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Cumulative drought and land-use impacts on perennial vegetation across a North American dryland region

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Keywords
Aridity; Climate change; Enhanced vegetation index; Moderate-Resolution Imaging Spectroradiometer; Protected areas; Remote sensing; Soil properties; Visitor use; Wildfire

Abbreviations
AIC = Akaike's information criterion; BLM = Bureau of Land Management; MODIS = Moderate-Resolution Imaging Spectroradiometer; EVI = enhanced vegetation index; TM = thematic mapper.

Nomenclature
US Department of Agriculture Plants Database (http://plants.usda.gov, Accessed: 10 Jan 2015)

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Abstract

Question: The decline and loss of perennial vegetation in dryland ecosystems due to global change pressures can alter ecosystem properties and initiate land degradation processes. We tracked changes of perennial vegetation using remote sensing to address the question of how prolonged drought and land-use intensification have affected perennial vegetation cover across a desert region in the early 21st century?

Location: Mojave Desert, southeastern California, southern Nevada, southwestern Utah and northwestern Arizona, USA.

Methods: We coupled the Moderate-Resolution Imaging Spectroradiometer Enhanced Vegetation Index (MODIS-EVI) with ground-based measurements of perennial vegetation cover taken in about 2000 and about 2010. Using the difference between these years, we determined perennial vegetation changes in the early 21st century and related these shifts to climate, soil and landscape properties, and patterns of land use.

Results: We found a good fit between MODIS-EVI and perennial vegetation cover (2000: R^2 = 0.83 and 2010: R^2 = 0.74). The southwestern, far southeastern and central Mojave Desert had large declines in perennial vegetation cover in the early 21st century, while the northeastern and southeastern portions of the desert had increases. These changes were explained by 10-yr precipitation anomalies, particularly in the cool season and during extreme dry or wet years. Areas heavily impacted by visitor use or wildfire lost perennial vegetation cover, and vegetation in protected areas increased to a greater degree than in unprotected areas.

Conclusions: We find that we can extrapolate previously documented declines of perennial plant cover to an entire desert, and demonstrate that prolonged water shortages coupled with land-use intensification create identifiable patterns of vegetation change in dryland regions.

Introduction

Perennial vegetation is the foundation of ecosystems because it forms the base of food webs and wildlife habitat, sequesters carbon, contributes to nutrient cycling and reduces soil erosion (Havstad et al. 2007; Munson et al. 2011). In dryland regions, sparsely distributed perennial vegetation is at great risk of decline or loss due to global change pressures, which can result in land degradation. Protracted drought and elevated temperatures forecasted for many dryland regions (Dai 2010; Seager & Vecchi 2010) can reduce already limited plant water availability. This pressing background of decreasing water in drylands can be punctuated by human land uses that accelerate perennial vegetation declines. Plant damage or mortality due to climate and land use can have long-lasting effects on dryland vegetation because growth and establishment of dryland plants is often slow within decadal-scale measurement periods (Webb 1980; Cody 2000).

In the North American Mojave Desert, elevated temperatures and pronounced drought have emerged as the

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climate of the early 21st century, and warming and drying trends are expected to become more severe in the future compared to historical conditions (Cayan et al. 2010). This recent, rapid change in climate has resulted in declines and mortality of multiple perennial plant species (Munson et al. 2015). In addition to climate, changes in water availability and associated plant performance can be influenced by the complex topography and soil types of the region (McAuliffe 1994). For example, south-facing slopes and fine-textured surface soils may lose water quickly to high-evaporative demand. Given the large spatial heterogeneity in climate, topography and soils across the Mojave Desert, changes in perennial vegetation are unlikely to be uniform across the region.

Changes in water availability across the Mojave Desert, like many global drylands, have occurred concurrently with rapid human population growth. The desert houses Las Vegas, Nevada, one of the fastest-growing cities in the US, and is a short drive for 40 million people in southern California and central Arizona (http://www.census.gov/popest, Accessed: 3 Apr 2015). This large and growing population has increased land-use disturbances from energy development, wildfire and recreational use (Lovich & Bainbridge 1999; Hughson 2009), further reducing perennial vegetation and placing considerable strain on the desert ecosystem. National parks, military installations and large tracts of Bureau of Land Management (BLM) land occur throughout the Mojave Desert and provide varying degrees of protection from land-use disturbances. Determining if protected areas buffer perennial vegetation from declines can help inform efforts to conserve natural resources.

Although observational studies (Beatley 1980; Webb et al. 2003; Miriti et al. 2007; Munson et al. 2015) and experimental manipulations (Huxman et al. 1998; Hamerlynck et al. 2000) demonstrate large shifts in the condition of perennial vegetation with warming, elevated CO_2, drying and land-use disturbance, these studies are often limited in spatial extent or restricted to a short window of time. Remote sensing can expand our understanding of spatial and temporal climate and land-use effects on perennial vegetation. In a previous study, we determined the spatial distribution and abundance of perennial vegetation cover in the year 2000 for the entire Mojave Desert by coupling Moderate Resolution Imaging Spectroradiometer Enhanced Vegetation Index (MODIS-EVI) satellite data with plot-based measurements of perennial vegetation (Wallace et al. 2008). Since 2000, the Mojave Desert has experienced a multi-year drought, high temperatures and additional land-use pressures. The goal of our present study was to determine the impact of cumulative water deficit and land-use pressures across the entire Mojave Desert from 2000 to 2010 to help inform how future global change is likely to impact dryland ecosystems.

