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Regional signatures of plant response to drought and elevated temperature across a desert ecosystem

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Abstract. The performance of many desert plant species in North America may decline with the warmer and drier conditions predicted by climate change models, thereby accelerating land degradation and reducing ecosystem productivity. We paired repeat measurements of plant canopy cover with climate at multiple sites across the Chihuahuan Desert over the last century to determine which plant species and functional types may be the most sensitive to climate change. We found that the dominant perennial grass, *Bouteloua eriopoda*, and species richness had nonlinear responses to summer precipitation, decreasing more in dry summers than increasing with wet summers. Dominant shrub species responded differently to the seasonality of precipitation and drought, but winter precipitation best explained changes in the cover of woody vegetation in upland grasslands and may contribute to woody-plant encroachment that is widespread throughout the southwestern United States and northern Mexico. Temperature explained additional variability of changes in cover of dominant and subdominant plant species. Using a novel empirically based approach we identified "climate pivot points" that were indicative of shifts from increasing to decreasing plant cover over a range of climatic conditions. Reductions in cover of annual and several perennial plant species, in addition to declines in species richness below the long-term summer precipitation mean across plant communities, indicate a decrease in the productivity for all but the most drought-tolerant perennial grasses and shrubs in the Chihuahuan Desert. Overall, our regional synthesis of long-term data provides a robust foundation for forecasting future shifts in the composition and structure of plant assemblages in the largest North American warm desert.

Key words: aridity; Chihuahuan Desert; climate change; climate pivot point; desertification; forecasting plant community composition; land degradation; long-term vegetation dynamics; plant canopy cover; species richness.

Introduction

Future warming and changes in the patterns of precipitation can have a strong impact on plant species already stressed by low water availability in arid and semiarid ecosystems. In North American deserts an ensemble of climate change models predicts lower annual and winter precipitation, more severe and protracted drought, and large increases in temperature, especially in the summer (Christiansen et al. 2007, Seager et al. 2007). Summer precipitation of these regions is especially difficult to predict because it is driven by complex land–sea contrasts and convective events that are not easily simulated (Giorgi et al. 2001). Although some models predict an increase in summer precipitation, an increase in evaporation due to rising temperatures in the summer months may offset any additional water input and reduce soil moisture available for plant growth and survival.

An evaluation of plant species responses to increased aridity in the Chihuahuan Desert is important because this ecosystem is prone to land degradation that is marked by the transition from grass to shrub dominance, invasion by nonnative species, and the loss of total perennial vegetation cover (Buffington and Herbel 1965, Gibbens et al. 2005). These changes can dramatically change productivity, soil erosion rates, carbon and nutrient cycling, and feedback to climate through the

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alteration of surface albedo in relatively abrupt and often irreversible pathways (Okin et al. 2009). Although human land use has influenced the rate of land degradation across the Chihuahuan Desert, especially in the late-19th and early-20th centuries when livestock grazing was at its peak (Buffington and Herbel 1965), increased aridity can accelerate the impact of past and current land-use practices and has led to recent and broad-scale effects on vegetation (Peters et al. 2012).

An accurate prediction of future plant species assemblages requires an assessment of the sensitivity of different plant species to various aspects of climate. Plant species in the Chihuahuan Desert region differ in their resistance to elevated temperature and drought based on their structural and physiological adaptations (Fernández and Reynolds 2000, Gibbens and Lenz 2001). Equally important to making a prediction is an understanding of the direction and magnitude of plant species responses and whether these responses are shared among species that have similar functional traits. Although conceptually well-defined thresholds of change exist for plants and ecosystems with respect to climate, empirically based early-warning signs of approaching threholds are rare (Scheffer et al. 2001). A shift from positive to negative plant species performance over a range of climatic conditions can serve as an indicator and be used to predict future species assemblages. If dominant species or a large number of species cross these "climate pivot points," novel plant species assemblages may result, with major alterations to ecosystem structure and function.

Past climate–vegetation relationships provide a basis to predict future changes in plant assemblages. At present, climate-envelope definitions are used to predict climatic responses at a regional scale, yet these assume that species are currently in equilibrium with climate and will respond if climate changes (Pearson and Dawson 2003). Results from monitoring vegetation in permanent plots provides a robust approach to assess how plants have changed through time and with respect to climate because that approach does not assume a climate–vegetation equilibrium, and instead integrates the full suite of biotic and abiotic conditions that can influence plant performance. A long-term record of vegetation monitoring encompasses changes in plant cover over a range of climatic conditions, particularly the hot, dry climatic regime that occurred in the mid-20th and early-21st century, which may be similar to future conditions. A regional assessment of the response of plant species to climate can be greatly improved through the synthesis of data across multiple sites.

We conducted a regional synthesis of long-term vegetation monitoring data to understand how drought and elevated temperatures have influenced plant species across the Chihuahuan Desert region and to predict future plant species assemblages. Our specific objectives for this study were to: (1) determine which plant species and functional types in the Chihuahuan Desert may be most sensitive to climate change, (2) assess the relative importance of climate variables in explaining plant species responses, (3) document the magnitude of plant responses that have occurred over a range of climatic conditions, and 4) identify critical points over a range of climatic conditions that are indicative of changes in plant cover.

