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Decadal shifts in grass and woody plant cover are driven by prolonged drying and modified by topo-edaphic properties

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Abstract. Woody plant encroachment and overall declines in perennial vegetation in dryland regions can alter ecosystem properties and indicate land degradation, but the causes of these shifts remain controversial. Determining how changes in the abundance and distribution of grass and woody plants are influenced by conditions that regulate water availability at a regional scale provides a baseline to compare how management actions alter the composition of these vegetation types at a more local scale and can be used to predict future shifts under climate change. Using a remote-sensing-based approach, we assessed the balance between grasses and woody plants and how climate and topo-edaphic conditions affected their abundances across the northern Sonoran Desert from 1989 to 2009. Despite widespread woody plant encroachment in this region over the last 150 years, we found that leguminous trees, including mesquite (*Prosopis* spp.), declined in cover in areas with prolonged drying conditions during the early 21st century. Creosote bush (*Larrea tridentata*) also had moderate decreases with prolonged drying but was buffered from changes on soils with low clay that promote infiltration and high available water capacity that allows for retention of water at depth. Perennial grasses have expanded and contracted over the last two decades in response to summer precipitation and were especially dynamic on shallow soils with high clay that have large fluctuations in water availability. Our results suggest that topo-edaphic properties can amplify or ameliorate climate-induced changes in woody plants and perennial grasses. Understanding these relationships has important implications for ecosystem function under climate change in the southwestern USA and can inform management efforts to regulate grass and woody plant abundances.

Key words: aridity; climate change; desert; land degradation; shrub encroachment; Sonoran Desert; *Larrea tridentata*; *Prosopis* spp.

INTRODUCTION

The cover of grasses and woody plants in dryland regions can be highly dynamic at decadal timescales (Archer 1996). Woody plant encroachment into grasslands has been documented in many parts of the world (Archer et al. 1988, Aguiar et al. 1996, Brown and Carter 1998) and has important effects on ecosystem structure and function, including shifts in diversity (Ratajczak et al. 2012), changes in net primary production (Huenneke et al. 2002, Knapp et al. 2008), and alterations in ecohydrology (Kurc and Small 2004); although the magnitude and direction of these effects may depend on the specific site and traits of the woody plants (Eldridge et al. 2011). Grasses can spread rapidly into arid and semi-arid regions (D'Antonio and Vitousek 1992), accelerating fire and nutrient cycles, drawing down shallow soil moisture, and increasing herbivore diversity (Scholes and Archer 1997). Because grasslands, savannas, and shrublands

compose 30–35% of terrestrial net primary productivity (Field et al. 1998) and are inhabited by 38% of the global human population (MEA 2005), changes in the abundances and distributions of grasses and woody plants play a large role in the global carbon, nutrient, and water cycles (Schlesinger et al. 1996) and affect resources for human well-being.

Shifts in the cover of grasses and woody plants, and overall declines of both vegetation types, have strong implications for land management. Woody plant encroachment can limit livestock forage, and brush management efforts are frequently carried out to recover herbaceous components of rangelands (Archer and Predick 2014). Habitat functionality for wildlife can be largely modified by conversion from open grassland to relatively dense woody plant cover (Lloyd et al. 1998). This modification is especially important in the southwestern USA, which provides major flyways for migratory birds in primarily woody plant assemblages and supports a high diversity of overwintering birds in perennial grasslands, which are both actively managed habitats (Lloyd et al. 1998, Krueper et al. 2003). Woody plant encroachment

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and overall declines in perennial vegetation can lead to land degradation, including increases in soil erosion (Munson et al. 2011) and associated nutrient losses, which managers actively attempt to mitigate.

The causes of shifts in vegetation types remain controversial and have been attributed to local land management practices, including grazing by domestic livestock, alterations in fire frequency, and brush management (Archer et al. 1995). Changes in climate and increasing CO₂ can drive grass and woody plant dynamics at broader spatial scales (Brown et al. 1997, Smith et al. 2000). Less clear is how topographic and soil properties can affect the abundance of grass and woody plants through their influence on the spatial distribution and timing of water availability across dryland regions (McAuliffe 1994). For example, areas with shallow slopes and sandy soils may experience increased water availability through run-on and drainage, respectively, which can improve the condition of dryland vegetation (Munson et al. 2015). The influence of topo-edaphic properties can result in differential access of water to perennial grass and shrub species based on their rooting distributions (Walter 1971). Heterogeneity in topo-edaphic properties can also influence the magnitude and rate at which changes in the balance between grass and woody plant species occurs (Browning et al. 2008). Understanding how climate, soils, and topography broadly affect grass and woody plant abundance provides a baseline to which compare how management actions accelerate or deter compositional shifts at a more local scale. Determining the influence of these environmental variables is also critical to predict the magnitude and direction of compositional shifts under future climate change.

In the southwestern USA, woody vegetation, primarily creosote bush and mesquite, has encroached on arid and semi-arid grasslands over the last 150 years (Grover and Musick 1990, Van Aiken 2000). Both species have occurred in the region for over 4,000 years (Van Devender and Spaulding 1979), but according to surveys in the 1880s, were mainly restricted to drainages (mesquite) and foothills (creosote bush; York and Dick-Peddie 1969). Since that time, mesquite cover has more than doubled in southern Arizona (McClaran et al. 2003, 2010) and creosote bush has largely expanded its distribution throughout the southwestern USA (Grover and Musick 1990). Recent studies suggest that woody plants in uplands (disconnected from riparian areas and groundwater) of the southwestern USA have reached an upper limit or have slightly declined in the last couple of decades based on reductions in water availability of the region (Browning et al. 2008, Munson et al. 2012). The degree to which climate influences the abundance of grass and woody plants is particularly timely because the southwestern USA experienced extreme wet conditions in the early 1980s and subsequent dry conditions over much of the subsequent three decades. In southern Arizona, annual precipitation has decreased 25–40% from the early 1980s to 2009 (Fig. 1). This drying trend is enhanced

by large increases in temperature that have occurred throughout the regions since the 1970s (Weiss and Overpeck 2005). Understanding the influence of climate on vegetation dynamics within a soils and topography context can help resolve heterogeneity in the magnitude and direction of grass and woody cover changes across the region. This knowledge can inform land management practices targeted at promoting or maintaining a specific balance between grasses and woody plants in face of a rapidly changing climate.

Remote sensing data can be used to monitor decadal changes of grass and woody plant abundance in dryland ecosystems, including woody plant encroachment (Browning et al. 2008, Sankey and Germino 2008). However, assessing changes in different vegetation types in drylands remains a challenge because of sparse plant cover, spectral similarities among species, and bright soil backgrounds (Okin and Roberts 2004). Recent advancements in analyzing satellite imagery allow for the separation of vegetation types and species within image pixels (Xian et al. 2012a, Homer et al. 2015). We conducted an assessment of changes in grass and woody plant cover in the Sonoran Desert of southern Arizona from 1989 to 2009 using estimates generated by these remote sensing improvements. The Sonoran Desert is an ecosystem that has experienced widespread woody plant encroachment and is experiencing large changes in climate (Munson et al. 2012). Our primary objectives are to (1) determine where dominant woody plant species and perennial grasses have increased or decreased and (2) define the climate, soils, and topographic drivers of these changes.