Methods

Study area

Our study area includes the Mojave Desert region in southeastern California, southern Nevada, southwestern Utah and northwestern Arizona. The region contains basin-and-range topography, with basin elevations ranging from −80 to 1,500 m. Soils are highly variable across a range of lithologies, depositional environments and surface ages (Bedford et al. 2009). Mean annual precipitation in basins across the Mojave Desert is 186 mm and ranges from 47 to 370 mm, with 66–82% falling in the cool-season months (Oct–Apr; Fig. 1). Seven out of 10 yrs between 2000 and 2010 experienced annual precipitation below the mean. The proportion of cool- to warm-season (Jul–Sept) precipitation increases from west to east such that areas >117° longitude receive biseasonal patterns of precipitation (Hereford et al. 2006). Mean annual temperature in basins across the Mojave Desert is 18.8 °C (range of 12.3–25.1 °C), and warming trends have occurred since the late 1970s (Redmond 2009). Low precipitation supports woody plant and sparse perennial grass cover, including dominant shrubs *Larrea tridentata* (creosote bush), *Ambrosia dumosa* (white bursage) and *Atriplex* spp. (saltbushes) at the lower elevations of 0–1,400 m; *Coleogyne ramosissima* (blackbrush), *Yucca brevifolia* (Joshua tree) and *Artemisia tridentata* (big sagebrush) at the middle elevations of 1,000–1,500 m; and *Juniperus californica* (California juniper) and *Pinus monophylla* (single-leaf pinyon) at elevations >1,300 m.

Plot-based perennial vegetation measurements

We used measurements of total perennial vegetation cover taken in large plots (ranging from 100 to 1,000 m^2 in area) or parallel transects (totaling 100–500 m in length) across the Mojave Desert (herein referred to as plots; Wallace et al. 2008). Cover of perennial vegetation was measured using line and line-point intercepts in the spring months of March–May during peak productivity following cool-season precipitation. Line intercept was conducted by extending a measuring tape within a plot and recording the start and end of each plant canopy that overlapped with the tape (Webb et al. 2003), while line-point intercept was conducted by recording if a plant was intercepted by a vertical pin dropped every 1 m from the tape (Herrick et al. 2005). Canopy cover of perennial vegetation was calculated by totaling the intercept measurements and dividing by the entire length or number of points sampled. A total of 477 plots were measured from 2000 to 2002 (~2000)

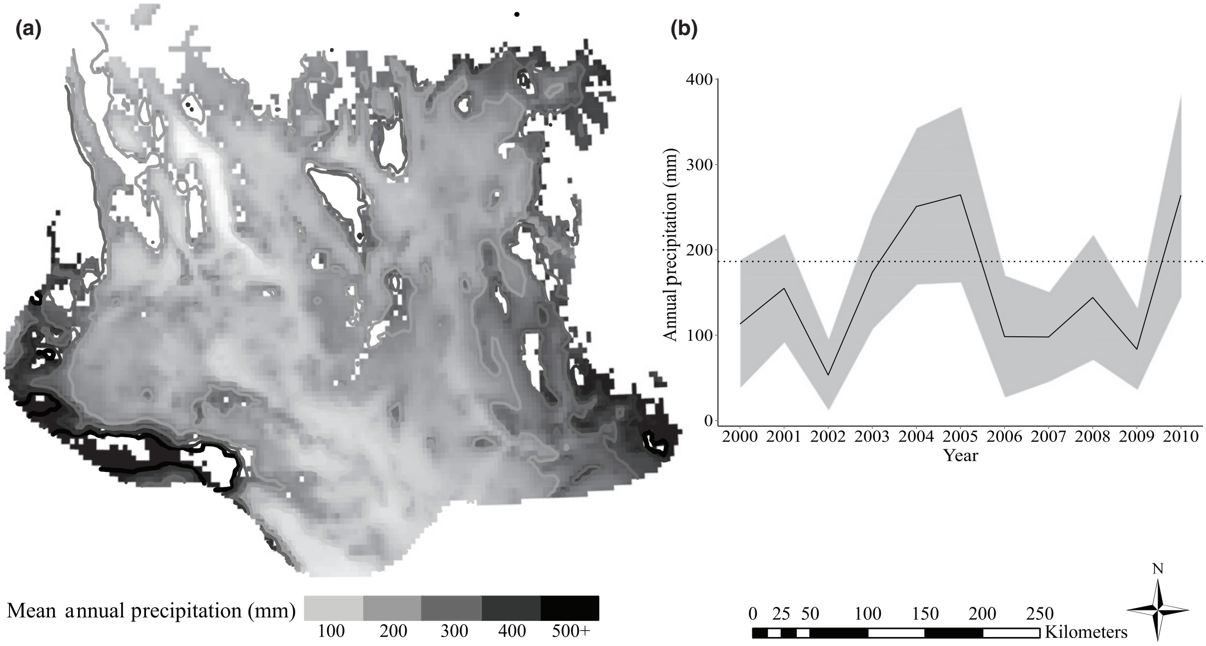

Fig. 1. **(a)** Long-term (1981–2010) mean annual precipitation across the Mojave Desert in space, and **(b)** annual precipitation of the Mojave Desert through time (2000–2010). The grey region in annual precipitation through time represents ±1 SD of precipitation across the Mojave Desert, and the dotted line represents the long-term mean annual precipitation for the entire region (186 mm).

and 144 plots were measured from 2010 to 2012 (~2010). A total of 124 of the plots measured in the 2010 period were repeat measurements of the same plots measured in the 2000 period.

Satellite-based enhanced vegetation index

We used images from MODIS acquired during the same time period as plot-based vegetation measurements (2000–2002 and 2010–2012). These images have been processed to remove operational external noise through improved calibration, atmospheric correction, cloud and cloud shadow removal and standardization of sun-surface-sensor geometries with bidirectional reflectance distribution function models (Huete et al. 2002). We used the enhanced vegetation index (EVI), which is a spectral measure of the amount of photosynthetically active vegetation calculated using the red (620–670 nm), near-infrared (NIR; 841–876 nm) and blue (459–479 nm) bands, as follows:

$$\mathrm{EVI} = G\frac{\rho_{\mathrm{NIR}} - \rho_{\mathrm{RED}}}{\rho_{\mathrm{NIR}} + C_1 \times \rho_{\mathrm{RED}} - C_2 \times \rho_{\mathrm{BLUE}} + L}, \qquad (1)$$

where ρ are atmospherically corrected or partially atmosphere corrected (Rayleigh and ozone absorption) surface reflectances, L is the canopy background adjustment that addresses nonlinear, differential NIR and red radiant transfer through a canopy, and C_1, C_2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band. The coefficients adopted in the EVI algorithm are, $L = 1$, $C_1 = 6$, $C_2 = 7.5$, and G (gain factor) = 2.5 (Huete et al. 2002). The MODIS-EVI data are delivered as a 16-bit digital number with a valid range from −2,000 to 10,000, and a 10,000 scale factor. The calculated EVI values are, therefore, −0.2 to 1.0, with non-land surfaces (such as water and snow) represented by negative values and land surfaces represented by positive values. As photosynthetically active vegetation in the imagery increases, the calculated EVI increases toward a maximum value of 1.0.