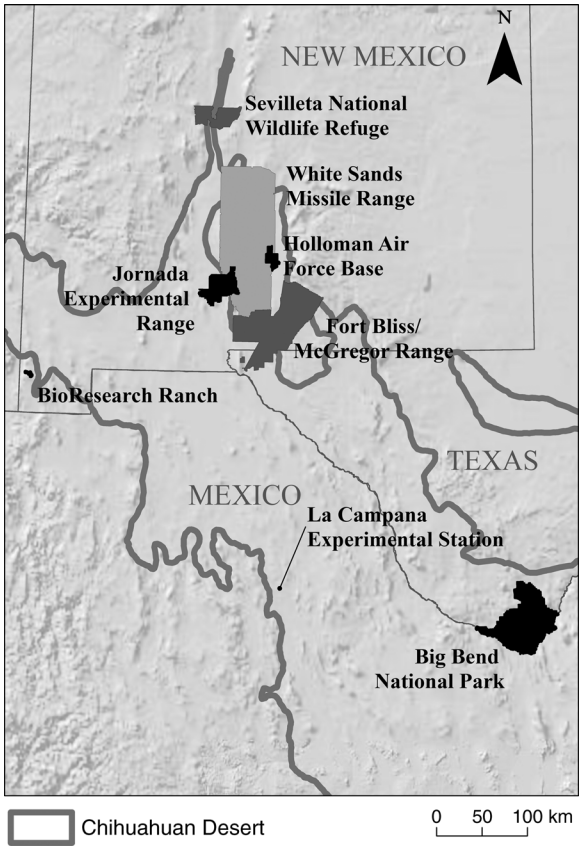

FIG. 1. Map of the long-term vegetation monitoring sites in the Chihuahuan Desert, USA and Mexico.

METHODS

We used repeat measurements of plant species canopy cover from eight sites (Fig. 1, Appendix A) in the northern Chihuahuan Desert in New Mexico (see Plate 1) and Texas, USA, and Chihuahua, Mexico. Sites range in elevation from 1210 to 1897 m and include lowlands characterized by low-lying or depression regions with fine-textured soils that periodically flood; uplands consisting of rolling plains and alluvial-fan piedmonts that have loamy sand to sandy clay loam soils, and in many cases, petrocalcic horizons at 10–50 cm below the surface; and foothills or the lower positions of colluvial hill and mountain slopes that have gravelly coarse-textured soils.

Repeat measurements of plant canopy cover at each site were done by (1) line and line-point intercept along

transects, (2) mapping the canopy outlines of individual plants in a quadrat (Wondzell and Ludwig 1995), or (3) assigning a cover value that represented the projected areal extent of a plant part, individual plant, or plant species in a quadrat (Huenneke et al. 2002; Appendix A). The line intercept and line-point intercept methods consisted of recording the species that crossed a transect line or was intercepted by a point projected down to the canopy level from the transect line, respectively. All measurements included in the analysis were made in late summer to early fall (August–October) and were taken 1 to 20 years apart from each other, depending on the study. The objectives of plant measurements of the original studies were to assess how vegetation varied according to site characteristics and changed with climate and disturbance (Appendix A). All sites were influenced by historic land uses, but we minimized their potential effects by using undisturbed control or reference quadrats and transects for studies that examined disturbance due to livestock, small mammals, and military training.

Mean monthly temperature (minimum, mean, and maximum) and precipitation measurements were obtained from long-term weather stations nearest to the quadrats and transects [$n = 1$ station per site, except White Sands Missile Range ($n = 18$ stations), Sevilleta ($n = 3$ stations), and Jornada ($n = 2$ stations)]. Precipitation measurements were supplemented at the Jornada site with an extensive network of 14 rain gauges. We also used the Palmer Modified Drought Index (PMDI), which is a calculation of the balance between moisture supply and demand that uses both temperature and precipitation variables. Unlike the Palmer Drought Severity Index, the PMDI is continuous and is able to better capture transitions between wet and dry periods (Heddinghaus and Sabol 1991). Monthly temperature, precipitation, and drought variables were aggregated into annual, summer (June–September), and winter (October–March) periods that preceded a vegetation measurement.

Canopy cover of each species was calculated by summing the area, intercept lengths, or points occupied by all vegetative units of a plant species divided by the total area of the quadrat, transect length, or points sampled, respectively. Nonmetric multidimensional scaling and hierarchical cluster analyses were performed to designate plant communities using the cover of all plant species in quadrats or transects (vegan package in R; Oksanen et al. 2008). Plant species were aggregated into plant functional types based on lifespan and on structural and physiological traits to test broader group responses to environmental conditions. We used the average cover value of all quadrats or transects within a plant community for each year a study was conducted.

As vegetation data were collected using different methods for different studies and sites, we normalized estimates of cover with a calculation of the change in cover of plant species per unit time:

$$\text{Change in cover} = \frac{\ln(\text{cover}_{t2}/\text{cover}_{t1})}{t2 - t1}$$

where cover_{t2} is plant cover in year t2, and cover_{t1} is plant cover in the previous sampling year, t1. The denominator scales the change in cover according to how much time elapsed between plant measurements, which also varied among studies and sites. A positive value of this index indicated that a plant species increased in cover over the observation interval, whereas a negative value indicated that it decreased in cover.

While the magnitude and timing of short-term climate events (e.g., frost, monsoon storm) can influence increases and decreases in plant cover, plant measurements were too far apart in time to assess climate–plant relationships at a fine scale. Instead, we related the change in cover of plant species to the means of climate variables over the plant measurement interval, which characterized the average climate regime. Scaling the change in cover index by time elapsed between measurements limited the influence of plant measurements taken at long time intervals, which may have included multiple short-term increases and decreases in plant cover. We did not include measurements of annual plants if they were measured more than one year apart. To determine which plant species and functional types were most sensitive to climate change and the relative importance of climate variables in explaining plant species responses (objectives 1 and 2), we used a two-stage approach that handled spurious correlation and shared explanatory power among climate variables better than comparable methods (Murray and Conner 2009). First, we used zero-order correlations between the change in plant cover and each climate variable. We also included the year of the vegetation measurement as a potential correlate to determine if there were interannual changes in cover not explained by the climate variables.

