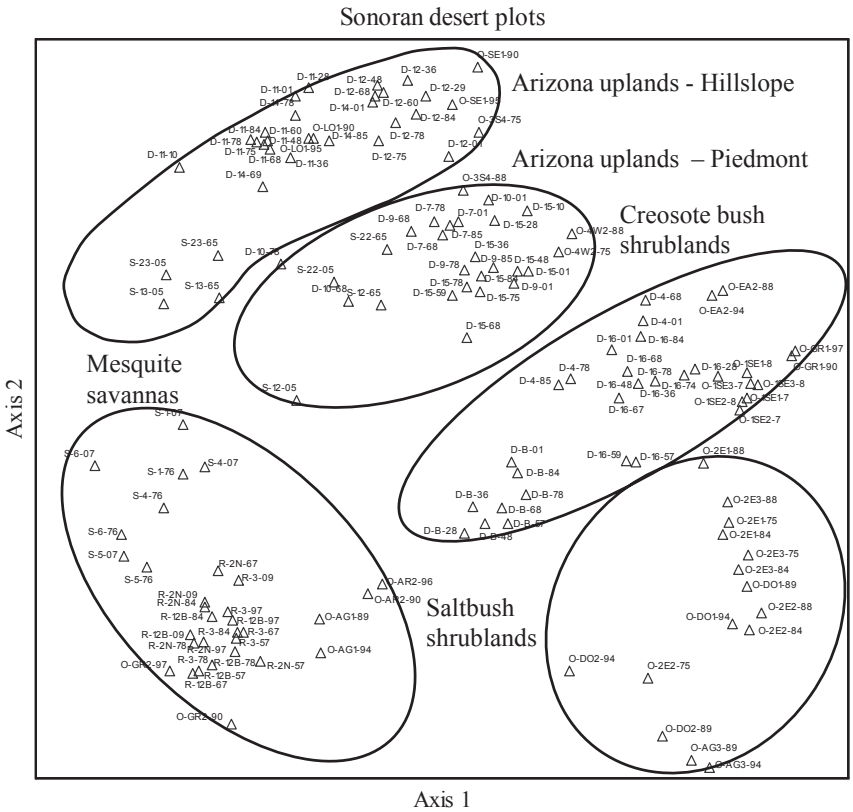

Fig. 3 Nonmetric multidimensional scaling of plant species cover at each plot across all years of monitoring, which shows five plant communities: (1) Savannas dominated by *Prosopis velutina* (mesquite); (2) Arizona Uplands (Sonoran desertscrubs) on hillslope and (3) piedmont landscape positions, and two shrublands dominated by (4) *Larrea tridentata* (creosote bush) and (5) *Atriplex* species (*A. polycarpa* and *A. canescens* var. *linearis*; saltbushes). Individual plots are coded by site name – plot name – year (e.g., O-SE1–90 = Organ Pipe Cactus National Monument, plot SE1, year 1990). See Table 1 for plot characteristics.

perennial grass cover increased with increasing AP above a threshold of 390 mm (slope = 0.02, $r^2 = 0.39$, $P < 0.01$; Fig. 4b) and was negative with high aridity (slope = 0.29, $r^2 = 0.46$, $P < 0.01$; Fig. 4c) below 21.0 mm °C^{-1}. The change in forb cover (slope = 0.06, $r^2 = 0.44$, $P < 0.01$; Fig. 4d) was positive and increased above a WP threshold of 142 mm. The change in cacti cover increased with increasing MAT (slope = 0.65, $r^2 = 0.20$, $P < 0.01$; Fig. 4e) above a threshold of 17.8 °C.