METHODS

Study region

Our study region in southern Arizona includes two Landsat scenes from path 36, row 38 (centered on latitude 31.7470, longitude -111.3981) and path 37, row 38 (31.7470, -112.9431) that encompass Tucson, Arizona. Mean annual precipitation and the proportion of summer relative to winter precipitation increases from west to east across the study region (Sheppard et al. 1999). Plant community composition in uplands reflects this gradient of precipitation and ranges from communities dominated by creosote bush and white bursage (*Larrea tridentata*, *Ambrosia dumosa*, respectively) in the dry (<150 mm) western and low elevation reaches of the study region to Arizona Uplands dominated by leguminous paloverde trees (*Parkinsonia microphylla* and *P. florida*), shrubs (including creosote bush), and cacti at moderate precipitation (150–300 mm), and perennial grasslands and leguminous mesquite (*Prosopis velutina*) savannas in the wettest (>300 mm) eastern portion of the study region. In xeroriparian corridors, there is also relatively high (>30%) cover of mesquite species in the eastern part of the region and paloverde species in the western part of the

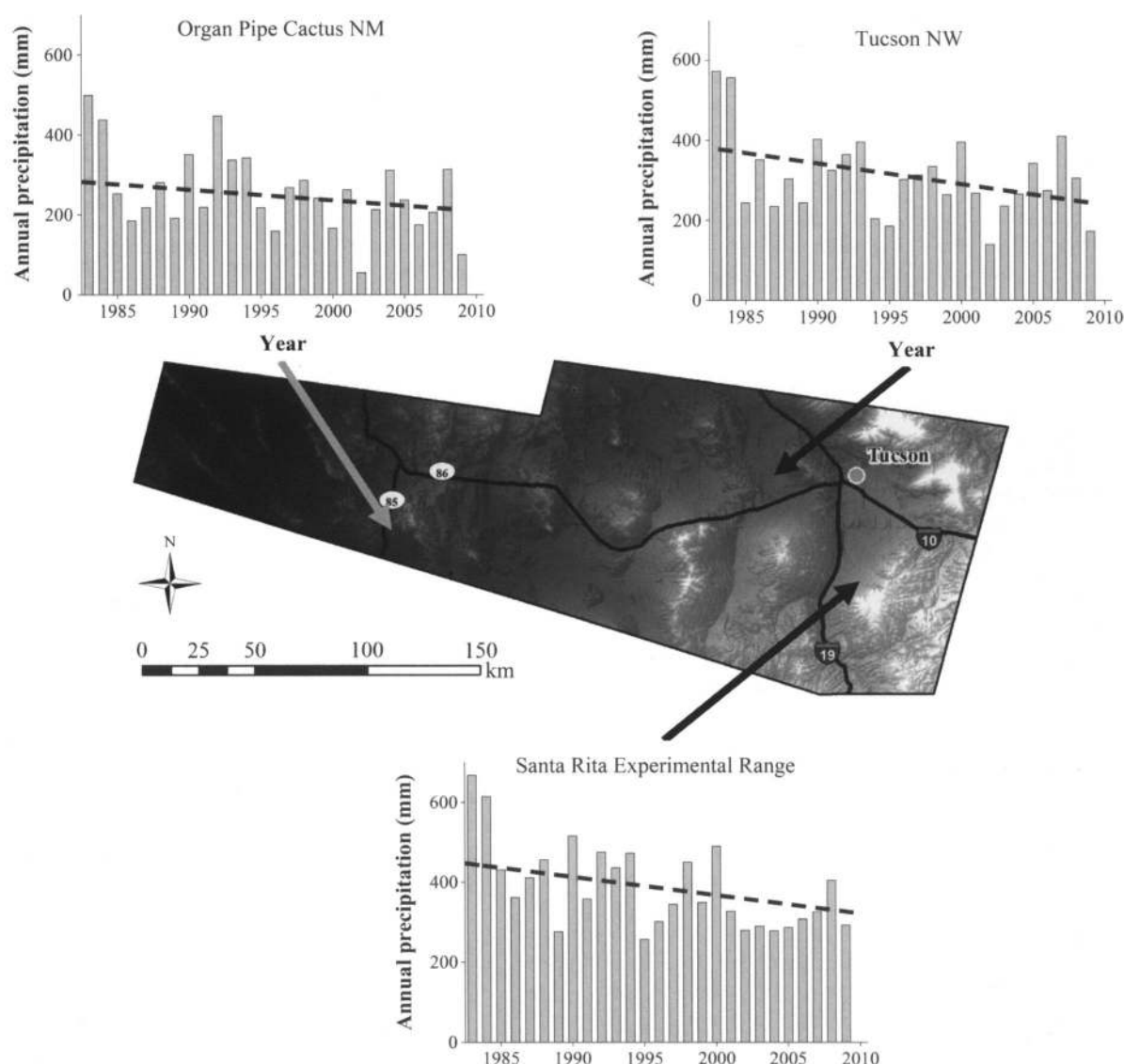


FIG. 1. Annual precipitation across three sites in southern Arizona shows a drying trend from the early 1980s to 2009. The dashed line is a linear regression of annual precipitation (all $P < 0.05$).

region (Warren and Anderson 1985). Soil texture and depth are highly variable across the study region due to different parent materials, ages of the surface, and complex topography (McAuliffe 1994). The study region has experienced numerous land uses, including livestock grazing, dryland cropping, urban growth, and mining (Bahre 1995).

Image classification

We acquired Landsat Thematic Mapper images from both path 36 and 37 in 1989, 1995, 1999, 2005, and 2009 for June and September of each year (except in 2009, when we used a July image in path 37 due to cloud cover in the June image). The acquisition of imagery at this time accounted for the initial green-up to peak greenness of

vegetation associated with precipitation from the North American Monsoon in the Sonoran Desert (Kurc and Benton 2010). All Landsat images were first standardized to at-satellite reflectance using the Multi-Resolution Land Characteristics Consortium image protocol (Chander et al. 2009). Following a previously developed approach (Xian et al. 2012b), the at-satellite reflectance images were further normalized to reduce the effects of seasonal phenology and atmospheric conditions between the image dates. In this approach, a linear regression algorithm relates each pixel of each spectral band in a subject image to a reference image to achieve normalization values. Applying these values minimizes the differences between the subject image and the reference image for pixels that do not experience either abrupt or gradual changes. The images from 1989, 1995, 1999, and 2005

TABLE 1. Cross-validation of regression models for different vegetation types in each Landsat scene of the baseline year 2009.

Vegetation type	Path 36, row 38				Path 37, row 38			
	<i>N</i>	Average error	Relative error	<i>R</i>	<i>N</i>	Average error	Relative error	<i>R</i>
Perennial grasses	947	8.6	0.70	0.66	858	2.9	0.39	0.87
Creosote bush	1,244	1.7	0.36	0.86	843	2.9	0.71	0.67
Leguminous trees	1,331	9.3	0.43	0.80	1,124	6.0	0.30	0.90

Note: *N* is the number of field measurement training samples and *R*, Pearson's correlation coefficient.

were normalized to the 2009 baseline images. Normalized and reference images from the same month were then used to calculate a change vector image that represented spectral feature differences and potential vegetation changes between the image years (Xian et al. 2012b).

In all of the Landsat images, we estimated sub-pixel cover of three vegetation types: perennial grasses, creosote bush, and leguminous trees (mesquite and paloverde). Between 843 and 1,331 field measurements of cover for each vegetation type were made between 2007 and 2011 for each Landsat scene inside 100-m² plots and used for classification training for the baseline image in 2009. Measurement locations that had clouds and shadows in the imagery were excluded from the training dataset. All field measurement polygons were converted to a raster format in 30-m resolution to match the Landsat image pixels. These rasterized training pixels were then used to create regression tree models. Covers of the three different vegetation types in the training samples were the dependent variables in the models, while the Landsat image pixels and ancillary data, including elevation and slope, were the independent variables. These models were created using the partitioning algorithm Cubist (Quinlan 1993), which built trees by recursively splitting the training samples into smaller subsets and producing a set of rules for predicting a target variable (e.g., percent cover of perennial grasses).