Second, using only climate variables that were significantly related to the change in plant cover, we used hierarchical partitioning (HP), a form of multiple regression that can account for multicollinearity among explanatory variables (Chevan and Sutherland 1991, Walsh and Mac Nally 2009: hier.part package in R). We only analyzed the effect of climate on plant species and functional types that had a sufficient sample size for analysis. We tested whether the inclusion of different data sets from several locations had an influence on climate–vegetation relationships with ANCOVA analyses, but found no significant differences among the data sets (Appendix B) and therefore grouped data sets together in subsequent analyses. Change in cover values that were significant outliers in the multiple regressions were identified and removed using a Bonferroni outlier test (Fox 2009: companion to applied regression package in R). Once the sensitivity of plant species to

different aspects of climate was determined, we used the change in cover index to document the magnitude of plant responses and identify critical points over a range of climatic conditions that were indicative of changes in plant cover (objectives 3 and 4). To meet these objectives, we used Akaike's information criterion (AIC) and AIC weights (w_i; relative likelihood of model) to determine the relative support for a linear vs. nonlinear (logarithmic and quadratic) model that related the change in cover and climate variables identified in the previous correlation and HP analyses.

The slope between the change in plant cover and a climate variable indicated the response of a plant species with respect to climate. The point where the regression slope intersected the x-axis (the x-intercept) indicated a transition between gains and losses of cover, which we define as a *climate pivot point*. To provide a greater context for plant sensitivity to climate, we compared plant responses and climate pivot points among plant species and functional types within a given plant community. We also compared plant species responses among plant communities when data sets had measurements that spanned multiple plant communities.

Results

Nonmetric multidimensional scaling and cluster analysis indicated 13 distinct grassland and shrubland assemblages represented by the long-term quadrats and transects, but only eight assemblages had sufficient sample size for analysis. Sites dominated by C_4 grasses had species compositions that were related to landscape position: (1) a lowland grassland dominated by *Pleuraphis mutica* (tobosagrass) (plant nomenclature follows USDA Plants Database, *available online*);[10] upland grasslands dominated by (2) *Bouteloua eriopoda* (black grama) or (3) mixed grasses [*Aristida purpurea* (purple threeawn), *Sporobolus* spp. (dropseeds), *Muhlenbergia* spp. (muhlys)]; and foothill grasslands dominated by (4) *Bouteloua gracilis* (blue grama) or (5) *Bouteloua curtipendula* (sideoats grama). Shrublands were in upland landscape positions and dominated by the C_3 shrubs (6) *Larrea tridentata* (creosote bush), (7) (*Prosopis glandulosa* (honey mesquite), or (8) *Flourensia cernua* (tarbush), which depended on soil texture and degree of slope.

Dominant grassland species and functional types

Climate variables and time explained 7%–80% of the variation in the changes in cover of plant species and functional types across plant communities (Appendix C). Because some of the foothill and lowland grassland communities had low sample sizes but related species compositions and landscape settings, we examined broader plant functional type responses within each of the more generalized grassland communities (lowlands, uplands, foothills). The change in cover of perennial grasses was related to summer precipitation in upland ($r^2 = 0.14$, $P < 0.0001$) and foothill ($r^2 = 0.19$, $P < 0.01$) grasslands and a decrease in cover occurred below pivot points of 115 ± 11 mm and 165 ± 14 mm (mean ± SE), respectively (Fig. 2a). In contrast, perennial grasses in lowland grasslands had large changes in cover, but these changes were not related to summer precipitation or other climate variables. The change in cover of woody vegetation increased with winter precipitation in upland grasslands ($r^2 = 0.20$, $P < 0.0001$) and was positive above a pivot point of 78 ± 6 mm, but there was no relationship in foothill or lowland grasslands (Fig. 2b).

In the upland black grama and mixed grasslands, perennial grasses were most sensitive to summer precipitation, but annual precipitation, summer temper-

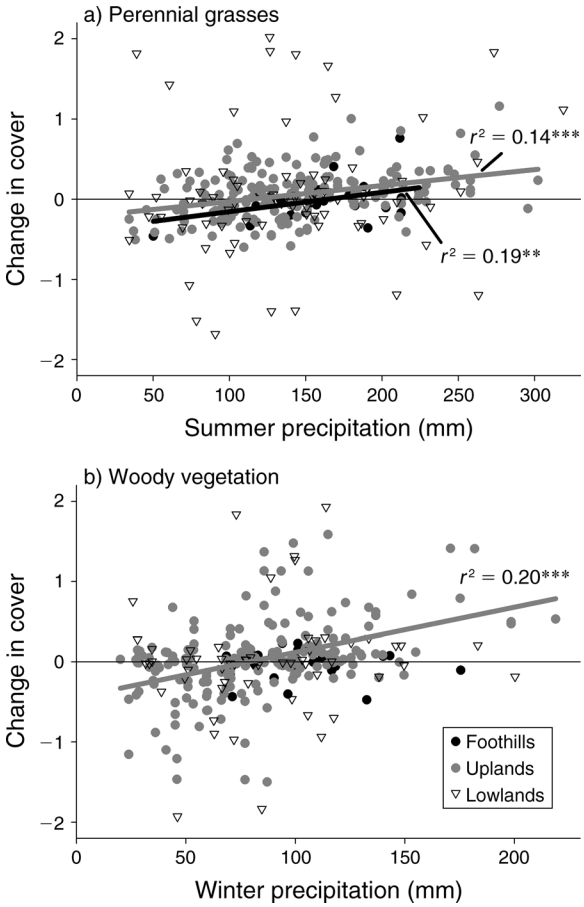

FIG. 2. Change in cover of (a) perennial grasses in relationship to summer precipitation and (b) change in cover of woody vegetation in relationship to winter precipitation in three grassland types: foothills, uplands, and lowlands. Perennial grasses regression are $y = 0.0020x - 0.23$ for uplands and $y = 0.0024x - 0.40$ for foothills; regressions for woody vegetation are $y = 0.0056x - 0.44$ for uplands. Change in cover $= [\ln(\text{cover}_{t2}/\text{cover}_{t1})]/(t2 - t1)$, where cover_{t2} is plant cover in year t2 and cover_{t1} is plant cover in the previous sampling year, t1.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[10] http://plants.usda.gov