In Arizona Upland communities on the hillslope landscape position, the change in cover of leguminous trees, primarily composed of *Cercidium microphyllum*, was significantly explained by year and MAT (Table 2). The change in cover of trees and *C. microphyllum* was negatively related to MAT, with losses in cover associated with high temperature (trees: slope = −0.26, $r^2 = 0.27$, $P < 0.01$; *C. microphyllum*: slope = −0.29, $r^2 = 0.30$, $P < 0.01$; Fig. 4f). A transition from gains to losses in cover between sampling years occurred for trees and *C. microphyllum* at a similar threshold MAT near 21.2 °C. The change in cover of *Janusia gracilis*, a vine that relies on other perennial plants for structural support, could be explained by time and climate variables (Adj. $R^2 = 0.69$, $P < 0.01$; Table 2), but no single variable was significant.

In Arizona Upland communities on piedmont landscape positions, below hillslopes, *C. microphyllum* and cacti cover were significantly explained by time and climate variables (*C. microphyllum*: Adj. $R^2 = 0.52$, $P = 0.03$; cacti: Adj. $R^2 = 0.64$, $P < 0.01$; Table 2), but no single variable independently explained cover. The change in cover of *L. tridentata* was related to WP (slope = 0.03, $r^2 = 0.48$, $P < 0.01$; Fig. 4g) and was negative when WP fell below 115 mm. The change in cover of subshrubs, mostly composed of *Ambrosia deltoidea*, was related to AP (subshrubs: slope = 0.03, $r^2 = 0.28$, $P = 0.01$; *A. deltoidea*: slope = 0.03, $r^2 = 0.31$, $P = 0.03$; Fig. 4h), with gains in cover between sampling years occurring above 289 and 283 mm, respectively. The change in cover of *Fouquieria splendens* could significantly be explained by MAT (slope = −0.68, $r^2 = 0.31$, $P = 0.04$; Fig. 4i) and was negative when MAT rose above a threshold of 21.5 °C.

In creosote bush shrublands, the change in shrub cover was related to AP and aridity (AP: slope = 0.01,

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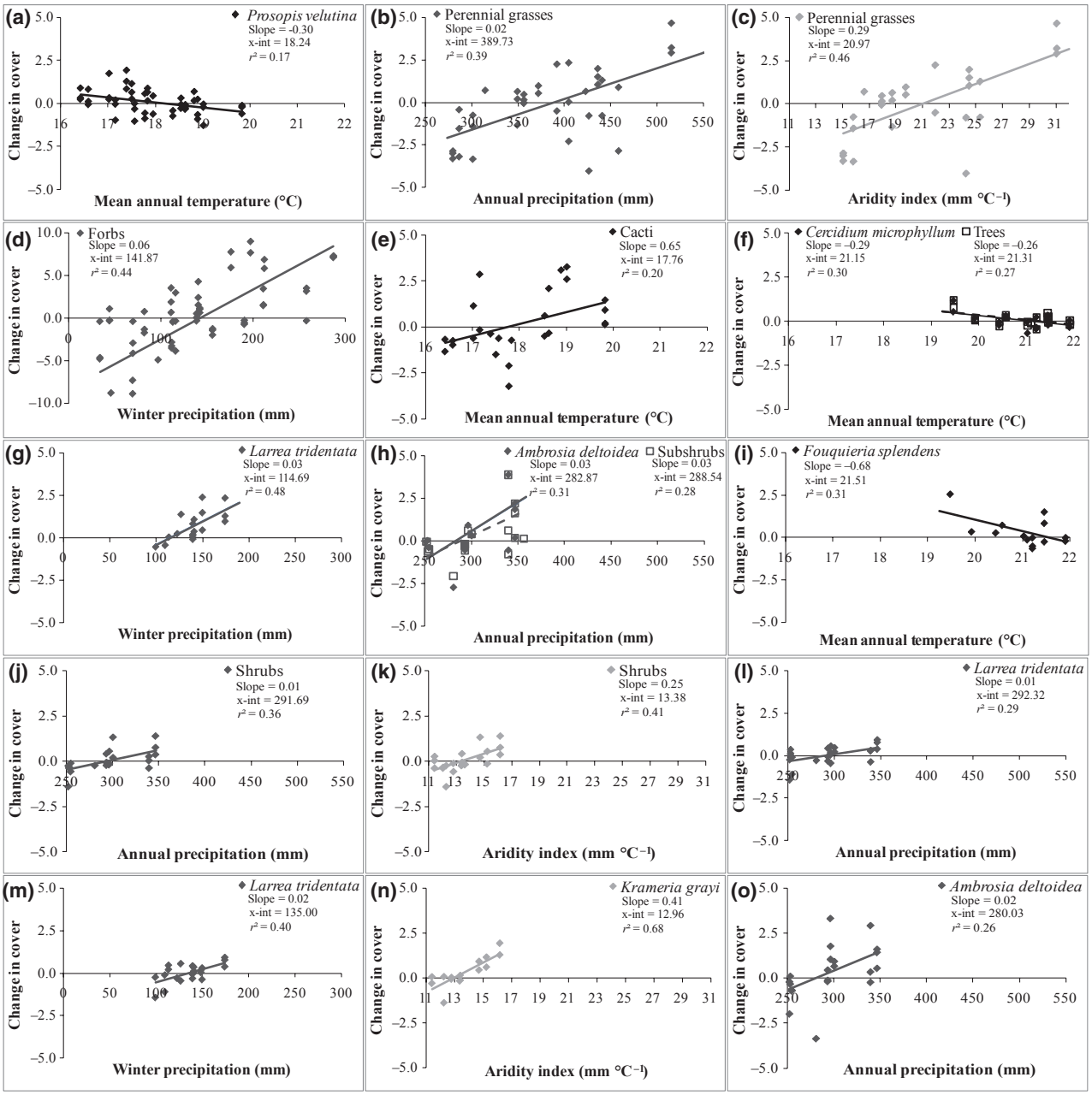