After a model was produced for each vegetation type with the use of the training polygons for the baseline year 2009, the model was extrapolated to calculate cover of each vegetation type in each pixel for the entire study region. These sub-pixel estimates in the baseline image and the change vector images from the earlier years were then differenced to estimate the vegetation type cover for those image dates (Xian et al. 2012b). In this procedure, the unchanged pixels in the subject images containing all ranges of cover of each vegetation type were used as a training dataset. The image differencing then quantified only the changed areas for a given image pair. The image pairs used in this procedure included 1989–1999 and 1999–2009 to estimate changes in cover for all vegetation types, and the additional pairs 1989–1995, 1995–1999, 1999–2005, and 2005–2009 for perennial grasses, which were expected to change more rapidly than woody plants. We used this procedure separately for the two Landsat scenes for each image date, then mosaicked cover estimates for the two scenes and adjusted differences using an edge matching approach. We then applied a mask to eliminate areas >1,500 m in elevation, and urban,

agricultural, roadway, and water body areas defined by the National Land Cover Database (*available online*) because our models were calibrated for low elevation native plant communities.⁶

Accuracy assessment

Historical field measurements collected on the image acquisition dates are the ideal way to validate regression tree modeling results, but these were not available for accuracy assessment. Instead, a model cross-validation strategy was employed to assess the classification results. The cross-validation strategy used 10% of training datasets to analyze model performance using the average error, relative error, and the Pearson's correlation coefficient. We used the average of each of these three parameters to evaluate the performance of regression tree models in the baseline year using a 10-fold cross-validation strategy (Table 1). Generally, model performance was relatively high to estimate leguminous tree cover ($r = 0.80$ – 0.90) in both paths. Models performed better to estimate creosote bush cover in path 36 ($r = 0.86$) and perennial grasses ($r = 0.87$) in path 37 than in the other paths ($r = 0.66$ – 0.67). The model performances for cover estimates prior to 2009 were similar to those in the baseline year.

Environmental variables

We acquired soil properties related to plant water availability from the NRCS State Soil Geographic (STATSGO) Database (*available online*) and derived topographic slope from the National Elevation Dataset (*available online*).^{7,8} The soil properties included available water holding capacity (0–0.25, 0.25–0.50, and 0.50–0.75 cm³ water/cm² of soil), which is the difference between soil moisture content at field capacity and permanent wilting point; percentage of clay (0–10%, 10–20%, 20–30%, and 30–40%), which is the amount of soil that has a particle size <0.002 mm; and soil depth (0–30 cm, 30–60 cm, and >60 cm), the maximum depth recorded or depth to bedrock. We used the representative mean value of soil properties in each sample polygon. Topographic

⁶ <http://www.mrlc.gov>
⁷ <http://websoilsurvey.nrcs.usda.gov>
⁸ <http://ned.usgs.gov>

slope included shallow (0–10%) and steep (>10%) landscape positions.

We extracted annual precipitation (January–December) from PRISM from 1980 to 2010 at a 4 km resolution (*available online*).⁹ We then calculated the average annual precipitation within 5-yr and 10-yr intervals that matched the intervals for perennial grass and woody vegetation changes, respectively. For 10-yr intervals, the temporal trend of precipitation for each pixel was analyzed using the Mann-Kendall (MK) non-parametric test. The MK tau (τ) coefficient (Neeti and Eastman 2011) ranges from -1 to 1 and was used to assess an upward (positive coefficient) or downward (negative coefficient) trend of precipitation through time. A MK τ coefficient near 0 indicates absence of a trend. Pixels with significantly ($P < 0.05$) negative MK tau coefficients in precipitation were classified as areas impacted by a drying trend, while all other pixels were classified as unimpacted (there were no significantly positive MK tau coefficients). Due to the relatively short 5-yr time interval for perennial grasses, we did not use a MK test for trend of precipitation (a minimum of eight years is recommended for the MK test). Instead, we compared the average annual precipitation at 5-yr intervals to the 30-yr (1980–2010) mean and used whether precipitation fell above or below the mean as a categorical variable. Because we expected changes in perennial grass cover to be related to summer (July–September) precipitation (McClaran et al. 2003), we also determined whether summer precipitation at 5-yr intervals was above or below the 30-yr mean summer precipitation and used it as a categorical variable. Although land-use activities also influence changes in grass and woody plant cover, we minimized many of their effects with our masking procedure (described previously) and focused instead on the importance of climate and topo-edaphic properties.

Change in cover of vegetation types and their relationship to environmental variables

We examined the classified images in pairs of consecutive time intervals for pixel-by-pixel comparisons to estimate vegetation type cover changes across the entire study region. We calculated change in cover at 5-yr intervals (1989–1995, 1995–1999, 1999–2005, and 2005–2009) for perennial grasses and 10-yr intervals (1989–1999 and 1999–2009) for leguminous trees and creosote bush, which are both long-lived. To account for the error in our regression models, we removed cover values that were below the average error determined from our accuracy assessment. We produced regional cover change maps of each vegetation type showing increases, decreases, and no change in pixels between consecutive time intervals. We then calculated the net change between areas experiencing increases and decreases in cover of each vegetation type and used a t test on a random sample

of 1,500 pixels of each vegetation type to determine if the net change was significantly different from zero.

To relate changes in cover of vegetation types to environmental variables at the landscape-scale, we generated 1,000 square polygons within the Landsat scenes. Each polygon was randomly generated to avoid spatial autocorrelation and included 100 pixels (10×10 pixels = 8.12 ha). To account for error in our cover estimates and to minimize the effects of propagating error when relating cover to environmental variables, we binned cover for each of the three vegetation types into classes of 10%: 0–10%, 10–20%, etc. We then determined if the cover class of a vegetation type increased, decreased, or had no change between consecutive time intervals for each pixel. The percent of pixels falling into the categories of increase, decrease, and no change in cover within each polygon was used as the response variable to relate to the environmental variables.

Statistical analysis

We tested if increases and decreases of cover within each sample polygon (response variables) were different among categories of environmental predictor variables sampled at the polygon center using analysis of variance (ANOVA). Changes in cover of each vegetation type at each time interval were analyzed using separate ANOVAs. Environmental variables included precipitation, topographic slope, and soils properties (depth, percentage of clay, available water holding capacity). We also included the interactions between precipitation and slope, and precipitation and soil properties, because water availability in dryland ecosystems is a function of climate mediated by site physical attributes. When an environmental variable or interaction had a significant effect ($P < 0.05$) on change in cover, we performed pair-wise post hoc comparisons among environmental variable categories using a Tamhane's test with a Bonferroni correction. Although we included all environmental variables and their interactions as predictors in our analyses, we only report those which were significantly related to change in cover of each vegetation type in each time interval.