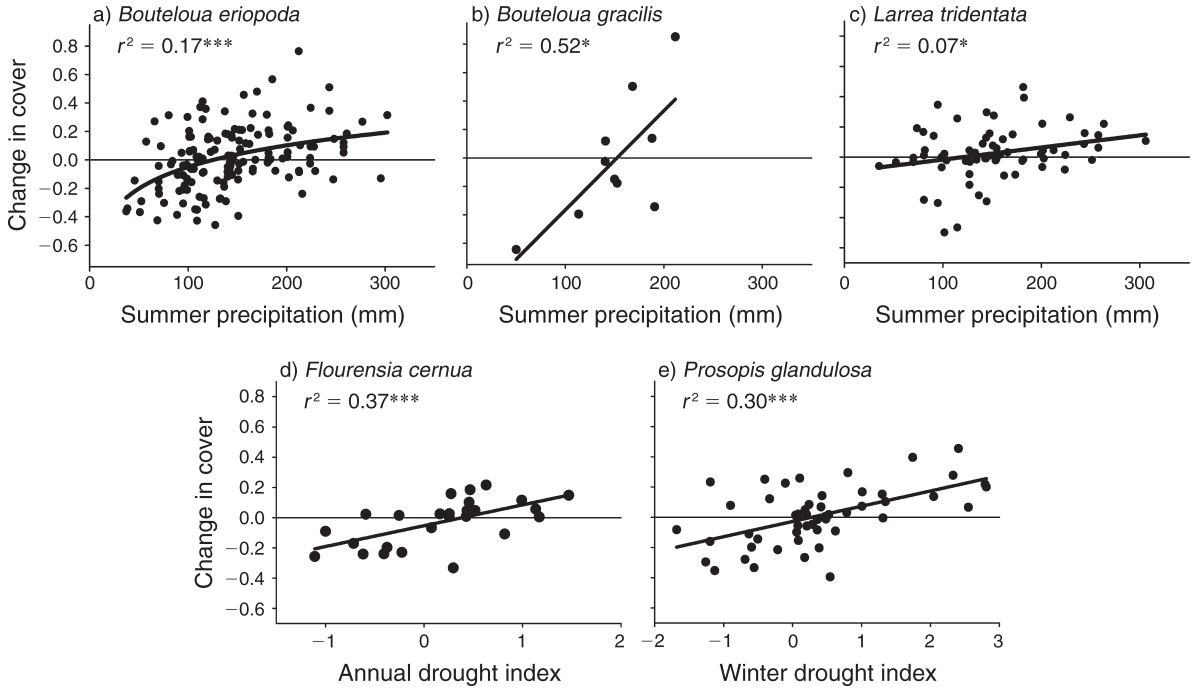

FIG. 3. Changes in cover of dominant plant species in relationship to climate variables for (a) *Bouteloua eriopoda* [$y = 0.22 \ln(x) - 1.06$], (b) *Bouteloua gracilis* ($y = 0.007x - 1.06$), (c) *Larrea tridentata* ($y = 0.0008x - 0.097$), (d) *Flourensia cernua* ($y = 0.14x - 0.054$), and (e) *Prosopis glandulosa* ($y = 0.10x - 0.028$). Change in cover = [$\ln(\text{cover}_{t2}/\text{cover}_{t1})$]/(t2 – t1), where cover_{t2} is plant cover in year t2 and cover_{t1} is plant cover in the previous sampling year, t1.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

atures and drought also influenced their changes in cover (Appendix C). There was support in the data that the change in cover of *B. eriopoda* in black grama grasslands was nonlinear (logarithmic AIC = −50.04, $w_i = 0.69$; quadratic, AIC = −48.01, $w_i = 0.25$; Appendix D) instead of linear (AIC = −44.98, $w_i = 0.06$) with respect to summer precipitation ($r^2 = 0.17$, $P < 0.0001$), increasing above a pivot point of 125 ± 13 mm and decreasing at an accelerated rate below this amount (Fig. 3a). In blue grama foothill grasslands, *B. gracilis* had a large increase in cover when summer precipitation was above 153 ± 15 mm ($r^2 = 0.52$, $P < 0.05$; Fig. 3b). The changes in cover of all annual grass and most annual forb species, which comprised a large part of species richness, were positively related to summer precipitation and the summer drought index, and negatively related to summer maximum temperatures in black grama grasslands and shrub communities (Appendix C). While the changes in cover of many perennial forbs were related to summer precipitation in grasslands, annual precipitation was a more important driver. Winter precipitation and the winter drought index were most important in explaining the change in cover of subshrubs.

Dominant shrubland species and functional types

Shrub responses to climate in shrublands varied according to the dominant species. The change in cover of *L. tridentata* in shrublands in which it was dominant was related to summer precipitation ($r^2 = 0.07$, $P < 0.05$), and was negative below a pivot point of 121 ± 29 mm (Fig. 3c). The changes in cover of *Flourensia cernua* and *P. glanulosa* were sensitive to annual and winter precipitation, in addition to annual and winter drought indices in the plant communities in which they were dominant (Appendix C). The change in cover of *F. cernua* was most related to the annual drought index ($r^2 = 0.37$, $P < 0.001$) and decreased below 0.39 ± 0.18 PMDI (Fig. 3d), whereas the change in cover of *P. glandulosa* was strongly linked to the winter drought index ($r^2 = 0.30$, $P < 0.0001$) and decreased below 0.28 ± 0.22 PMDI (Fig. 3e). Both these drought pivot points are considered near-normal conditions, with most decreases in cover occurring during dry conditions indicated by a negative PMDI.