Fig. 4 Change in plant cover in relation to climate variable (black = temperature, dark gray = precipitation, light gray = aridity) for (a) *Prosopis velutina*; (b and c) perennial grasses; (d) forbs; (e) cacti in mesquite savannas; (f) *Cercidium microphyllum* and trees in Arizona Uplands-hillslope; (g) *Larrea tridentata*; (h) *Ambrosia deltoidea* and subshrubs; (i) *Fouquieria splendens* in Arizona Uplands-piedmont; (j and k) shrubs; (l and m) *Larrea tridentata*; (n) *Krameria grayi*; and (o) *Ambrosia deltoidea* in creosote bush shrublands. Slope, *x*-intercept (*x*-int), and coefficient of determination (r^2) shown for each plant species/functional type.

$r^2 = 0.36$, $P < 0.01$; aridity: slope = 0.25, $r^2 = 0.41$, $P < 0.01$; Fig. 4 j,k) and was positive above thresholds of 292 mm and 13.4 mm °C^{-1}, respectively. Plant species and functional types responded similarly to climate as the Arizona Upland communities on the piedmont. The change in *L. tridentata* cover increased when AP and WP (AP: slope = 0.01, $r^2 = 0.29$, $P < 0.01$, WP: slope = 0.02, $r^2 = 0.40$, $P < 0.01$; Fig. 4l and m) were above 292 and 135 mm, respectively. *Krameria grayi*, a hemiparasitic shrub, was more abundant in *Larrea*-dominated communities than in Arizona Upland ommunities on the piedmont and like all shrubs in the Arizona Upland community, the change in cover was low with high aridity (slope = 0.41, $r^2 = 0.68$, $P < 0.01$; Fig. 4n) and was negative when aridity reached 13.0 mm °C^{-1}. Similar to Arizona Upland communities

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Table 2 The independent effects (% of R^2) of temperature (°C), precipitation (mm), aridity (mm °C^{-1}), and time (year) to explain change in plant species and functional type canopy cover as determined by hierarchical partitioning