Daily MODIS-EVI data are combined into single 16-d composites using an improved Constrained View Maximum Value Composite scheme that reduces sun-target-sensor angular variations. Each year is represented by 23 16-d composites, with each composite representing a relatively cloud-free view of the surface greenness. To create the 2010 perennial vegetation cover model, we used 69 composites from 2010, 2011 and 2012 with plot-based cover measurements from the same time period. To create the 2000 perennial vegetation cover model in our previous study (Wallace et al. 2008), we used 66 (the year 2000 only has 20 composites) MODIS EVI composites from 2000, 2001 and 2002 with plot-based cover measurements from the same time period.

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Image analysis

To bridge the satellite and plot-based data sets, we evaluated the larger footprint of plot locations to determine whether they were situated in homogeneous native vegetation and could be considered representative of an entire 250 m MODIS pixel. We used Landsat Thematic Mapper (TM) imagery (30-m resolution) to quantify landscape heterogeneity (Wallace et al. 2008). The TM imagery chosen was identical to the imagery used to develop the 2000 cover model and consisted of standardized, orthorectified, preprocessed scenes primarily from Jun–Aug of 1993 produced for the Multi-Resolution Land Characteristics (MRLC) data set and accessed through the Mojave Desert Ecosystem Program (http://www.mojavedata.gov; Accessed 13 Nov 2014). Although the TM imagery was more than a decade older than the plot-based measurements collected for the 2010 cover model, these value-added images are still useful for the purpose of assessing overall neighbourhood heterogeneity, especially given the remote locations of our study sites. The six-band stack of non-thermal TM data (visible, near-infrared and short-wave-infrared) were mosaicked and clipped to the boundary of the Mojave Desert ecoregion (Bailey 1995) with a 50-km buffer zone. The TM data were then input into an unsupervised classification routine (ERDAS Imagine 8.5) and output as 20 classes that ranged in the overall amount of vegetation: with class 1 mostly barren, including playas, and class 20 densely vegetated, including low-elevation forests (Wallace et al. 2008). To identify locations most representative of 250 m MODIS pixels, the landscape heterogeneity was evaluated within a buffer of 125 m radius around the centre of the plot location. Heterogeneity was calculated as the range (the difference between the highest and lowest class number) of the classified Landsat TM image pixels within the buffer area. To be consistent with our previous study, we considered a plot location to have low heterogeneity and therefore representative of a MODIS pixel if the range value was <6. Note that plots longer than 250 m sampled more than one MODIS pixel, but we used the pixel that contained the plot centre and only used the cover value of the plot if the neighbourhood around the plot centre was relatively homogeneous. The 2010 cover model was trained using 124 relatively 'pure' pixels to calibrate the relationship between plot measured cover and MODIS-EVI.

Perennial vegetation model

We used the 69 EVI composites from 2010, 2011 and 2012 as independent variables in a step-wise linear regression to predict total perennial vegetation cover (Tibco Spotfire S-PLUS v 8.1; Insightful Corp., Seattle, WA, US). As in the 2000 cover model, we also included elevation as an independent variable because the type of perennial vegetation cover is stratified according to elevation, with vegetation dominated by *L. tridentata* and *A. dumosa* occupying low elevations and vegetation dominated by *C. ramosissima* and *A. tridentata* occupying mid-elevations (Wallace et al. 2008). The initial 2010 cover model was refined by identifying and eliminating three outliers in the plot-based cover estimates (dependent variable) determined using Cook's distance. A subset of composite EVI composites was selected by evaluating ten realizations of the step-wise model. Each realization was run using a randomly selected 80% subset of the plot-based cover estimates and all EVI composites. The EVI composites were retained for inclusion in the final cover model if they were significant ($P < 0.05$) in at least five out of ten realizations.

We validated our perennial vegetation model using a modified bagging technique, which produces replicate samples of the training data to improve the stability and accuracy of the model (Quinlan 1996). We created and evaluated ten realizations of the final linear regression model using ten randomly selected 80% subsets of the plot-based data. For each realization, a training R^2 and a testing R^2 were calculated. The training R^2 evaluated the fit between the measured and predicted cover for 80% of the plot-based data used to train the model, and the testing R^2 evaluated the fit between the measured and predicted cover of the 20% of the data withheld from model development. The training and testing R^2 for the ten model realizations provide a measure of the final model performance; since the final model uses all appropriate plot-based data, its performance should be better than any of the random trials.

The 2010 perennial vegetation cover map was created from the final model and compared to the existing 2000 perennial vegetation map. We observed that the 2010 perennial vegetation map had a striping artifact running approximately WNW–ESE (affecting < 1% of the map) due to our model amplifying noise caused by aging of the sensor array (Kamel Didan, pers comm, 2013). This striping was not evident in the 2000 or 2010–2000 difference map (see below), and we consider the impact of striping noise to be minimal for analysis and interpretation of regional patterns and trends. Our perennial vegetation cover model was evaluated for stability across space by calculating the coefficient of variation for the ten realizations of the step-wise regression model. The coefficient of variation was <5% across more than 90% of the Mojave Desert and suggests that the model accuracy is ±5% of the plot-based cover values (Wallace et al. 2008). As such, estimated differences between the 2000 and 2010 cover models should be significant if they are more than 10% of the total cover value estimated for either 2000 or 2010.