Subdominant grassland and shrubland species and functional types

The sensitivity of many dominant plant species to summer precipitation was shared by a full suite of subdominant plant species spanning functional types across plant communities (Appendix C). We show plant species responses and pivot points relative to the long-term climate means in black grama grasslands and creosote bush shrublands, which had the highest number of plant species responsive to summer precipitation and

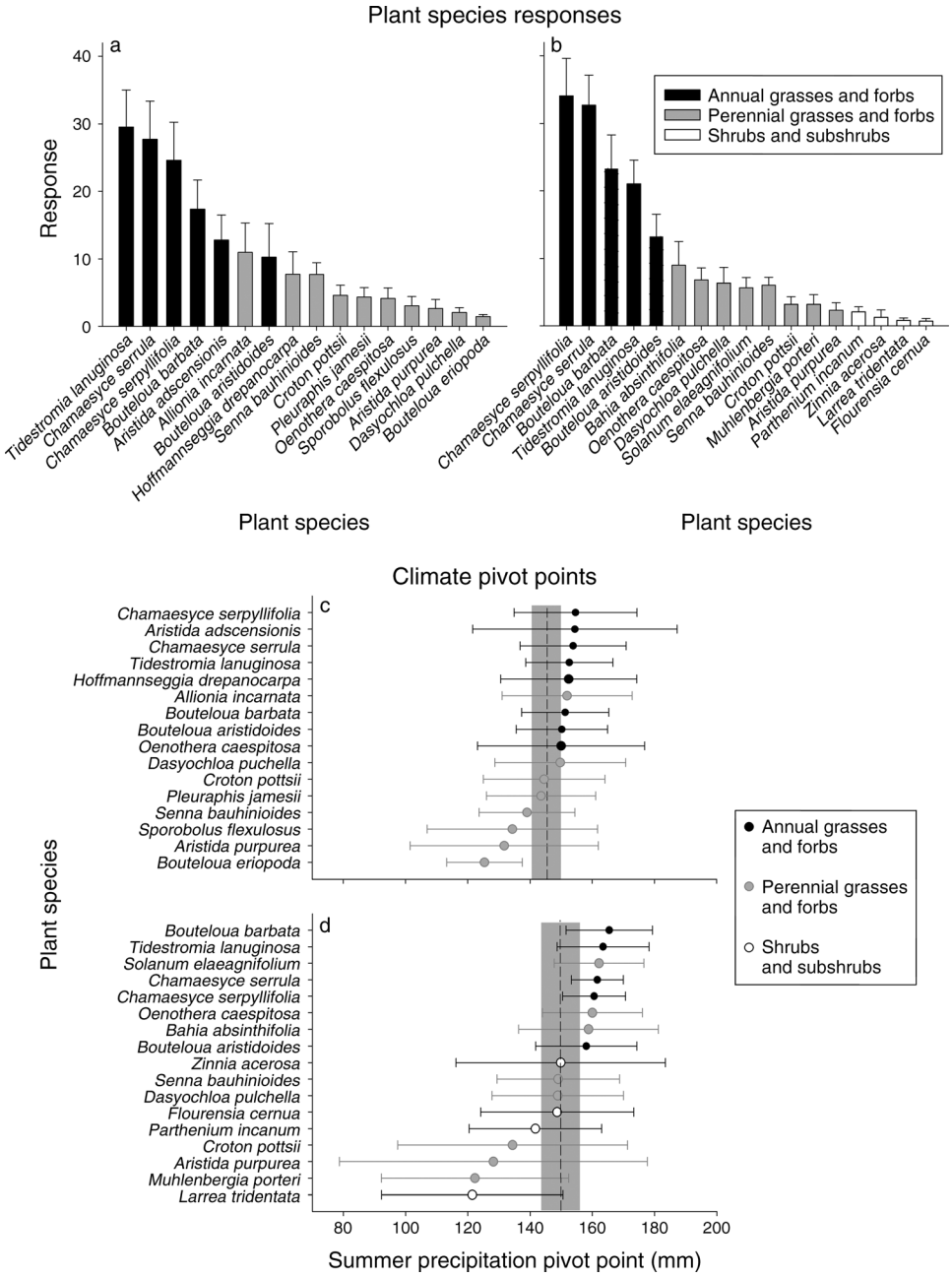

FIG. 4. (a, b) Plant species responses (×1000, mean + SE) in (a) black grama grassland and (b) creosote shrubland. Response was measured as percentage change in cover per mm summer precipitation. (c, d) Climate pivot points for species in (c) black grama grassland and (d) creosote bush shrubland in relation to summer precipitation. A plant species response is the change in cover of a species in relation to climate (slope), and a climate pivot point is the transition between gains and losses of cover of a species in relation to climate (x-intercept). Mean summer precipitation is shown by the vertical dashed line (±SE is shown by the light-gray shaded region).

had similar climate–vegetation relationships as other plant communities. The magnitude of plant species responses in black grama grasslands and creosote bush shrublands ranked according to their plant functional types: shrub and subshrub species (only in creosote bush shrublands) had the smallest responses, perennial grass and forb species had moderate responses, and annual grass and forb species had the largest responses (Fig. 4a, b). There was a significant positive relationship between plant species responses and their pivot points across these two plant communities ($r = 0.46$, $P < 0.01$), which meant that annual grass and forb species generally had higher precipitation pivot points than perennial grass and forb, subshrub, and shrub species