RESULTS

Leguminous trees

From 1989 to 1999, the vegetation change detection analysis indicated that leguminous trees increased on 314,106 ha (25.8% of leguminous tree range) and decreased on 255,567 ha (21.0%; Fig. 2a; Appendix S1), resulting in a net increase ($P < 0.0001$; Fig. 3). Soil depth had a significant ($P = 0.01$; Table 2) effect on decreases of leguminous trees, with locations of 30–60 cm soil depth having marginally greater decreases than locations >60 cm depth (Bonferroni-adjusted $P = 0.07$). The soil depth interaction with the 1980s (1980–1989) precipitation trend had a significant effect on increases of

⁹<http://www.prism.oregonstate.edu>

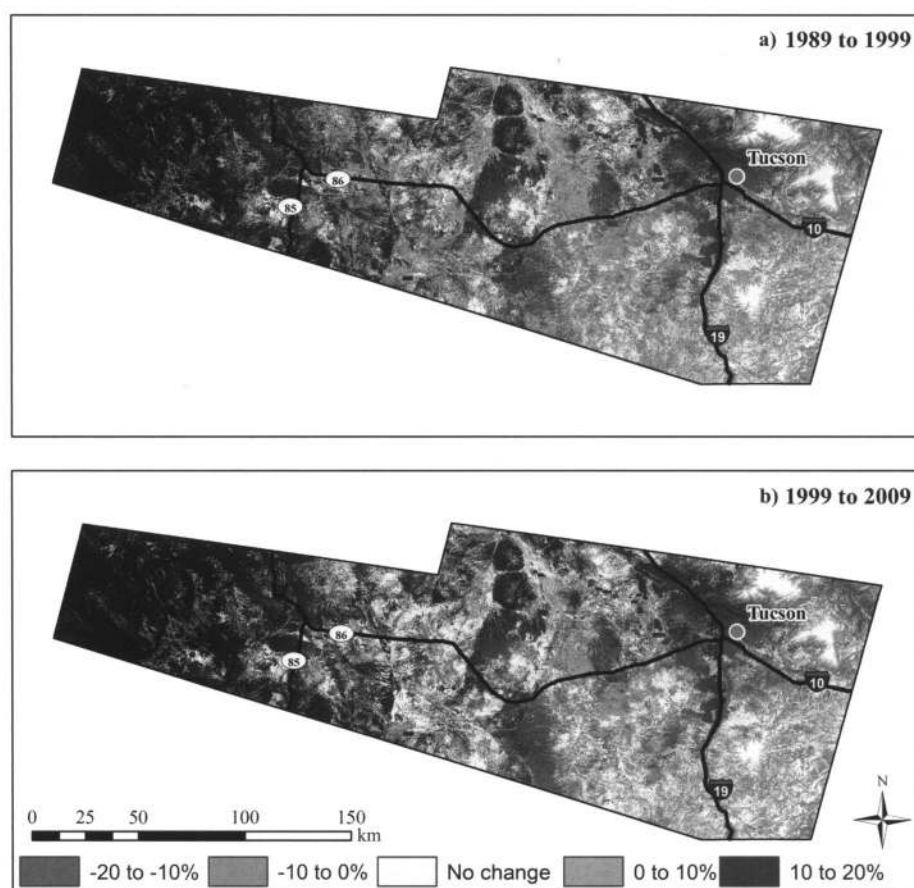


FIG. 2. Increases, decreases, and no change of leguminous trees from (a) 1989 to 1999 and (b) 1999 to 2009 in southern Arizona.

leguminous trees ($P = 0.02$) such that increase was significantly lower on shallow soils (0–30 cm) experiencing a drying trend compared to unimpacted areas (Fig. 4a). The significant interaction was also associated with greater leguminous tree increase on deep soils (>60 cm) experiencing a drying trend compared to unimpacted areas. Furthermore, the 1980s precipitation trend interaction with topographic slope had a significant effect on increases of leguminous trees ($P = 0.02$), such that increase on shallow slopes was significantly lower in areas experiencing a drying trend compared to unimpacted areas (Bonferroni-adjusted $P = 0.04$).

From 1999 to 2009, leguminous trees increased on 146,933 ha (12.9%) and decreased on 221,170 ha (19.4%; Fig. 2b), resulting in a net decrease ($P < 0.0001$; Fig. 3). Soil depth was again significant ($P = 0.03$; Table 2), with greater leguminous tree decline associated with areas that have 0–30 cm soil depth. The soil depth interaction with 1980s precipitation trend had a marginally significant effect on leguminous tree decreases ($P = 0.08$), such that areas with 0–30 cm soil depth that experienced a drying trend over the 1980s had greater leguminous trees decreases than unimpacted areas (Bonferroni-adjusted $P = 0.03$). Furthermore, the 1990s (1989–1999)

precipitation trend was marginally significant for leguminous tree decreases ($P = 0.05$) and in its interaction with soil depth ($P = 0.07$). Leguminous tree decrease was significantly greater on shallow soils in unimpacted areas compared to areas experiencing a drying trend over this decade (Bonferroni-adjusted $P = 0.01$). Although a majority of the sample polygons ($N = 520$) were in areas not impacted by a drying trend over the 1990s, approximately a quarter of the unimpacted areas were impacted by a drying trend in the previous decade, indicating a lag effect.

Creosote bush

From 1989 to 1999, creosote bush increased on 251,816 ha (14.0% of creosote bush range), while it decreased on 345,406 ha (19.2%; Fig. 5a; Appendix S1), resulting in a net decrease ($P < 0.001$; Fig. 3). Soil depth was marginally significant ($P = 0.08$) for explaining creosote bush decrease. There was a significant interaction between the 1980s precipitation trend and soil depth on creosote bush decreases ($P = 0.02$; Table 3), such that areas experiencing a drying trend with a soil depth of >60 cm had significantly greater decreases compared to

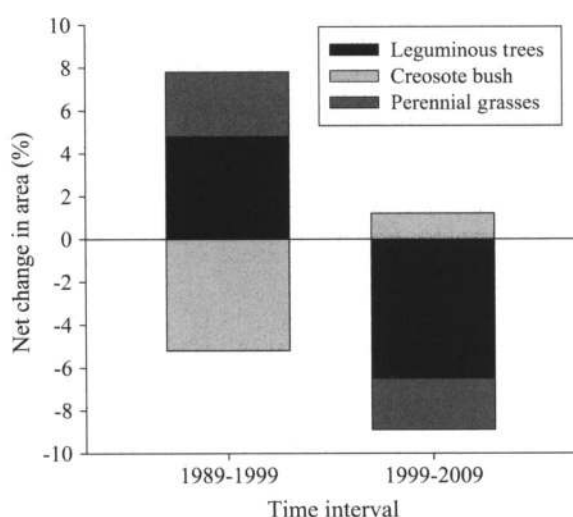


FIG. 3. Net change between areas experiencing increases and decreases of leguminous trees, creosote bush, and perennial grasses from 1989 to 1999 and 1999 to 2009 in southern Arizona ($P < 0.01$ for all net changes).

the same soil depths in unimpacted areas (Fig. 4b). Creosote bush increase was significantly lower in areas that had high clay content (20–30% and 30–40%) compared to areas with low clay content (0–10% and 10–20%; Bonferroni-adjusted $P = 0.001$).

From 1999 to 2009, creosote bush increased on 222,720 ha (12.4%) and decreased on 201,704 ha (11.2%; Fig. 5b), resulting in a slight net increase ($P < 0.001$; Fig. 3). The 1980s precipitation trend with soil depth interaction had marginally significant effects on creosote bush increases ($P = 0.07$; Table 3), such that areas with a soil depth of 0–30 cm unimpacted by drying had a tendency for greater increases compared to areas experiencing a drying trend (Bonferroni-adjusted $P = 0.08$). The 1990s precipitation trend interaction with slope had a significant effect on increases of creosote bush

($P = 0.03$). Creosote bush increases tended to be greater in areas with steep slopes unimpacted by drying compared to areas with steep slopes experiencing drying trends (Bonferroni-adjusted $P = 0.08$). Over this decade, soil available water-holding capacity (AWC) was also important for creosote bush decreases, as there was a significantly greater decline at sites with low (0–0.25 cm) relative to high (0.50–0.75 cm) AWC (Bonferroni-adjusted $P = 0.02$; Table 3).

