Warming as a Driver of Vegetation Loss in the Sonoran Desert of California

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Abstract  Dryland ecosystems cover large regions of the Earth and have important impacts on global biogeochemistry and the carbon cycle. The plant species that occupy dryland environments have traits that enable them to withstand harsh environmental conditions, and some researchers have hypothesized that dryland vegetation may be comparatively resilient to changing climate, while others have pointed out that dryland vegetation often operates close to the physiological limits of many species, implying a possible vulnerability to warming. Here we use the Landsat archive to analyze vegetation dynamics for part of the Sonoran Desert and adjacent mountains in southern California. We show that large decreases in vegetation cover occurred over the last 34 years (1984–2017), especially across the xeric portions of our study region, where we observed a normalized difference vegetation index (NDVI) decline of 1.1 ± 0.3% yr−1. Changes in precipitation explain most of the year-to-year variation but are unable to fully explain the observed long-term decline in NDVI. Statistical models that combined summer temperature and mean annual precipitation explained more of the spatial and temporal structure of NDVI trends and implicate climate warming as an important driver of declining vegetation cover. The impact of warming contributed to a change in the precipitation-vegetation relationship through time for this desert region, indicating a structural change in ecosystem function during the study period. These results suggest that recent climate change has already had significant impact on these drylands and highlight the potential for future warming to increase risks for dryland ecosystems in other regions.

Plain Language Summary  Dryland ecosystems are widespread across much of the globe. Plants occurring in these drylands are adapted to prolonged periods without rainfall and it is often assumed that drylands will be relatively resilient under present and future climate change. Here we use 34 years (1984–2017) of satellite data to assess vegetation changes over part of the Sonoran Desert and adjacent mountain areas in southern California. We observed a strong decline in vegetation cover, with the drier locations showing the strongest decline. Changes in rainfall could only explain part of the observed trends, with the long-term vegetation trends closely related to warming climate. These results indicate that dryland ecosystems may be more susceptible to changing climate than previously thought.

1. Introduction

Dryland ecosystems cover about 41% of Earth’s terrestrial surface, making them one of the most widespread ecosystems worldwide (Cherlet et al., 2018). Dryland systems are known for high numbers of endemic species and account for 20% of the major centers of global plant diversity (White & Nackoney, 2003). Drylands are characterized by extended periods when potential evapotranspiration exceeds precipitation input (Lal, 2004). Vegetation in dryland ecosystems is characterized by adaptations to endure stressful conditions (Smith et al., 2012). While annual primary productivity is low (Schlesinger et al., 2009), dryland ecosystems often react strongly to changing water availability, with plants rapidly increasing photosynthesis and growth after rain events and soils metabolizing carbon with minor wetting (Noy-Meir, 1973; Sala et al., 2012). This however depends on precipitation amount, timing, and duration, as well as vegetation characteristics, and as a consequence in some situations dryland ecosystems may have a dampened response to individual precipitation events (Fernández, 2007). Dryland systems are widespread and play a key role in global biogeochemical cycles and Earth’s energy balance (Jickells et al., 2005; Okin et al., 2004). For example, the response of net primary production to interannual variability in precipitation in global dryland ecosystems...
explains much of the year-to-year variability in the growth rate of atmospheric CO$_2$ (Poulter et al., 2014). Across multiple continents, there is an accumulating body of evidence that dryland ecosystems have a high level of sensitivity to various drivers of global environmental change, including temperature, precipitation, nutrient deposition, elevated CO$_2$, fire, and invasive species (Burrell et al., 2020; Cherlet et al., 2018; Lovich & Bainbridge, 1999). Understanding the response of dryland vegetation dynamics to climate change is essential for understanding past and future changes in global biogeochemistry and the carbon cycle, and for protecting and preserving the biodiversity of these vulnerable regions.

It is currently unclear how dryland vegetation will respond to climate change. It is expected that CO$_2$ fertilization may increase photosynthesis and water-use efficiency (Farquhar, 1997), though observational and experimental evidence is mixed (e.g., Donohue et al., 2013; Shaw et al., 2005; Smith et al., 2000). Future climate projections also indicate shifts in precipitation across global drylands, with a general decrease in overall precipitation (but including localized increases) and increases in temporal variability (e.g., Dai, 2012; Feng & Fu, 2013; Swain et al., 2018). While it is well known that changes in precipitation can drive long-term dynamics in dryland systems, including shifts in overall vegetation density or the relative proportion of alternative life-history strategies (e.g., Goldberg & Turner, 1986; Hereford et al., 2006; Miritti et al., 2007; Tucker et al., 1991; Venable, 2007; Venter et al., 2018; Welzian et al., 2003), it remains uncertain how projected changes in precipitation magnitude and interannual variability will impact dryland systems. Predicting future vegetation outcomes is challenging, in part, because compared with plants in other biomes, dryland vegetation is often adapted to drought conditions and interannual variability in precipitation (Kimball et al., 2012; Noy-Meir, 1973; Smith et al., 2012).