We removed all open water, developed and agricultural pixels as classified by the National Landcover Dataset (Homer et al. 2015) from both the 2000 and 2010 perennial vegetation maps in a GIS (ArcGIS 10.2 ESRI, Redlands, CA, US). We also removed all pixels above 1,500 m in elevation, to eliminate densely vegetated forests that are not a part of the Mojave Desert region. To calculate the change in perennial vegetation cover, we subtracted the 2010 vegetation cover map from the 2000 vegetation cover map. We used the Species Distribution Modelling Tools package (http://www.rforge.net/SDMTools, Accessed: 21 Mar 2015) in R (v. 2.14.1; R Foundation for Statistical Computing, Vienna, AT) to calculate the number of patches and mean patch size of areas of increase, decrease and no change in perennial vegetation cover from the cover change map.

Environmental and land-use variables

We extracted monthly precipitation for the study area in 2000–2010 from the 4-km gridded PRISM data set (http://prism.oregonstate.edu, Accessed: 2 May 2015), and then calculated annual precipitation for each year, as well as mean precipitation for cool- (Oct–Apr) and warm-seasons (Jul–Sept) in each year. These two seasons represent dominant storm trajectories in the Mojave Desert from the Pacific Ocean and Gulfs of Mexico and California, respectively (Hereford et al. 2006). To account for the strong elevation and latitude gradient in precipitation and temperature across our study region, we differenced each annual, cool- and warm-season precipitation value from its 30-yr (1981–2010) normal (e.g., 2002 annual precipitation – 30-yr normal of annual precipitation), which resulted in an annual and seasonal precipitation anomaly for each year. We also extracted seasonal and annual measures of the standardized precipitation–evapotranspiration index (SPEI) from the Global SPEI Database (http://sac.csic.es/spei; Accessed 4 May 2015). SPEI is a drought severity index that incorporates both precipitation and potential evapotranspiration calculated using the Penman-Monteith method (Vicente-Serrano et al. 2010).

Topography and soil properties can influence water availability and the growth of perennial vegetation. We used a 90 m digital elevation model to derive elevation, slope and aspect (http://nationalmap.gov/elevation.html; Accessed 15 May 2015). We acquired percentage sand (particles 0.05–2.0 mm), silt (particles 0.002–0.05 mm), clay (particles < 0.002 mm), surface fragment cover (% occupied by particles 2–74 mm in diameter) and depth to restrictive layer (bedrock or other layer that impedes water movement) from the Soil Survey Geographic Database (http://websoilsurvey.nrcs.usda.gov, Accessed: 18 May 2015).

Visitor recreational use impacts vast parts of the Mojave Desert and can reduce perennial vegetation cover. We quantified visitor use on BLM lands (a large subset of the entire Mojave Desert region) using a spatial layer that uses a network-based accessibility modelling approach (Theobald 2008). The spatially explicit modelling approach quantifies the number of visitors based on three components of recreation: population centres that supply visitors, transportation infrastructure, and the location of recreation features that attract visitors (e.g., recreation sites and trailheads). The layer accounted for aquatic (e.g., boaters), non-motorized (e.g., hikers) and motorized (e.g., off-highway vehicle recreation) recreational users. We determined the protected area status using the Protected Areas Database (http://gapanalysis.usgs.gov/padus, Accessed: 22 May 2015), and classified areas as protected if they were within a national park or wilderness area boundary and unprotected if they were not contained in these protected areas.

Finally, fire can alter the type and amount of perennial vegetation that grows following a burn. We extracted perimeters of fires that had actively burned during our study period using the Geospatial Multi-Agency Coordination database (http://www.geomac.gov, Accessed 22 May 2015), which uses incident intelligent sources, GPS data and infrared imagery from remote sensing platforms to determine perimeters. We classified areas as burned if they were within a 2000–2010 fire perimeter and unburned if they were not.

Data analysis

We calculated perennial vegetation cover change for each 250 m × 250 m pixel as:

$$\text{cover change} = \ln\left(\frac{\text{cover}_{2010}}{\text{cover}_{2000}}\right), \qquad (2)$$

where cover_{2010} is total perennial vegetation cover in 2010 and cover_{2000} is total perennial vegetation cover in 2000 estimated from the MODIS-EVI-derived models in each respective year. Cover change, environmental and land-use values were extracted from 5,000 randomly selected points from the perennial vegetation change and associated environmental and land-use rasters (R 'raster' package; https://cran.r-project.org/web/packages/raster/, Accessed: 2 Apr 2015). We did not include elevation in our model because it was correlated with SPEI variables ($r > 0.5$). We determined the relationships between perennial vegetation cover change and explanatory variables by performing multiple regressions with both forward and backward step-wise model selection using

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Akaike's information criterion (AIC). Continuous explanatory variables of the highest ranked models were then binned by quartiles (0–25%, 25–50%, 50–75%, 75–100%) to simplify the very large data set and allow for clear examination of trends driven by environmental and land-use variables. ANOVA was performed on perennial vegetation cover change to determine if gains or losses of cover were different among classes of each environmental and land-use variable. A Tukey's multiple comparison adjustment was used to compare differences among groups and a *t*-test to determine whether cover changes were significantly different from zero.

Results

The final 2010 cover model included 19 EVI images selected by step-wise linear regression and the 121 refined plot-based cover estimates (Average Training R^2 = 0.74, Average Testing R^2 = 0.69; Table 1). The 2010 cover model was compared to the existing 2000 cover model (Average Training R^2 = 0.83, Average Testing R^2 = 0.74; Table 1) to produce the 2000–2010 difference map of perennial vegetation cover across the Mojave Desert (Fig. 2). The area that lost perennial vegetation cover between 2000 and 2010 (46,635 km^2 or 32% of total area) was similar to the areas with no change (47,359 km^2, 33% of total area) or gains in cover (49,243 km^2 or 35% of total area).