Perennial grasses

From 1989 to 1995, perennial grasses increased on 236,735 ha (19.2% of perennial grass range) and decreased on 180,673 ha (14.6%; Fig. 6a; Appendix S1). The summer precipitation anomaly and soil depth over this time interval were significant predictor variables for grass increases and decreases (all $P < 0.05$; Table 4). Grass increases were significantly greater on shallow soils of 0–30 cm depth compared to areas of 30–60 cm soil depth (Fig. 4c; lacking sufficient data to evaluate changes in perennial grass cover on deep >60 cm soils), especially where there was above average summer precipitation on low clay content soils (Bonferroni-adjusted $P < 0.001$). Grass decreases, however, were significantly greater only on shallow soils of 0–30 cm depth compared to soils of 30–60 cm depth where there was below average summer precipitation (Bonferroni-adjusted $P < 0.0001$).

From 1995 to 1999, perennial grasses increased on 223,652 ha (18.2%) and decreased on 228,187 ha (18.6%; Fig. 6b). Summer precipitation significantly explained both grass increases and decreases ($P < 0.001$ and 0.002, respectively; Table 4). Soil depth alone and in an interaction with summer precipitation and clay content explained increases and decreases in perennial grasses (all $P < 0.001$). Perennial grass increases were significantly greater in areas with shallow soils of 0–30 cm depth and 0–10% clay, where there was greater than average summer precipitation (Bonferroni-adjusted $P < 0.0001$) compared

TABLE 2. Effects of environmental variables on increases and decreases of leguminous tree cover at different time intervals as determined from ANOVA tests.

Time interval	Environmental variable	Response variable	df	Error df	MS	F	P
1989–1999	Soil depth	increase	2	864	287.45	0.88	0.18
		decrease	2	864	650.35	1.16	0.01
	1980s precipitation × soil depth	increase	2	866	628.31	3.80	0.02
		decrease	2	866	87.19	0.69	0.50
	1980s precipitation × slope	increase	2	866	650.51	3.94	0.02
		decrease	2	866	161.73	1.28	0.28
1999–2009	1990s precipitation	increase	1	869	41.67	0.54	0.46
		decrease	1	869	1,288.91	3.80	0.05
	Soil depth	increase	1	868	18.99	0.24	0.62
		decrease	1	868	1,568.13	4.62	0.03
	1980s precipitation × soil depth	increase	2	868	77.95	0.34	0.72
		decrease	2	868	339.13	2.53	0.08
	1990s precipitation × soil depth	increase	5	865	35.73	0.49	0.81
		decrease	5	865	685.49	2.03	0.07

Notes: Only environmental variables with significant main and interaction effects are shown. MS is mean square, and df, degrees of freedom.

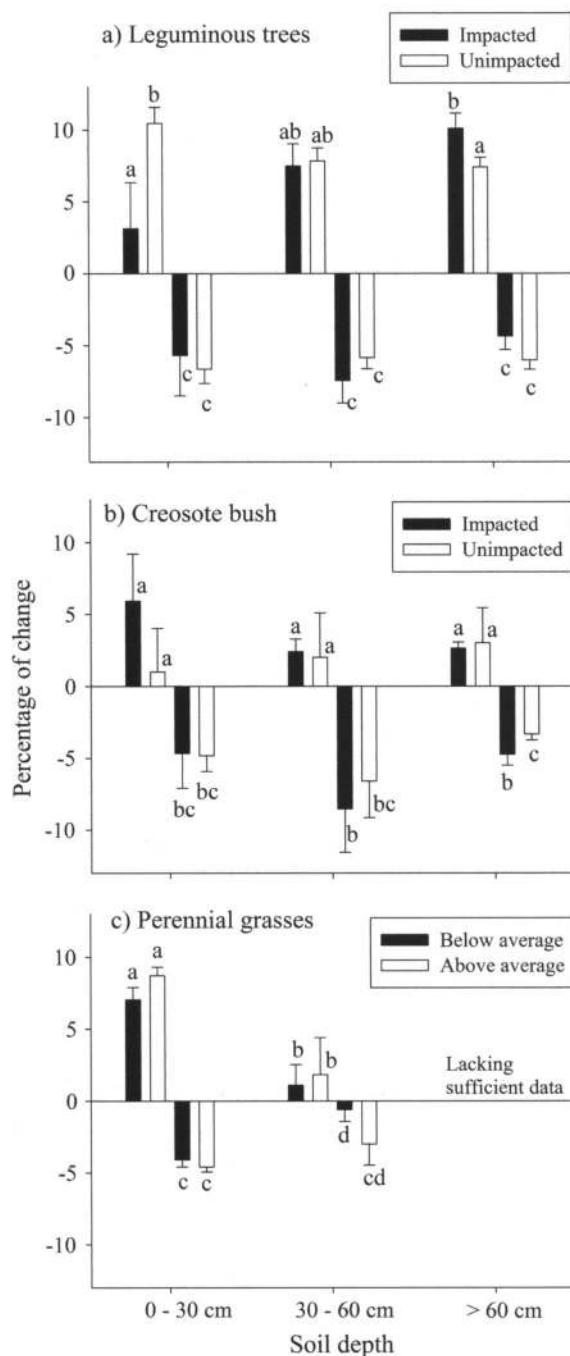


FIG. 4. Mean increases and decreases (\pm SE) of (a) leguminous trees from 1989 to 1999, (b) creosote bush from 1989 to 1999, and (c) perennial grasses from 1989 to 1995 on three soil depths as determined from sample polygons within Landsat scenes. For leguminous trees and creosote bush, changes in cover by soil depth are shown in areas experiencing a drying trend (from 1980 to 1989; black bars) and unimpacted areas (normal annual precipitation from 1980 to 1989; white bars), and for perennial grasses, changes in cover by soil depth are shown in areas experiencing below (black bars) and above (white bars) average summer precipitation. Different letters indicate significant (Bonferroni-adjusted $P < 0.05$) differences in the percent change of vegetation types.

to other areas. Perennial grass decrease was significantly greater on shallow soils of 0–30 cm, where summer precipitation was below compared to above average (Bonferroni-adjusted $P < 0.0001$).

From 1999 to 2005, perennial grasses increased on 214,118 ha (17.8%) and decreased on 213,621 ha (17.7%; Fig. 6c). Both summer precipitation and annual precipitation from this 5-yr interval were lower than the 30-yr mean across the entire study region, so there was no categorical analysis of precipitation above vs. below the 30-yr mean. Instead, we found that perennial grass decreases were related to the magnitude of annual precipitation below the 30-yr mean ($P = 0.001$). Soil depth interacted with summer precipitation such that there were significantly greater grass decreases on shallow soils of 0–30 cm depth in areas that experienced large summer precipitation shortfalls compared to areas that experienced above average summer precipitation (Bonferroni-adjusted $P < 0.0001$).

From 2005 to 2009, perennial grasses increased on 131,625 ha (10.9%) and decreased on 153,145 ha (12.7%; Fig. 6d). Increases in perennial grasses were significantly greater in areas with high summer precipitation, soil depth of 0–30 cm, and high clay content $>20\%$ compared to other areas (Bonferroni-adjusted $P = 0.001$).

Changes in perennial grasses at the longer decadal time interval consisted of net increases from 1989 to 1999 ($P = 0.003$) and net decreases from 1999 to 2009 ($P < 0.0001$; Fig. 3; Appendix S1 and S2). Unlike the two woody vegetation types, we found that the 1980s and 1990s precipitation trends did not explain changes in perennial grass cover over the longer decadal time interval ($P > 0.05$).