		Mean temperature			Precipitation					
	Year	Annual	Minimum	Maximum	Annual	Monsoon	Winter	Aridity index	Adjusted R^2	*P*-value
Mesquite Savanna										
Trees	4.31	16.49	9.96	7.48	10.68	9.63	21.63	19.82	0.09	0.21
Prosopis velutina	9.66	**31.71**	15.71	10.33	8.36	10.32	4.21	9.70	**0.41**	≤ **0.01**
Shrubs	9.72	12.16	12.25	6.36	13.49	8.31	20.89	16.82	0.20	0.16
Subshrubs	13.62	10.84	9.88	10.91	9.18	17.23	15.38	12.96	0.13	0.19
Grasses	2.39	11.65	6.15	4.05	**24.21**	12.18	14.42	**24.95**	**0.68**	≤ **0.01**
Forbs	7.09	10.58	1.08	1.32	10.28	6.02	**51.46**	12.17	**0.56**	≤ **0.01**
Cacti	11.41	**27.36**	8.30	6.17	13.32	4.85	14.53	14.06	**0.39**	**0.03**
Arizona Uplands-Hillslope										
Trees	**30.35**	**27.35**	5.55	4.84	5.65	7.80	10.32	8.14	**0.53**	≤ **0.01**
Cercidium microphyllum	**26.25**	**27.43**	4.16	4.57	4.99	10.62	9.33	12.65	**0.51**	≤ **0.01**
Shrubs	10.37	11.75	10.18	9.38	16.15	19.61	9.44	13.12	0.07	0.40
Lycium spp.	12.88	11.30	12.94	10.25	17.00	17.05	9.25	9.33	0.14	0.29
Subshrubs	8.00	10.29	9.39	9.01	15.42	18.10	12.34	17.45	0.16	0.33
Encelia farinosa	9.16	11.36	11.99	7.73	14.54	17.32	13.72	14.18	0.19	0.24
Cacti	10.15	9.42	19.14	12.57	10.29	18.86	5.12	14.45	0.38	0.14
Janusia gracilis	18.38	19.61	7.01	6.79	13.74	17.17	8.81	8.49	**0.69**	≤ **0.01**
Arizona Uplands-Piedmont										
Trees	12.23	10.53	10.63	8.41	17.80	13.13	13.45	13.82	0.26	0.19
Cercidium microphyllum	14.72	13.53	13.49	10.55	9.59	18.18	8.24	11.70	**0.52**	**0.03**
Shrubs	14.78	11.79	9.69	12.18	8.11	6.83	20.69	15.93	0.20	0.41
Larrea tridentata	2.79	4.90	6.18	7.99	23.35	16.13	**31.95**	6.71	**0.46**	**0.04**
Fouquieria splendens	**28.15**	**27.00**	11.76	9.70	5.81	4.83	5.69	7.06	**0.81**	≤ **0.01**
Subshrubs	3.89	6.42	6.54	7.75	**31.13**	23.95	13.28	7.04	**0.49**	**0.04**
Ambrosia deltoidea	3.02	6.13	6.71	7.06	**30.68**	22.61	13.62	10.17	**0.41**	**0.04**
Cacti	15.58	18.28	13.03	10.12	7.10	13.24	8.76	13.89	**0.64**	≤ **0.01**
Janusia gracilis	20.13	15.64	9.49	6.59	15.73	13.82	8.64	9.96	0.31	0.24
Creosote bush shrublands										
Shrubs	4.60	7.72	6.88	7.21	**29.81**	9.91	8.22	**25.65**	**0.44**	**0.03**
Larrea tridentata	9.23	7.94	3.45	8.26	**25.50**	3.57	**28.09**	13.96	**0.59**	**0.02**
Krameria grayi	4.24	6.87	7.00	7.56	15.90	10.22	16.92	**31.29**	**0.84**	≤ **0.01**
Ambrosia deltoidea	4.73	7.66	5.20	7.90	**34.14**	7.36	19.03	13.98	**0.46**	**0.03**
Trees	10.11	8.42	10.61	12.15	11.95	14.79	12.41	19.56	0.29	0.18
Cacti	7.51	9.13	20.89	14.08	14.31	14.65	12.98	6.45	0.18	0.27
Saltbush shrublands										
Atriplex spp.	6.16	7.89	16.14	5.00	17.66	17.28	11.51	18.36	0.30	0.15
Subshrub	20.21	18.52	10.84	19.81	6.79	6.87	10.22	6.74	0.18	0.49