There were fewer contiguous areas (patches) and larger patch sizes that lost cover (56,885 patches with a mean area of 0.84 km^2) compared to patches that gained cover (58,359 patches with a mean area of 0.82 km^2). The amount of area experiencing losses or gains in cover decreased exponentially with the magnitude of change in cover (Table 2) such that only 2% of the Mojave Desert had >50% losses or gains between 2000 and 2010. In general, the gains in cover were clustered in the northeastern (west of St. George, UT) and southeastern (east of Joshua Tree National Park) parts of the Mojave Desert, whereas decreases occurred in the southwest (west of Barstow, CA), the far southeast (southeast of Kingman, AZ) and central (south of Las Vegas, NV, into the Mojave National Preserve) portions of the Mojave Desert (Fig. 2).

The highest ranked models (ΔAIC < 3) to explain changes in perennial vegetation cover included the 10-yr annual precipitation anomaly, visitor use, soil depth to restrictive layer, fire history and protective area status (Table 3). Cover increased (mean change in [Δ] cover = 0.30 ± 0.02 SE) in areas of the Mojave Desert that experienced near to above average precipitation over the last 10 yrs (−4 to 45 mm; Fig. 3a). This increase in cover was significantly higher than areas of the Mojave Desert that experienced 10-yr deficits in annual precipitation of −20 to −4 mm (Δ cover = 0.12 ± 0.03; t = 25.4, P < 0.0001) and −45 to −20 mm (Δ cover = 0.04 ± 0.03; t = 56.0, P < 0.0001), and areas that experienced <−45 mm deficits lost cover (Δ cover = −0.14 ± 0.02; t = 176.6, P < 0.0001). There were gains in cover on shallow soils <40 cm (0–32 cm: Δ cover = 0.19 ± 0.04; t = 7.3, P < 0.0001; and 32–40 cm: Δ cover = 0.19 ± 0.04; t = 8.0, P < 0.0001; Fig. 3b) compared to no significant changes (Δ cover = −0.04 ± 0.04; t = −1.29, P = 0.20) on soils with a moderate depth of 40–55 cm and losses on deep soils >55 cm (Δ cover = −0.17 ± 0.03; t = −6.2, P < 0.0001).

Changes in perennial vegetation cover were not significantly different as recreational use increased (0–1,500, 1,500–5,700 and 5,700–14,200 visitors yr^{-1}: Δ cover = 0.19 ± 0.04, 0.18 ± 0.04, 0.14 ± 0.04, respectively; all P > 0.05) until the number of visitors exceeded 14,200 yr^{-1}. Areas of the Mojave Desert that received visitor use higher than this amount experienced decreases in perennial vegetation cover (Δ cover = −0.18 ± 0.03; t = −6.1, P < 0.0001; Fig. 3c). Protected areas of the Mojave Desert had larger increases in perennial vegetation cover than unprotected areas (protected: Δ cover = 0.17 ± 0.03, unprotected: Δ cover = 0.05 ± 0.01; t = 16.53, P < 0.0001, not shown), and burned areas had larger decreases in perennial vegetation cover than unburned areas (burned: Δ cover = −0.19 ± 0.07, unburned: Δ cover = 0.09 ± 0.01; t = 14.21, P = 0.0002, not shown).

Discussion

We found that the Mojave Desert, which mostly has evergreen and deciduous shrubs that respond to cool-season precipitation, had both areas that gained and lost perennial

Table 1. Ten realizations (or trials) of the 2000 and 2010 perennial vegetation cover models using a modified bagging technique that calculates a testing (20% of plot-based field data) and training (80% of plot-based field data) goodness of fit (R^2).

Trial	2000 Testing R^2	2000 Training R^2	2010 Testing R^2	2010 Training R^2
1	0.77	0.82	0.65	0.75
2	0.79	0.82	0.73	0.72
3	0.62	0.85	0.72	0.74
4	0.81	0.82	0.79	0.72
5	0.76	0.83	0.63	0.74
6	0.79	0.82	0.69	0.72
7	0.63	0.85	0.64	0.76
8	0.69	0.84	0.65	0.74
9	0.76	0.82	0.74	0.72
10	0.83	0.82	0.63	0.76
Average	0.74	0.83	0.69	0.74