Balance between woody plants and perennial grasses

Across southern Arizona, there were overall net increases in leguminous tree and perennial grass cover from 1989 to 1999 and net decreases from 1999 to 2009, whereas creosote bush had changes that were in the opposite direction of perennial grasses in both decades ($P < 0.01$ for all net changes; Fig. 3). When we examined whether there were spatial relationships between changes in leguminous tree and grass cover, and creosote bush and grass cover, at the scale of individual pixels, there was only a positive relationship between changes in leguminous tree and grass cover from 1999 to 2009 ($r = 0.31$, $P < 0.05$), while all other relationships were not significant ($P > 0.05$; Appendix S3).

DISCUSSION

Leguminous trees

Mesquite encroachment has been widely documented across the southwestern USA over the last century (Archer et al. 1995). Although mesquite continued to

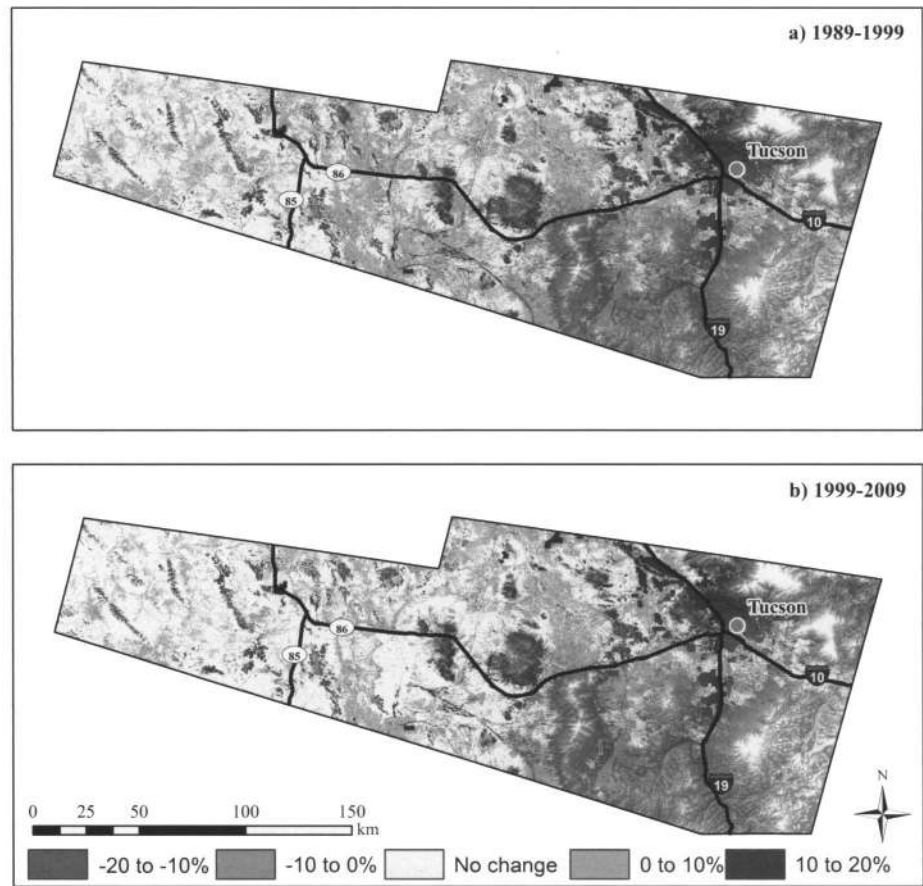


FIG. 5. Increases, decreases, and no change of creosote bush from (a) 1989 to 1999 and (b) 1999 to 2009 in southern Arizona.

have a net increase across the study region from 1989 to 1999, our analysis reveals that this widespread increase in a dominant woody plant might be changing in areas with water deficit. Repeat photography and field visits confirm that leguminous tree declines from 1999 to 2009 in the central and eastern portions of the study region are attributable to mesquite (Villarreal et al. 2013). Even in

areas where leguminous tree cover increased from 1989 to 1999, these changes were significantly lower in areas experiencing a drying trend and on shallow (0–30 cm) soils. Leguminous tree decreases from the 1999 to 2009 time interval were observed in areas with shallow soils, especially in areas that were impacted by a drying trend over the previous decade. Mesquite is generally a

TABLE 3. Effects of environmental variables on increases and decreases of creosote bush cover at different time intervals as determined from ANOVA tests.

Time interval	Environmental variable	Response variable	df	Error df	MS	F	P
1989–1999	Soil depth	increase	2	868	66.99	1.38	0.25
		decrease	2	868	261.95	2.52	0.08
	Clay	increase	3	867	266.72	5.60	0.00
		decrease	3	867	73.09	0.70	0.55
	1980s precipitation × soil depth	increase	2	868	107.78	2.23	0.11
		decrease	2	868	381.27	3.67	0.02
1999–2009	1980s precipitation × soil depth	increase	2	868	207.7	2.69	0.07
		decrease	2	868	83.17	1.59	0.20
	1990s precipitation × slope	increase	2	868	258.56	3.35	0.03
		decrease	2	868	36.69	0.70	0.49
	AWC	increase	1	869	10.49	0.13	0.71
		decrease	1	869	276.8	5.32	0.02

Notes: Only environmental variables with significant main and interaction effects are shown. MS is mean square, df is degrees of freedom, and AWC is available water-holding capacity.

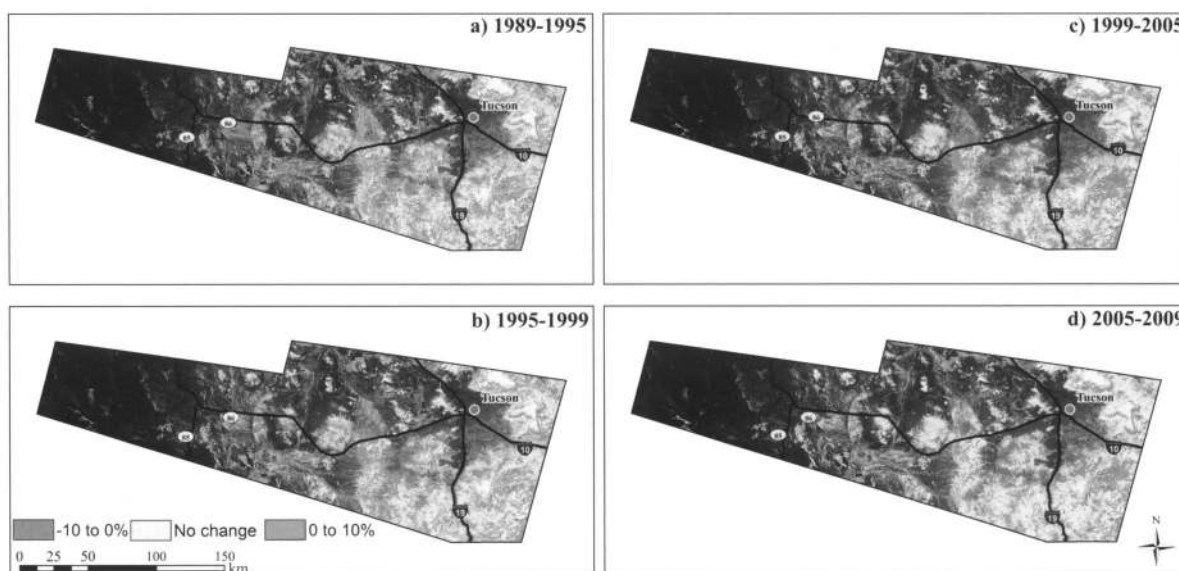


FIG. 6. Increases, decreases, and no change of perennial grasses from (a) 1989 to 1995, (b) 1995 to 1999, (c) 1999 to 2005, and (d) 2005 to 2009 in southern Arizona.

deep-rooted (>5 m) species and drought does not necessarily affect its growth when it occurs on deep soils. However, our results indicate that mesquite can be susceptible to increasing dryness in areas of exposed bedrock and where restrictive layers are close to the surface because water movement and root growth may be limited (Eggemeyer and Schwinning 2009). Soils with shallow restrictive layers may also keep water near the soil surface, where it is susceptible to evaporative losses. Consistent with our findings, paloverde has been found to be susceptible to decline with drought, especially among older, larger trees that occur on steep slopes on bedrock or shallow soils (Bowers and Turner 2001). The response of leguminous trees to precipitation shortfalls can be exacerbated by increasing temperatures, which were found to negatively influence the cover of both mesquite and paloverde in southern Arizona (Munson et al. 2012).