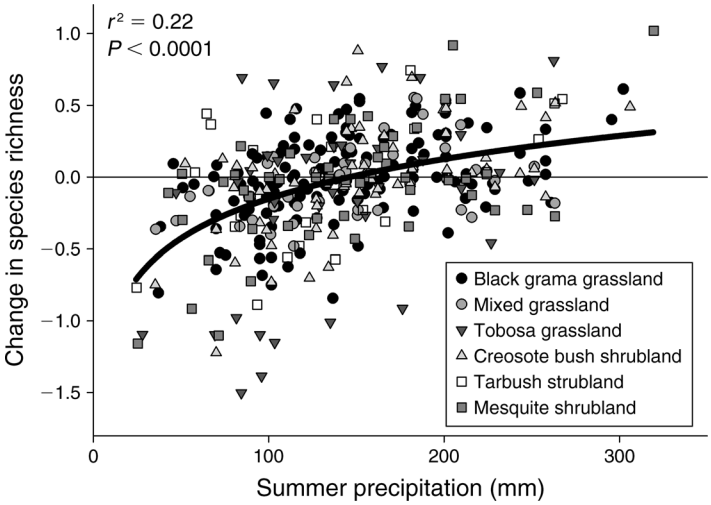

FIG. 5. Change in plant species richness in relationship to summer precipitation for six plant communities [$y = -0.40 \ln(x) - 1.99$; $P < 0.0001$]. Change in species richness = [ln(spp. richness$_{t2}$/spp. richness$_{t1}$)]/(t2 − t1), where spp. richness$_{t2}$ is plant species richness in year t2 and spp. richness$_{t1}$ is plant species richness in the previous sampling year, t1. Species richness in foothill grasslands (blue grama and sideoats grama dominated) was not significantly related to summer precipitation (not shown).

(Fig. 4c, d). However, the errors associated with pivot point estimates were large and indicated considerable overlap among species and functional types. The responses of each plant functional type were 20% (annual grasses) to 110% (perennial grasses) larger in creosote bush shrublands relative to black grama grasslands.

Species richness

Species richness data were combined for regression with summer precipitation across plant communities because the responses to summer precipitation and pivot points were not significantly different among communities ($F = 0.84$, $P = 0.43$). There was more support in the data that the relationship between species richness and summer precipitation was nonlinear (logarithmic, AIC = 244.14, $w_i = 0.90$; quadratic, AIC = 248.73, $w_i = 0.09$; Appendix D) instead of linear (AIC = 253.91, $w_i = 0.01$). Species richness showed a moderate positive change above 144 ± 6 mm and a large negative change below this pivot point (Fig. 5).

DISCUSSION

The synthesis of long-term monitoring results from multiple sites revealed regional signatures of plant response to climate across the Chihuahuan Desert and provides an extensive understanding of how a future warmer and drier southwestern United States may affect plant species assemblages, which is a critical need (Rosenzweig et al. 2007).

Dominant grassland species and functional types

Plant species and functional types across the Chihuahuan Desert varied in their sensitivities to different aspects of climate. The changes in cover of perennial grasses in upland and foothill settings were most sensitive to summer precipitation, which is consistent with previous studies (Nelson 1934, Muldavin et al. 2008). Summer convective storms generally produce episodic pulses of shallow soil moisture that are rapidly lost due to high evaporation rates at this time of year. The perennial grasses in this region are well suited for this type of water input because they have a water-efficient C_4 photosynthetic pathway and extensive shallow root systems for rapid water uptake (Gibbens and Lenz 2001). Despite these adaptations, many perennial grass species in upland settings showed a sensitivity to summer temperatures and the drought index (calculated with temperature), which has been observed in other deserts (Munson et al. 2011, 2012) and likely indicates the constraints on plant water availability when there is a high atmospheric demand for water. The large changes in perennial grass cover in lowland grasslands was not related to summer precipitation and might be better explained by the timing of water run-on from upland landscape settings and flooding events relative to the timing of plant growth (Huenneke et al. 2002).

While there was a regional signature of perennial grass response to climatic variables in upland and foothill settings across the Chihuahuan Desert comparable to other deserts (Munson et al. 2011, 2012), there was a substantial amount of variation in the change in cover that was not explained by climate over the measurement interval. This additional variation in the changes in cover of grasses and other plant functional types is likely attributable to environmental factors that modify water availability and directly affect plant abundance at smaller spatial scales (e.g., landscape position, soil texture; Yao et al. 2006). Plant responses are also likely dependent on individual climatic events (e.g., frost), the timing and size of precipitation events, and antecedent soil moisture conditions from previous events (Reynolds et al. 2004).

There are several possible explanations why the dominant upland grass *Bouteloua eriopoda* had moderate increases in cover during wet summers compared to large decreases during dry summers. The limited

response of this grass to wet summers may be attributable to its low seedling recruitment, establishment, and meristem density that can constrain its growth and reproduction when soil moisture conditions are favorable (Peters 2000, Peters et al. 2012, Reichmann et al. 2013). In contrast to the limitations on increases in cover of *B. eriopoda*, drought can reduce grass cover rapidly and extensively across space (Herbel et al. 1972). Our result of a nonlinear response of *B. eriopoda* to summer precipitation was corroborated by a seven-year experimental water manipulation at the Sevilleta, which found that this perennial grass species responded more strongly to drought than to water addition (Báez et al. 2012).

Bouteloua gracilis had large responses to summer precipitation, the magnitude of which was not expected because this grass spreads very slowly through the production of tillers and has infrequent recruitment (Peters et al. 2000). However, *B. gracilis* had higher and more rapid increases in leaf-level photosynthesis and pre-dawn water potential compared to *B. eriopoda* where the two species co-occurred following simulated monsoon rainfall events at the Sevilleta, which suggests a water-use advantage following dry periods (Thomey 2012). Our results suggest that *B. gracilis* requires more summer water input (138–167 mm = pivot point ± standard error) than *B. eriopoda* (112–139 mm) to increase in cover, in part because it is dominant in grasslands that receive more precipitation (Appendix E). Furthermore, the pivot point for *B. eriopoda* is below the summer precipitation mean (145 mm) for black grama grasslands, suggesting that this drought-tolerant grass can maintain positive increases in cover even under extremely dry summer conditions, whereas *B. gracilis* has a pivot point near the mean (163 mm) for blue grama grasslands. Despite these differences, the shared sensitivity to summer precipitation of the two *Bouteloua* species with other perennial grasses in the Chihuahuan Desert indicates that there is likely strong competition for water at this time of year and a high potential for widespread losses of perennial vegetation cover during consecutively dry summers.