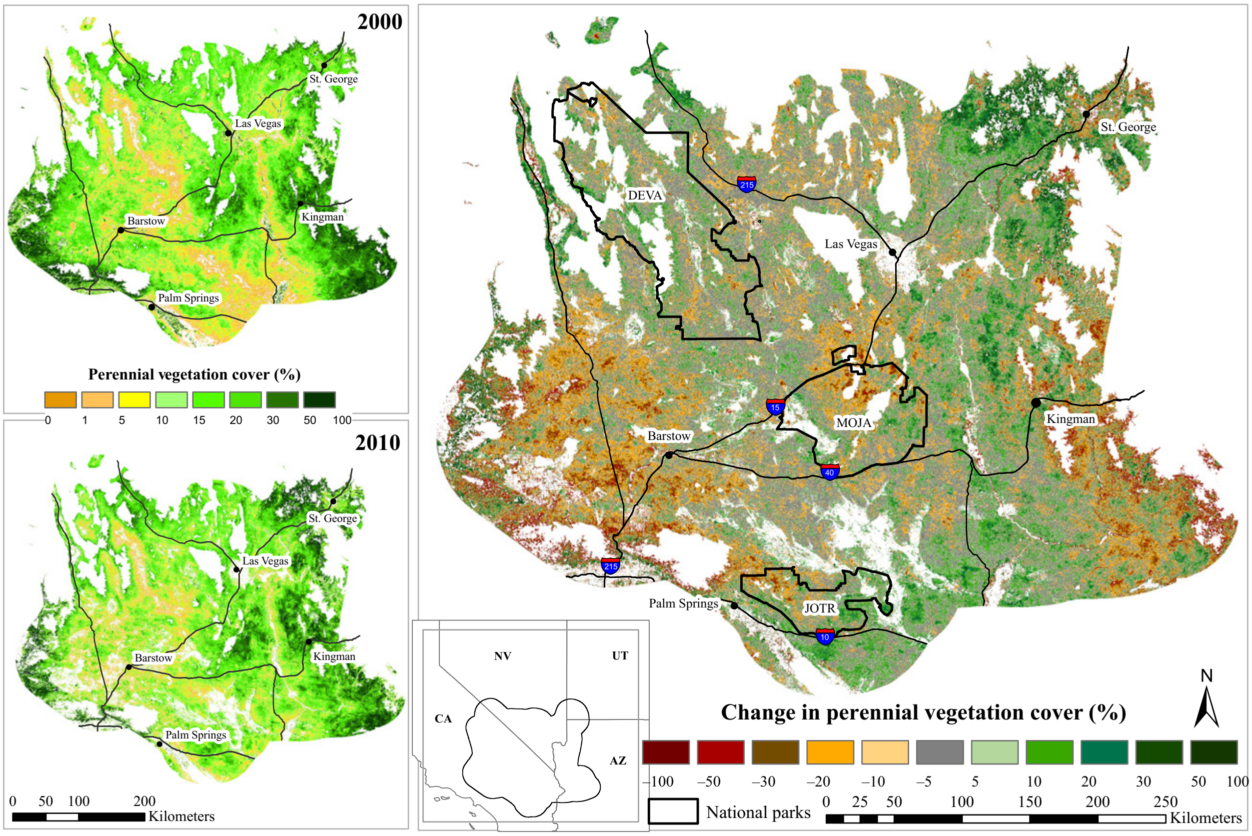

Fig. 2. Map of 2000 and 2010 perennial vegetation cover (left insets), and change in perennial vegetation cover between 2000 and 2010. Abbreviations: DEVA, Death Valley National Park; JOTR, Joshua Tree National Park; MOJA, Mojave National Preserve.

Table 2. Area and proportion of total area for change in cover classes between the 2010 and 2000 perennial vegetation maps.

Change in Cover (%)	Area (km^2)	Proportion of Total Area (%)
−100 to −50	1,440	1
−50 to −30	3,840	2
−30 to −20	6,516	5
−20 to −10	17,645	12
−10 to −5	17,193	12
−5 to 5	47,359	33
5 to 10	19,349	14
10 to 20	19,473	14
20 to 30	6,111	4
30 to 50	3,288	2
50 to 100	1,022	1

vegetation cover from 2000 to 2010. While there was large heterogeneity in these changes, the southwestern, far southeastern and central Mojave Desert showed marked declines in cover. Plot-based data show 30% average reductions in cover of the dominant shrub *L. tridentata* southwest of Death Valley National Park (western Mojave), and 50% average reductions at Joshua Tree National Park (south-central Mojave) and Mojave National Preserve (central Mojave) in the 2000s (Munson et al. 2015). The area east of Death Valley National Park (north-eastern Mojave) had 15% average reductions of the shrub during the same time period. McAuliffe & Hamerlynck

Table 3. Rank of best models, number of parameters (*K*) and model selection using AIC and ΔAIC (AIC of model – AIC of best model), and Akaike weights (w_i).

Rank	Model	*K*	AIC	ΔAIC	w_i
1	AP, Visitors, Depth, Fire	6	−2,107.9	0.0	0.39
2	AP, Visitors, Depth, Fire, Protected	7	−2,106.4	1.5	0.18
3	AP, Visitors, Depth, Protected, Fire	7	−2,106.4	1.5	0.18
4	AP, Visitors, Depth	5	−2,105.1	2.8	0.10
5	AP, Visitors, Fire	5	−2,103.9	4.0	0.05
6	AP, Visitors, Depth, Protected	6	−2,103.6	4.3	0.05
7	AP, Visitors, Fire, Protected	6	−2,102.2	5.7	0.02
8	AP, Visitors	4	−2,101.3	6.6	0.01
9	AP, Visitors, Protected	5	−2,099.7	8.2	0.01
10	AP, Depth	4	−2,050.1	57.8	0.00

AP: 10-yr annual precipitation anomaly; Visitors: recreational visitor use; Depth: soil depth to restrictive layer; Fire: fire history; Protected: protected area status.

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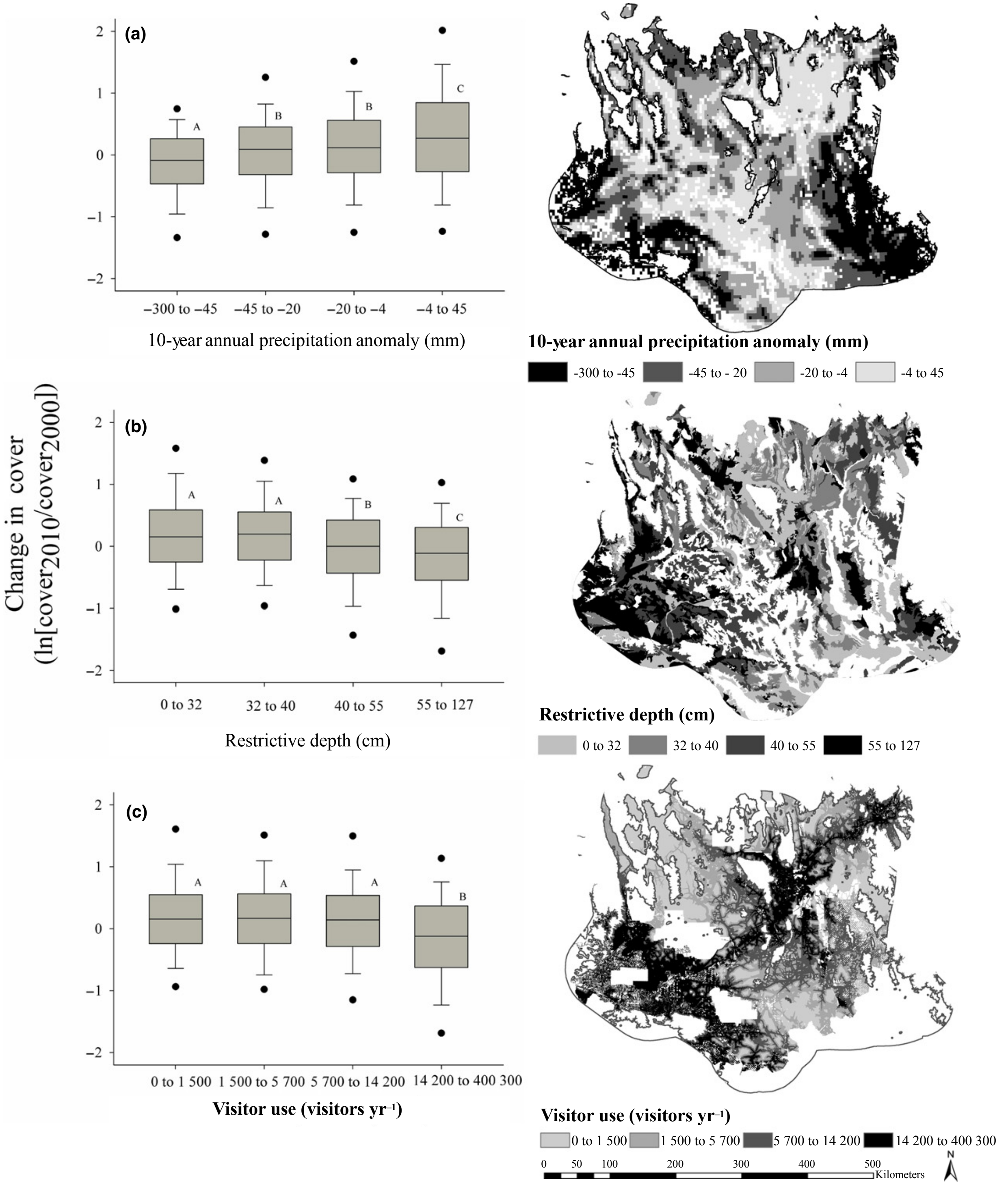