Bold, underlined values designate significant independent effects based on the upper 95% confidence level of *Z*-scores generated by a randomization routine (Walsh & Mac Nally, 2009).

on the piedmont, the change in cover of *A. deltoidea*, which was the only common subshrub, was positive when AP was above a threshold of 280 mm (slope = 0.02, r^2 = 0.26, P < 0.01; Fig. 4o).

In saltbush shrublands, the change in cover of dominant *Atriplex* species and subshrubs could not be explained by time and climate variables.

Discussion

Climate change and its impact on plant community composition is occurring at a regional scale, which requires a shift from assessing site-specific plant responses to understanding plant dynamics at a large spatial scale. Equally important for forecasting the

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responses of long-lived Sonoran Desert plants to climate change is an assessment of how long-term vegetation measurements correlate with past climate variability. We used the change in cover between sampling periods as an index of overall plant species performance because it integrates changes in the growth rate of previously existing individuals with recruitment and mortality events. Our cross-site analysis of long-term data provides a novel and useful approach to assessing plant vulnerability to climate change.

Plant community composition of the Sonoran Desert monitoring plots was strongly related to changes in elevation, which influence temperature and precipitation (Whittaker & Niering, 1965). As our plots decreased in elevation and became warmer and drier, mesquite savannas transitioned into Arizona Upland desertscrub, and then to communities dominated by drought-tolerant shrubs. The responses of plants to increased aridity within a plant community were similar to these downslope changes in composition. For example, mesquite savannas lost perennial grass cover in years when AP fell below 390 mm and had increases in cacti when MAT was greater than 17.8 °C, which are changes that shift the composition toward life forms more characteristic of Arizona Upland communities.

The loss of perennial grasses has been documented in drylands worldwide and is an indicator of desertification, which has large implications for ecosystem productivity (Archer *et al.*, 1995). Although land use (fire and grazing) can influence this transition, our results show that climate is a strong driver. Perennial grasses likely showed large responses to AP because they are fast-growing and shallow-rooted, and several species turn over every 5–15 years in this region (Canfield, 1957). Other research has shown that AP influences perennial grass density and cover to a greater extent than the livestock grazing system in this plant community (Mashiri *et al.*, 2008). Similar to our results, a threshold of 350 mm AP has been shown to limit grass recruitment in the Sonoran Desert (McClaran & Angell, 2006). The relationship between perennial grass cover and AP was improved if MAT was accounted for as an aridity index. Because temperature controls evapotranspiration, this improved relationship demonstrates that atmospheric demand for water was also potentially important. Perennial grasses were not responsive to SP, which has been previously shown (Cable, 1975). Associated with perennial grass response to climate was a correlation between WP and forb cover in mesquite savanna communities. Forbs compose most of the species in the community, and therefore WP has important implications for species diversity.

The increase of cacti with warmer temperatures has been documented across the southwestern United States (Webb, 1996; Turner *et al.*, 2003). Episodic climate events (not just climate means), such as frost, can have a long-term influence on plant community composition in the Sonoran Desert. A decreased frequency of extreme freezes indicates less potential for tissue damage and mortality of succulents (Nobel, 1988). Freezing events have become less frequent in the Sonoran Desert; the annual number of nights with freezing temperatures has decreased from 40 to 20 at SRER, the coldest site, and from 20 to <10 at OPCNM, the warmest site, over the last 50 years [Western Regional Climate Center (WRCC), 2011].