A decrease in cover of the dominant perennial grasses may equate to enhanced degradation of ecosystem condition, including the reduction of productive capacity (Huenneke et al. 2002). The decrease of perennial grass cover also increases the relative dominance of woody vegetation in upland settings, and our results show that woody vegetation increases when winter precipitation exceeds 72–84 mm. Subshrubs (e.g., *Gutierrezia sarothrae*, *Ephedra trifurca*) were a more abundant woody vegetation component in perennial grasslands than shrubs, but their increase with winter precipitation marks an important shift in vegetation structure and demonstrates the importance of precipitation seasonality in influencing the balance of herbaceous and woody vegetation.

Dominant shrubland species and functional types

Despite the generalized relationship between winter precipitation and woody vegetation cover in upland grasslands, dominant shrubs varied in the degree to which their performance in shrublands was influenced by wet winters in the descending order: *Prosopis glandulosa* > *Flourensia cernua* > *Larrea tridentata*. *Prosopis glandulosa* is a leguminous shrub that has widely increased from being restricted to channels and playas to spreading across uplands in the Chihuahuan Desert since the mid-19th century (Buffington and Herbel 1965, Gibbens et al. 2005). There is support from our analysis that winter water availability may have influenced its expansion into grasslands. The shrub is extremely deep rooted (>5 m; Gibbens and Lenz 2001), allowing it to exploit subsurface water sources, maintain higher phototosynthetic rates, and remain physiologically active for a longer time during the growing season than more shallow-rooted species (Throop et al. 2011). *Flourensia cernua* also benefits from wet winters, but its stronger link to annual moisture conditions suggests that it additionally uses more summer precipitation than does *P. glandulosa*. This is supported by higher water potentials of *F. cernua* following experimental shallow water addition compared to the other two dominant shrubs (Montaña et al. 1995).

The change in cover of the drought-tolerant evergreen shrub *L. tridentata* showed no relationship to winter precipitation and instead was weakly explained by summer precipitation. Previous observational studies have shown that winter precipitation can be a driver of the abundance of this species across warm deserts in southwestern North America (Beatley 1974, Muldavin et al. 2008, Munson et al. 2012), while a long-term simulation found no relationship between *L. tridentata* and annual or seasonal precipitation across these warm deserts (Reynolds et al. 2004). Despite the results of other studies, summer precipitation comprises the largest proportion of total water input in the Chihuahuan Desert compared to other warm deserts, and *L. tridentata* has been shown to be physiologically responsive to summer precipitation (Reynolds et al. 1999). One study estimates that ~65% of the stem growth of *L. tridentata* in the Chihuahuan Desert is attributable to summer precipitation (Sponseller et al. 2012), in part due to its extensive system of fine roots in the top 30 cm of soil (Gibbens and Lenz 2001).

Our results demonstrate a regional signature of shrub species responses to climate in the Chihuahuan Desert, but changes in the intensity of livestock grazing and fire have likely also influenced the abundance and distribution of shrubs (Archer et al. 1995). Increases in CO_2 may interact with climate in the Chihuahuan Desert and in some cases increase the performance of shrub species (Scheiter and Higgens 2009), although increases in CO_2 do not necessarily confer a water-saving advantage to plants in desert ecosystems (Nowak et al. 2004).

PLATE 1. Repeat photographs looking southwest near a long-term black grama grassland quadrat taken in the early fall following (top) wet (302 mm precipitation in 2008) and (bottom) dry (93 mm in 2003) summers at the Jornada Experimental Range, New Mexico, USA. *Bouteloua eriopoda* (black grama) and *Sporobolus flexuosus* (mesa dropseed) are the dominant perennial grasses, and *Yucca elata* (soaptree yucca) is the dominant shrub. Photo credits: J. P. Anderson.

Subdominant grassland and shrubland species and functional types

Annual grasses and many annual forbs that co-occurred with dominant species in black grama and shrubland plant communities were also responsive to summer precipitation, in part due to their shallow root systems and C_4 photosynthetic pathways that allow for efficient uptake and retention of pulsed summer moisture. Although our study addressed mean seasonal precipitation, annual plant species are sensitive to the size and timing of precipitation within a season (Reynolds et al. 2004), which can stimulate germination and growth. Importantly, there was also a temporally distinct assemblage of predominantly C_3 annual forb species (e.g., *Eriogonum* spp.) that was sensitive to winter precipitation, which were underrepresented in this study because vegetation measurements occurred at the end of the summer growing season. Annual forb and grass species had large responses to changing climatic conditions in the Chihuahuan Desert compared to species of other functional types, and their high summer precipitation pivot points relative to the long-term summer precipitation mean of the plant communities in which they occurred demonstrate that they were the first functional groups to decline during the onset of drought. Similar to perennial grass species, annual grasses and forb species were sensitive to summer temperatures and the drought index. The importance of annual precipitation increased with forb longevity, which may be explained by perennial forbs having a longer window of time to be physiologically active and respond to water input than do annual forbs.