Fig. 3. Change in perennial vegetation cover between 2000 and 2010 in relationship to **(a)** 10-yr annual precipitation anomaly, **(b)** soil depth to restrictive layer, and **(c)** recreational visitor use. Boxes depict the 25th, 50th (median) and 75th percentiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles of change in cover values. Different uppercase letters designate significant differences among explanatory variable quartiles.

(2010) noted high mortality of *Larrea* in the southwestern Mojave Desert and on the west side of Joshua Tree National Park that they attributed to the 2002 drought, but relatively low mortality of this dominant species occurred in the northeastern Mojave Desert (Webb et al. 2003). These spatial patterns of dominant shrub loss are related to our detection of changes in perennial vegetation at the larger scale and indicate that mortality is partially contributing to reductions in cover.

The contribution of *Larrea* decline to losses in perennial vegetation cover across the Mojave Desert is important because it is widely distributed across the other warm deserts of North America. As a long-lived evergreen species, it is generally slow to change (Cody 2000) and requires larger water deficits to decrease in abundance compared to short-lived and deciduous species (Smith et al. 1997; Munson et al. 2015). Indeed, *A. dumosa*, a drought deciduous sub-shrub, experienced even higher mortality rates in the southern and central Mojave Desert than *Larrea* following the early 21st century drought (McAuliffe & Hamerlynck 2010), and perennial grass populations have experienced 100% mortality during these extreme drought events (Hereford et al. 2006). The reductions of live shrub cover we detected are associated with the shedding of branches, or drought pruning, which increases dead biomass cover. The declines of perennial plant cover in a desert ecosystem expand on similar losses across less drought-tolerant grasslands (Moran et al. 2014), low- (Breshears et al. 2005) and high- (Ganey & Vojta 2011) elevation forests in the southwestern US attributable to extensive drought and high temperatures in the early 21st century.

The large perennial cover changes we detected in this study have been scaled down to the condition of individual plants in other efforts. Long-term tracking of plants at Joshua Tree National Park demonstrates that six of the seven most common perennial species had sharp die-offs in both juvenile and adult life stages following the 2002 drought after 15 yrs of near stasis (Miriti et al. 2007). Although we could not distinguish cover changes between different life stages, these concurrent results suggest that both adult individuals with the potential to reproduce and juvenile individuals that can indicate new recruitment, likely declined across multiple species. The abrupt mortality events determined by long-term tracking of plants occurred for both short- and long-lived species, emphasizing again the severity of drought conditions in the early 2000s.

Seven yrs between 2000 and 2010 of below-average annual precipitation across much of the Mojave Desert resulted in a 10-yr annual precipitation anomaly that ranged from −300 to +45 mm (mean: −29 mm). The areas in which this cumulative drought was most pronounced (10-yr annual precipitation anomaly <−45 mm), including large parts of the southwestern Mojave Desert, had reductions in perennial vegetation cover. Previous work has shown that it is the accumulation of drought conditions rather than short dry intervals that drive large and widespread decline of perennial species (McAuliffe & Hamerlynck 2010; Ponce-Campos et al. 2013). Although protracted drought conditions have occurred historically, most notably the drought of the 1950s, multi-year drought conditions and enhanced aridity are expected to become the new climatology of the southwestern US (Seager & Vecchi 2010). Shortfalls in cool-season precipitation largely influence perennial vegetation growth in the Mojave Desert (Beatley 1974), and the strongest deficits in 2002 and 2007 were most strongly correlated to change in perennial vegetation cover ($r = 0.32$, $P < 0.001$, $r = 0.30$, $P < 0.0001$, respectively). Although the standardized precipitation–evapotranspiration index incorporates the impact of increased temperatures on water demand, the index did not explain more of the variability than precipitation anomalies alone. Warming trends in the Mojave Desert are expected to intensify with climate change (Redmond 2009) and will likely impact future perennial vegetation growth by exacerbating soil moisture deficit.

Areas of the Mojave Desert that did not experience severe drought conditions, including the northeastern area, increased in cover, possibly in response to above average precipitation in 2005. It is also possible that perennial species affected by drought and disturbance in the early 2000s could have resprouted from roots and stems to produce new growth, thereby regaining lost cover by the end of the decade. McAuliffe & Hamerlynck (2010) determined that resprouting occurred following drought-induced declines in plant condition, even from presumed dead *Larrea* and *Ambrosia*. Areas of the Mojave Desert that exhibit vegetation resistance and resilience to drought, and possibly disturbance from land use, serve as refugia to maintain important ecosystem processes and recolonize impacted areas. Extreme wet or dry climatic regimes over decadal scales can result not only in changes in abundance of individuals, but shifts in plant community composition (Hereford et al. 2006).