The expansion of *P. velutina* has been a striking change across many sites in the Sonoran Desert during the 20th century (Turner *et al.*, 2003), but the drivers of this change remain controversial (Archer *et al.*, 1995). Our results suggest that increases in temperature have negatively influenced the growth of this leguminous tree. Browning *et al.* (2008) demonstrate a slowing rate of increase in the 21st century and a possible carrying capacity near 30% canopy cover based on water availability for the region. Other studies have concluded that water availability constrains the structure and photosynthetic capacity of *P. velutina* (Stromberg *et al.*, 1993; Resco *et al.*, 2009). Temperature could influence cover by modulating soil water through evapotranspiration rates. Our results suggest that a threshold MAT near 18 °C may cause significantly more water stress, especially in years with low precipitation or in an upland setting. Although *P. velutina* has deep roots, it also acquires water from the upper 30 cm of the soil profile (Cable, 1977), a region that is often subjected to rapid drying from evaporation when temperatures are high. The cost of water losses from mesquite savannas may exceed the benefit of increased water-use efficiency and photosynthesis of *P. velutina* gained from increasing CO_2 during the last century.

In the more xeric Arizona Upland communities, plant community composition and plant response to climate depended on landscape position. *Cercidium microphyllum*, a dominant drought-deciduous tree, likely experienced extended periods of low water availability on hillslope positions due to poorly developed shallow soils and steep slopes, where runoff can be high. Our results show that the cover of *C. microphyllum* decreased when MAT exceeded 21 °C and much of this decline was due to mortality as opposed to the reduction of living plant cover. Previous research has documented high mortality of this species when the diameter of trees was >50 cm (Bowers & Turner, 2001), suggesting that periods of high temperature and resultant low water availability likely have the greatest influence on older senescing trees. High temperatures might strongly limit the effectiveness of SP, which has been

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shown to influence the growth of this plant species (Bowers & Turner, 2001). The greatest decline in cover of *C. microphyllum* occurred on a south-facing plot, where evapotranspiration was presumably highest. Importantly, the decline of older *C. microphyllum* trees coupled with low recruitment in the Sonoran Desert can have cascading effects on plant community structure and function, as it serves as a nurse plant for *C. gigantea* and other species (Bowers & Turner, 2001).

In contrast to its response to climate on hillslopes, *C. microphyllum* growth was not related to any single climate variable on piedmonts/bajadas, where soils are more developed and runoff is not as high. The cover of *L. tridentata* was significantly explained by WP and began to decline below 112 mm. A cross-site study in the Sonoran and Mojave Deserts demonstrated a widespread decline of *L. tridentata* in response to low precipitation in the early 21st century, especially during the winter months (McAuliffe & Hamerlynck, 2010). Results from the same study showed that mortality was high at the Sonoran-Mojave Desert boundary, where October–March precipitation was less than 100 mm. A greater number of plots had declines in cover of *L. tridentata* and a higher WP threshold (135 mm) existed for the shrub where it was dominant in alluvial and valley bottom settings compared with Arizona Uplands on piedmont settings. Large rocks and gravel in piedmont positions may slow the evaporative loss of water relative to valley bottoms. McAuliffe (1994) demonstrated the decline of *L. tridentata* was only evident on older geomorphic surfaces, which have shallow impermeable layers, particularly petrocalcic horizons. These layers may limit the soil volume available to plant roots and restrict water infiltration, holding water at shallow depths where it is more susceptible to evaporation.