Our results further indicate that areas with shallow soils that did not experience significant drying trends from 1999 to 2009 continued to lose leguminous tree cover from increasing dryness experienced in the previous decades. The sustained drought impact on mesquite and paloverde populations lagging at a decadal time scale is particularly interesting because it suggests that many of the areas impacted by the particularly intense drought from 2002 to 2003 may continue to decline through 2020. This sustained impact of drying on woody plants may reduce the need for prescribed burning or cutting, which are both used in brush management operations.

Regardless of the time vegetation is affected, the reduction in leguminous tree cover in areas affected by water deficit in southern Arizona may be more widespread than our study region, including other parts of the Southwest that have been encroached by woody vegetation over the last several

decades. This slowing down of encroachment is likely attributable to a carrying capacity of woody plant populations imposed by water limitation (Browning et al. 2008). If reductions in leguminous tree cover in drying areas result in mortality, there may be large shifts in carbon storage, decreases in evapotranspiration and albedo, and increases in runoff with feedbacks to the regional climate (Scholes and Archer 1997).

The declines in leguminous tree cover along ephemeral flowing streams are particularly noteworthy, including the San Simon, Vamori, and Brawley Washes (south-central portion of Fig. 2b). Although record high streamflows occurred in the early 1980s, there have generally been declines since then, and this reduced amount is largely claimed for agricultural irrigation (ADWR 2009). Mesquite can use groundwater and can be invariant to climate in xeroriparian settings (Barron-Gafford et al. 2012). However, declines in groundwater and ephemeral water flow have historically resulted in declines of leguminous tree and other riparian vegetation along some rivers and tributaries in the region (Webb et al. 2007, Villarreal et al. 2013). This contraction of riparian vegetation reduces habitat for wildlife and corridors for migration, including deterioration of flyways for birds (Krueper et al. 2003). Although composing a relatively small part of the landscape, riparian areas are critical for a large number of breeding birds of the southwestern USA and declines in riparian vegetation likely affect these avian populations.

Creosote bush

Drying impacts on creosote bush are important because the shrub is a drought-tolerant evergreen that can maintain or increase cover during periods of low

TABLE 4. Effects of environmental variables on increases and decreases of perennial grass cover at different time intervals as determined from ANOVA tests.

Time interval	Environmental variable	Response variable	df	Error df	MS	F	P
1989–1995	Summer precipitation	increase	1	791	1,580.5	9.37	0.00
		decrease	1	791	339.47	6.13	0.01
	Soil depth	increase	2	789	2,768.92	16.78	0.00
		decrease	2	789	436.16	8.00	0.00
	Soil depth × summer precipitation	increase	3	789	1,588.22	9.63	0.00
		decrease	3	789	371.46	6.82	0.00
	Soil depth × clay × summer precipitation	increase	13	779	524.12	3.18	0.00
		decrease	13	779	136.84	2.51	0.00
1995–1999	Summer precipitation	increase	1	791	2,989.1	17.78	0.00
		decrease	1	791	901.27	9.36	0.00
	Soil depth	increase	1	790	3,281.11	16.78	0.00
		decrease	1	790	1,881.77	8.00	0.00
	Soil depth × summer precipitation	increase	2	790	3,135.11	19.10	0.00
		decrease	2	790	1,391.52	14.81	0.00
	Soil depth × clay × summer precipitation	increase	8	784	933.81	5.70	0.00
		decrease	8	784	416.56	4.43	0.00
1989–1999	Soil depth	increase	2	865	419.68	3.17	0.04
		decrease	2	865	34.19	0.35	0.70
	Clay	increase	3	867	468.45	3.53	0.01
		decrease	3	867	128.82	1.33	0.26
1999–2005	Annual precipitation	increase	1	164	175.07	0.97	0.59
		decrease	1	164	195.46	1.56	0.00
	Soil depth	increase	1	791	486.94	2.77	0.09
		decrease	1	791	3,808.45	21.60	0.00
2005–2009	Soil depth × summer precipitation	increase	2	790	138.63	0.78	0.45
		decrease	2	790	3,663.77	21.29	0.00
	Summer precipitation	increase	1	791	2,138.6	18.25	0.00
		decrease	1	791	151.04	0.91	0.34
2005–2009	Soil depth × clay × summer precipitation	increase	9	783	361.02	3.08	0.00
		decrease	9	783	97.29	0.58	0.80
1999–2009	N.S.	N.S.

Notes: Only environmental variables with significant main and interaction effects are shown. No significant (N.S.) effects of environmental variables were found for perennial grass cover changes from 1999 to 2009. MS is mean square, and df is degrees of freedom.

water availability (Munson et al. 2015). Our results of declines of creosote bush cover in the western portion of the study region is consistent with a Sonoran-Mojave Desert survey in 2003, which attributed creosote bush decline to intense drought in the preceding years (McAuliffe and Hamerlynck 2010). Other shrub species that co-occur with creosote bush in the region showed much higher rates of decline across the desert at the turn of the 21st century, and their shared responses indicate the severity and duration of the drought (Bowers 2005, McAuliffe and Hamerlynck 2010).

Soil properties were important on their own and in their interaction with the 1980s and 1990s precipitation trends in explaining changes in creosote bush cover. This deeply rooted shrub had dampened increases on fine-textured soils and was buffered from declines when it occurred on soils with high available water capacity. These results are consistent with findings that show how coarse-textured soils with high water storage can promote creosote bush growth (McAuliffe 1994) by allowing infiltration and retention of water at depth, where it is not lost to high atmospheric demand in the Sonoran Desert. Coarse-textured soils have also been shown to promote more rapid woody plant encroachment and support higher woody cover than fine-textured soils (Browning et al. 2008).

A drying trend from 1989 to 1999 resulted in greater decreases in creosote bush on deep soils in the same decade and less increases on shallow soils in the following decade (1999–2009) relative to areas unimpacted by the drying trend. The former result contradicts findings that show that a lack of subsurface horizons can enhance the amount of water availability and increase shrub growth (McAuliffe 1994), but sustained drying conditions across the region may have exceeded this buffering capacity. The latter result suggests a lagged effect of drying that can limit the recovery of creosote bush in soils that already have restricted water movement. Creosote bush also increased less in areas experiencing drying trends on steep slopes. While we tracked changes in creosote bush cover in this study, McAuliffe (1994) noted high mortality on side slopes compared to level areas in the Tucson Mountains. This influence of slope on creosote bush may be attributable to high levels of water runoff and solar radiation that limit water availability, or shallow soil conditions associated with soil loss. Collectively, results from our study suggest that heterogeneity in declines of woody plant cover is influenced by topo-edaphic controls that amplify or ameliorate declines in water availability during periods of drought.