Perennial plants in the Chihuahuan Desert tolerate periods of water shortages and have adaptations that limit water loss, such as low leaf surface-to-volume ratios and low stomatal conductance. However, these adaptations also limit the rate of photosynthesis, a cost that likely explains the low response to precipitation of perennial relative to annual plants. A positive relationship between plant species responses and their pivot points in our study may confirm that a trade-off exists between growth rate and drought resistance across functional types in the Chihuahuan Desert, which is in contrast to findings of a study that only considered perennial grasses (Fernández and Reynolds 2000). A large change in cover between measurements indicates high growth rate, whereas a high precipitation pivot point suggests that the plant requires more water input to increase in cover (low drought resistance). Perennial forbs and grasses declined less than annuals as conditions became drier, but several of their pivot points overlapped with annual species and were greater than the long-term summer precipitation mean in the plant communities where they occurred, demonstrating a potential for shared species decline. The additional cost of producing and maintaining woody tissue partially explains why subshrub and shrub species had lower responses than perennial grasses and forbs. These woody species were able to maintain small, but positive increases in cover above summer precipitation pivot points at or below the long-term summer precipitation mean due to their deep roots and drought-tolerance adaptations.

The larger functional type (combined species) responses to summer precipitation in creosote bush shrublands compared to black grama grasslands may have been in part due to the canopy of *B. eriopoda* overlapping with subdominant species and the strong competitive ability of the grass (Báez and Collins 2008). In contrast, the canopy of *L. tridentata* generally does not overlap with subdominant species and can facilitate subdominant growth.

Species richness

Although changes in the cover of plant functional types in relation to summer precipitation was influenced by the plant community in which they occurred,

the relationship between changes in species richness and summer precipitation was not differentially affected by plant community. The responses and pivot points of species richness in relation to summer precipitation were similar across grasslands and shrublands in the Chihuahuan Desert. This was unexpected, given the importance of biotic interactions and plant–soil feedbacks in influencing plant species turnover (Báez and Collins 2008). The shared response and pivot point suggests a regional control on species turnover, such as grasslands and shrublands collectively being constrained by a regional species pool. Our results provide further support for this broad trend because many plant species and functional types had similar responses to the same climate variable across grasslands and shrublands. Congruous changes in species richness among plant communities indicate that an increased frequency of summer drought in the future may broadly decrease the number of species that the Chihuahuan Desert can support. This decrease may be further accelerated by the spread of nonnative plant species or intensification of land-use activity in the region (Bock et al. 1986).

Similar to changes in the cover of *B. eriopoda*, we found support in the data that the response of species richness to summer precipitation was nonlinear, with greater losses of species below 138–150 mm than gains above this pivot point. The pivot point for species richness is similar to the one that marked shared declines in cover of annual and several perennial plant species, suggesting a threshold amount of water input, below which the presence and performance of multiple species reduces. This shared pivot point is near the long-term summer precipitation mean across plant communities (148 mm), which suggests that plant species assemblages in the Chihuahuan Desert are the result of long-term mean resource availability. Sustained drought conditions below this amount of water input may cause a permanent shift in plant community composition and accelerate ecosystem degradation. Increases in species richness appeared to saturate with extremely high summer rainfall, perhaps due to the limitation of resources other than water, increased competition with dominant plants, or a reduced seedbank. Vegetation measurements in this analysis were made in the fall, but additional spring measurements at the Sevilleta reveal that ~50% of annual species reach peak biomass in the spring and that this component of species richness is related to winter precipitation (Xia et al. 2010).

Conclusions

The climate pivot point that we highlight in our study is an empirically derived metric that represents an important transition in how a species responds over a range of climatic conditions. Importantly, the climate pivot point can be used to help understand historical vegetation dynamics and forecast future species assemblages under different climate regimes. The pivot points we identified in our broad-scale analysis had considerable margins of error, in part due to the broad spatial extent of our study that led to averaging across site-specific growing conditions. Climate pivot-point estimates can be further refined with local-scale information on the specific geomorphic, edaphic, and biotic factors that affect plant water availability. The development of an ecosystem water-balance approach that considers these conditions or direct soil water monitoring would improve our ability to predict plant responses in arid regions.

Plant species and functional types responded to seasonal and annual drought and warming across the Chihuahuan Desert, which are climatic conditions similar to those predicted for the future. Perennial grasses were most responsive to summer precipitation, with the dominant *Bouteloua eriopoda* showing a nonlinear response. In contrast, high water input during cooler winter months can increase woody vegetation performance in upland grasslands and may contribute to increasing shrub dominance throughout much of the Chihuahuan Desert. Despite this general trend, shrubs varied in their sensitivity to winter water availability in shrublands in which they were dominant, with *Prosopis glandulosa* the most sensitive and *Larrea tridentata* the least sensitive. While we detected a regional signature of grass and shrub response to climate, factors that influence water availability at smaller spatial scales, in addition to increasing CO_2, nutrient availability, and land-use activities, are also potentially important drivers.

In accordance with trade-offs between growth rate and drought resistance, many annual forb and grass species in grasslands and shrublands had larger responses to summer precipitation than did dominant perennial grass and shrub species, but required greater water input to increase in cover. Species richness had a similar nonlinear relationship with summer precipitation across most grasslands and shrublands. Declines in species richness and reduced cover of many species below the long-term summer precipitation mean across plant communities may indicate a decrease in productivity for all but the most drought-tolerant perennial grasses and shrubs in the Chihuahuan Desert.

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Supplemental Material

Appendix A

A table describing long-term vegetation measurements (*Ecological Archives* E094-185-A1).

Appendix B

A table presenting ANCOVA results that relate the changes in cover of dominant plant species/functional types and climate variables by data set (*Ecological Archives* E094-185-A2).

Appendix C

A table summarizing hierarchical partitioning results that explain the changes in cover of plant species/functional types with year of measurement and climate variables (*Ecological Archives* E094-185-A3).

Appendix D

A table summarizing the support for linear and nonlinear models that relate the changes in cover of dominant plant species/functional types and climate variables (*Ecological Archives* E094-185-A4).

Appendix E

A table presenting long-term mean annual and seasonal precipitation and temperature of Chihuahuan Desert plant communities (*Ecological Archives* E094-185-A5).