Subshrubs, largely composed of *A. deltoidea*, showed large fluctuations in cover in response to AP in Arizona Upland (piedmont) and at lower elevation in creosote bush shrubland communities. The drought-deciduous *A. deltoidea* can rapidly increase its photosynthetic rate in response to increasing water availability, but is very sensitive to water stress (Szarek & Woodhouse, 1976). High rates of subshrub mortality were indicated by the loss of individuals between consecutive census maps, but there were also several periods of new recruitment. *Ambrosia deltoidea* is a relatively short-lived plant, but likely has a persistent seedbank and germinates more frequently than other Sonoran Desert species, allowing it to readily fill open spaces in wet years (Bowers, 2002). This colonizing potential and its ability to serve as a nurse plant for woody species strongly influence plant community composition in the Sonoran Desert (McAuliffe, 1986). As cover for this facilitative species increased above 290 mm AP in both communities, this may indicate an important potential threshold for new recruitment in this region.

Like many Sonoran Desert semisucculent species, *F. splendens* can be vulnerable to extremely low temperatures and has been shown to be tolerant of high temperatures (Nobel, 1988). This tolerance is contradictory to our results showing a decline in cover, largely attributed to mortality of individual plants, with increasing MAT in Arizona Upland-piedmont communities. Declines of the shallow-rooted (5–40 cm) *F. splendens* were high on south- and west-facing slopes, where seedling recruitment is low and roots can be susceptible to direct heat damage and low water availability when temperatures are high (Nobel & Zutta, 2005). As a decline in *F. splendens* cover was also significantly explained by time, an environmental factor that covaried with temperature through time may have also explained changes in cover.

Creosote bush shrublands are one of the most xeric plant communities in the Sonoran Desert. Associated with declines in *L. tridentata*, the dominant shrub, with decreasing WP were declines in its common root parasite, *K. grayi*. Although the partially parasitic shrub is palatable to livestock and may have initially increased in response to the removal of livestock in the early 20th century (Blydenstein *et al.*, 1957), current patterns indicate that aridity is the best explanatory variable for change in cover of *Krameria*. Changes in total shrub cover, mostly composed of the codominant shrubs, as well as the subdominant *Acacia* spp. and *Lycium* spp., were most closely associated with AP and aridity. Shrub cover declined in years with less than 292 mm of precipitation, which was similar to subshrubs in this plant community. Many of the same shrubs occur in the Mojave Desert, where AP is much lower. For example, Beatley (1974) found that *L. tridentata* was most abundant at sites in the Mojave Desert with AP less than 180 mm. However, the Mojave Desert receives a greater proportion of precipitation in the winter, which leads to water recharge of deep soil layers accessible to *Larrea*.

Increasing CO_2 may interact with water availability to influence shrub performance in the Sonoran Desert. In the Mojave Desert, an artificial 50% increase in atmospheric CO_2 enhanced production of *L. tridentata* due to an increase in photosynthetic rate and water-use efficiency in wet, but not dry years (Smith *et al.*, 2000). Unlike what is predicted in more mesic ecosystems, an increase in CO_2 may not increase soil water availability in desert soils because of the interaction of decreased leaf conductance (Nowak *et al.*, 2004). Therefore, decreasing transpiration is not necessarily important

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given limited water availability in an increasingly arid ecosystem. These results, albeit from a desert with a different climatic regime, suggests little to counterbalance the consequences of decreased AP on plant performance in the Sonoran Desert region.

In conclusion, many plant species and functional types across the Sonoran Desert responded to increasing temperature and drought conditions, which are predicted for the future. Mesquite savannas are likely to have reduced perennial grass and forb cover in response to decreasing precipitation, a slow reversal of the *P. velutina* expansion experienced in the 20th century, and an increase in cacti in response to increasing temperature. Arizona Upland communities may experience continued declines of *C. microphyllum*, a dominant leguminous tree on hillslopes, loss of *F. splendens* on piedmonts/bajadas, especially on south- and west-facing slopes in response to increasing temperature, and loss of subshrubs with increasing aridity. In creosote bush shrublands, the codominant species *L. tridentata* and *K. grayi* will be most vulnerable to decreases in cool season precipitation and increased aridity. These regional-scale predictions of plant performance are supported by long-term vegetation dynamics from multiple protected sites. Such integrated assessments of plant responses to climate are critical for understanding future shifts in plant community composition.

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