Perennial grasses

Perennial grass cover increased and decreased over large areas across the Sonoran Desert at 5-yr time intervals. These changes in grass cover were related to summer precipitation in the Sonoran Desert, which is consistent with previous findings (McClaran et al. 2003, McClaran et al. 2010). Most perennial grasses in this region are C_4 species, which have greater photosynthetic rates at high temperatures and use water more conservatively in the summer months than C_3 species. Drought has historically exerted a large control on the abundance of grasses in the southwestern USA (Moran et al. 2014) and much of the region has experienced declines in grasses partially attributable to land-use activities over the last century such that only 15% of former grasslands that once covered the southwestern USA currently remain (Gori and Enquist 2003). The southeastern part of the study region where most of the perennial grasslands reside, experienced declines, especially from 2005 to 2009, which encompasses years with large shortfalls in summer precipitation. Declines in grasses at the beginning of the 21st century, in combination with future water shortfalls, are likely to affect many endemic mammal and bird species that use these grasslands as habitat (Lloyd et al. 1998). These decreases will also limit forage for livestock and reduce opportunities for grazing in this region.

In contrast to woody plants, grasses are shallow-rooted and experience large fluctuations in water availability in the upper soil profile, which makes them particularly sensitive to changes in soil texture and depth that modify water movement and storage (McAuliffe 1994). Grasses generally had large increases and decreases on shallow soils that have large fluctuations in water availability. Although non-native perennial Lehmann lovegrass (*Eragrostis lehmannia*) and buffelgrass (*Pennisetum ciliare*) have spread into the study region, we did not distinguish these species from native perennial grasses. Future work separating native from non-native perennial grasses may reveal competitive interactions between them and differential responses to climate, topo-edaphic properties, and changes in woody plant cover (McClaran et al. 2003, 2010).

Balance between woody plants and perennial grasses

Several studies have shown that perennial grasses compensate for the loss of woody plant cover, or conversely that woody plant cover is enhanced following drought and associated reductions in grass cover (Archer 1996, Brown et al. 1997). We found no evidence in our study for competitive interactions between woody plant and perennial grass cover and instead found support that leguminous trees and perennial grasses simultaneously declined at the pixel (900 m²) and regional (30,000 km²) scales during drying trends. There was no relationship between changes in creosote bush and perennial grass cover at the pixel scale, and despite changes in cover between the two

vegetation types in opposite directions at the regional scale, their distributions did not overlap extensively. Effects of competition between woody plants and perennial grasses have been found at the plant scale (<10 m²) in southern Arizona but are restricted to areas directly under woody plant canopies and were not detected at larger spatial scales (McClaran and Angell 2006). Precipitation shortfalls on top of already dry conditions (<400 mm mean annual precipitation) may override the effect of grass and woody plant interactions, causing declines of both vegetation types in our study. Despite our results, large declines in perennial grasses during shrub proliferation have been detected at landscape scales with remote sensing (Browning et al. 2008) and broad field surveys (Gibbens et al. 2005), which can help provide understanding of grass and woody plant interactions.

Climate change

Our results of shifting abundance of woody plant species and perennial grasses have implications for a warmer and drier climate projected by climate models for dryland regions (Seager and Vecchi 2010). Although short-term water shortages can have the greatest impacts on shallow-rooted grasses, our results suggest that drought over the last three decades has also impacted deep-rooted woody plant species. Increases in aridity expected by climate change in this the Sonoran Desert region may ultimately result in less total perennial vegetation. The expansion of areas with low or no perennial vegetation cover in our study region could be studied further to inform where land degradation is likely to occur, including soil erosion losses (Sankey et al. 2013) and colonization by non-native plant species (Olsson et al. 2012). Our results demonstrate that the cover of grasses and woody plants in the future depends on the underlying topo-edaphic properties of the site, with shallow slopes and coarse-textured deep soils promoting woody plant drought resistance and fine-textured shallow soils encouraging rapid increases in grass cover following wet summers. Although we determined that areas experiencing declines in precipitation affected grass and woody plant abundance, increases in temperature also play a role in this region (Munson et al. 2012), largely by increasing evaporative demand and exacerbating water shortages. Increasing CO₂ that drives climate change may affect the balance of grass and woody plant abundance directly by promoting growth or indirectly by inducing stomatal closure and retention of soil water (Morgan et al. 2011).

Remote sensing approach

Combining plot-based measurements and medium-resolution Landsat imagery into regression tree models was an effective way of separating grasses from woody plants and tracking their cover changes over a large region. This approach has been successfully used to

monitor other dryland ecosystems (Xian et al. 2012a, b, Homer et al. 2015) and requires fewer resources compared to only using field-based measurements. Using our approach to monitor different components of ecosystems can expand the spatial scale and increase the frequency at which measurements are taken so changes can be rapidly detected. This detection is especially important given the accelerated land-use and climate change pressures dryland regions are expected to face in the future. We were able to utilize existing plot-based measurements in this study, but future monitoring could be improved by systematically sampling all the vegetation and soil components of the study region at the time of image acquisition.

Land management and other considerations

The effect of climate, soils, and topography on grass and woody plant abundance across southern Arizona determined in this study interacts with land-use practices at local scales. Livestock grazing has been a major driver in the balance between grasses and woody plants in this region, both in suppressing herbaceous growth and spreading seed of mesquite and other shrubs (Van Auken 2000). Fire frequency has generally decreased in the region over the last century and may contribute to the shift from grass to woody dominance (Bahre 1995). However, localized increases in fire frequency fueled by the spread of non-native grasses may reduce woody plant abundance (McLaughlin and Bowers 1982). Brush management efforts can also reduce woody plants and promote grasses, but the suppression of woody plants in the region generally had short-lived effects (McClaran et al. 2003). The timing and intensity of these management efforts should incorporate the impacts of droughts and wet periods determined in this study. Further consideration of the topo-edaphic properties that differentially affect the performance of these two vegetation types through modification of water availability is also warranted.

We did not account for plant interactions and demographic processes, which can modify the abundances of grass and woody plants at a plant to local scale. Creosote bush and mesquite both have high adult survivorship, and grasses can influence their abundance in the early stages of development (Grover and Musick 1990). Once established, woody plants can facilitate or compete with grasses (Scholes and Archer 1997). In addition to grass and woody plant interactions, we did not consider the size and distribution of shrubs, which varies by geomorphic surface and contributes to their resistance to drought (McAuliffe 1994). Similarly, variability in soil textures can influence grass density, which constrains their recovery following drought (Yahdjian and Sala 2006). The incorporation of land-use, plant interactions, and demographic process can complement our broad-scale understanding of climatic and topo-edaphic controls of changes in cover of grasses and woody plants.

CONCLUSIONS

Monitoring changes in grass and woody plant cover using a fusion of plot-based measurements and satellite imagery can allow scientists and land managers to continuously track important shifts in vegetation composition and structure at broad spatial scales. Using this approach, we found that a dryland region experiencing prolonged drying lost both grass and woody plant cover at a decadal scale; declines which were exacerbated if topo-edaphic properties decreased water retention and increased water loss. Broadly understanding how climate and topo-edaphic properties interact to drive changes in grass and woody plant cover provides a baseline to compare how management actions and disturbances influence functional composition more locally.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1389/supinfo>

DATA AVAILABILITY

Data is currently available online at <http://dx.doi.org/10.5066/F7959FNF>.