We found that perennial vegetation generally increased from 2000 to 2010 on soils with a shallow restrictive layer and decreased on deep soils. Shallow restrictive layers can keep upper soil layers wet by preventing water from moving below the rooting zone, allowing water to be accessible to plants. However, this pattern seems to be most evident for shallow-rooted perennial plants, as deep-rooted *Larrea* generally grows more prolifically and is less susceptible to drought on deep soils (Munson et al. 2015). Hamerlynck & McAuliffe (2008) found higher mortality of *Larrea* and *Ambrosia* on young, weakly developed soils than older, well-developed soils with shallow restrictive layers. However, some of this difference in plant response was attributed to rock fragments on the well-developed soils, which may have suppressed evaporation and slowed sheet flow. We did not find evidence for rock fragments or soil texture contributing to increases or decreases in perennial cover in

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this study. Alternatively, lower perennial vegetation cover on shallow compared to deep soils in 2000 ($r = 0.22$, $P < 0.0001$) means that less vegetation could be lost. The lack of soil texture and topographic properties explaining changes in perennial vegetation cover is somewhat surprising, given their importance in regulating the redistribution and availability of water in dryland ecosystems. However, these properties may be more closely associated with changes in cover at the plot- to landscape-scale or may affect changes in cover at periods longer than a decade (Browning et al. 2008; Munson et al. 2015).

Areas heavily impacted by visitor use lost perennial vegetation cover between 2000 and 2010. Although many of these previously impacted areas already had low vegetation cover, largely due to long-term exposure to recreational use, negative impacts were apparent over our 10-yr study period. The development of roads and use of off-highway vehicles can directly destroy perennial plants; and both roads and vehicles have been increasing since the early 20th century (Vogel & Hughson 2009). Vehicular travel can also impair perennial vegetation regrowth and seedling establishment by compacting soils or otherwise altering soil properties. Roadways enhance the human impacts of foot traffic, fire ignition, plant collection, introduction and spread of annual invasive plants and other disturbance activities that all reduce perennial vegetation cover (Brooks & Lair 2009). The loss of perennial vegetation cover in the southwestern Mojave Desert can be tied to its close proximity to major population centers of southern California. These reductions in perennial vegetation impacted by visitor use can take >50 yrs to recover (Webb 1980) and over 200 yrs to form similar species assemblages as undisturbed areas (Abella 2010).

Perennial vegetation increased in protected areas (national parks and wilderness areas) to a larger degree than unprotected areas from 2000 to 2010. This positive effect may be attributable to limits on land-use activities, including off-highway vehicle use, in these parts of the Mojave Desert. This protection can limit declines of perennial vegetation cover directly, or by promoting ecosystem processes that encourage plant growth (Hansen & DeFries 2007). Protected areas may become increasingly important to help buffer against vegetation losses as the human population and associated development and recreation continues to grow in dryland regions.

Wildfires that occurred during our study period reduced vegetation cover, as burning can result in damage or mortality to perennial plants. While herbaceous vegetation can grow rapidly post-fire and contribute to green-up (Brooks & Matchett 2006), many perennial species in the Mojave Desert are slow to recover from disturbance (Webb 1980; Cody 2000), which limits greenness in burned areas. Fires have been historically infrequent in desert ecosystems of the southwestern US, but have increased with the invasion of non-native annual grasses such as *Bromus* spp. (Brooks & Matchett 2006). These annual plants have a positive feedback on fire frequency because they leave abundant litter and dead biomass that can readily burn. Potential increases in the fire frequency of an ecosystem that is poorly adapted to resist or recover from fire may have long-term effects on plant cover and composition.

The changes in perennial vegetation cover we determined for the early 21st century attributable to climate and land-use effects can have a large impact on ecosystem properties. Reductions in perennial vegetation cover can accelerate soil erosion and dust storms because vegetation keeps soils intact, reduces wind momentum and traps moving soil particles (Munson et al. 2011). While wind erosion is a naturally occurring process in playas, sand dunes and other surfaces with trace amounts of vegetation, future increases in drought and human disturbances can expand the erosion footprint to areas that currently support higher amounts of perennial vegetation cover. Perennial plants in the Mojave Desert increase soil nutrient levels (Titus et al. 2002) and alter subsurface hydrology (Scanlon et al. 2005). Changes in the abundance of perennial vegetation that we detected, in addition to future shifts, can therefore feedback to affect plant growing conditions. Because perennial vegetation provides food and habitat for a large number of wildlife species, their populations can be altered by shifts in plant abundance and distribution. For example, decreases in the survival of the threatened desert tortoise that occurred from 1996 to 2002 were closely tied to persistent drought and associated declines of plant productivity (Lovich et al. 2014).

Use of MODIS-EVI proved to be an effective metric to monitor decadal changes in the condition of perennial vegetation across a broad desert region. Using MODIS-EVI, once properly validated, requires fewer resources compared to using plot-based measurements to detect changes in vegetation, making it a viable approach for natural resource management. Future application of MODIS-EVI in monitoring efforts could be improved by systematically sampling vegetation across a broader region of plots at the time of image acquisition, more explicitly examining changes in cover by vegetation type and incorporating additional plot-based sampling where the model had relatively low accuracy.

Conclusions

The satellite imagery used in our study expands the spatial extent of plot-based detection of early 21st century declines in perennial vegetation cover throughout the southwestern US. Reductions in the condition of vegetation that is drought-tolerant are particularly noteworthy, although this response was heterogeneous and many parts of the Mojave Desert had increases in perennial vegetation from 2000 to 2010. The heterogeneity in vegetation change and its response to climate and land use helps to define parts of the landscape that are vulnerable to expected increases in aridity and human population growth projected for this desert region. Continuous sampling of vegetation condition using remote sensing methods can document important trends and provide managers with an early warning sign to prepare for and possibly mitigate unwanted effects of losing perennial vegetation.

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