Drylands are dynamic, undergoing large changes in plant cover in response to interannual, decadal, and centennial changes in precipitation (Gherardi & Sala, 2015; Huxman et al., 2004; Sala et al., 2012). Most of this change is associated with large interannual changes in abundance of annual species (Ehleringer, 2001), with seasonal and interannual variability in precipitation influencing vegetation structure (Gherardi & Sala, 2015; Lauenroth et al., 2014). Increases in woody vegetation has been observed in mesic drylands (Brandt et al., 2017), with perennial vegetation shifts caused mainly by changes in the size of individual plants and canopy expansion or loss, rather than whole plant mortality or recruitment. As such, the relative abundance of perennial species composition does normally not change drastically over long time periods in these more arid drylands (Goldberg & Turner, 1986). This seems at odds with the observations over the last two decades in the Southwestern US where large-scale mortality has been documented during recent drought (Bobich et al., 2014; Breshears et al., 2005; Hereford et al., 2006; McAuliffe & Hamerlynck, 2010; Miritti et al., 2007; Van Mantgem et al., 2009). These vegetation mortality events seem to exceed natural variability in background mortality rates, as some species have experienced up to 100% mortality (McAuliffe & Hamerlynck, 2010; Miritti et al., 2007), possibly leading to local extinction, and differential impacts that may depend on life-history strategy (Winkler et al., 2019). The effect of the local disappearance of a species may ultimately go beyond a decrease in local biodiversity, with possible implications such as nutrient cycling and water redistribution within soil (Maestre et al., 2012) making the changes possibly irreversible over a period of decades to centuries.

Precipitation has received the main focus as the driver of dryland vegetation dynamics, and comparatively few studies have explored secondary climate drivers of dryland vegetation dynamics. Some studies have looked at the impact of VPD on vegetation dynamics (Yuan et al., 2019) and another set of studies has shown that some desert plant species exhibit sensitivity to long-term changes in air temperature (e.g., Li & Yang, 2014; Munson et al., 2012, 2013). Interactions between precipitation and temperature have been shown to be important too, with rising temperatures on their own increasing drought risk (Diffenbaugh et al., 2015).

Moreover, desert areas are heavily influenced by anthropogenic disturbance, such as overgrazing by livestock, wildfires, off-road recreational vehicles, and agriculture (Brandt et al., 2017; Lovich & Bainbridge, 1999). All of these influence vegetation dynamics and recovery, and all are potentially sensitive to interannual variability and long-term trends in climate.

Here we study regional vegetation change across a swath of dryland ecosystems in Southern California, including a section of the Sonoran Desert and adjacent mountains. Within the Sonoran Desert, field studies
have documented important perennial vegetation mortality events over the past several decades (McAuliffe & Hamerlynck, 2010; Munson et al., 2013). However, the magnitude, spatial extent, and drivers of these events are not well understood. We hypothesized that warming over recent decades has had a disproportional impact on the driest ecosystems within our study domain given the effect of increasing potential evapotranspiration and subsequent declining moisture availability. We focused our analysis on changes in perennial vegetation, as changes in water balance should have a more pronounced effect on perennial vegetation compared to annual vegetation as a consequence of differences in life-history responses to climate variability (e.g., Venable, 2007).

We examine long-term changes in perennial vegetation cover from Landsat imagery during 1984–2017, using the multidecadal satellite time series to attribute trends to long-term changes in environmental drivers. Recent improvements in the intercalibration and stability of satellite imagery time series, including Landsat, allow for the exploration of ever more detailed ecological questions (e.g., Robinson et al., 2019). The 34-year Landsat time series is powerful for differentiating the impacts of variable and decreasing precipitation and increasing temperatures on the desert perennial vegetation. Questions we address include: (a) What are the magnitude of vegetation changes across our study domain?, (b) Do hotter and drier lowland desert areas show larger decreases in NDVI than the more mesic ecosystems in adjacent mountains?, and (c) What are the drivers of interannual variability and long-term trends in vegetation change? In a final step, we explore the implications of a changing climate-vegetation relationship that is revealed from our analysis for changes in ecosystem function during the remainder of the 21st century.

### 2. Materials and Methods

#### 2.1. Study Site

We assessed changes in vegetation cover over an area of Southern California encompassing the Anza Borrego State Park, on the border with Mexico (Figure 1). Our study domain covers 1.27 million hectares and includes a large part of the Colorado Desert, part of the Sonoran Desert, and peninsular mountain range (Laguna, Palomar, and Santa Rosa Mountains). The study region is bounded to the east by the change in land cover from natural systems to agricultural areas adjacent to the Salton Sea and to the south by the border with Mexico due to the lack of climate data (indicated by the mask in Figure 1). Elevation ranges from –70 to 1,660 m across the study domain, with a large 1984–2017 mean annual precipitation gradient from...
73 mm y\(^{-1}\) in the desert to 770 mm y\(^{-1}\) in the mountains, and large interannual variability. Precipitation occurs during the winter and early spring, with occasional summer monsoons contributing additional precipitation across the lower elevation desert areas. Mean annual temperature also varies with elevation, from 10.7 °C in the mountains to 23.9 °C in the lowland desert.

A wide range of vegetation types occur across the study domain, in line with the large climatic gradient present. These can be largely divided in two groups (Keeler-Wolf et al., 1998), with higher elevation areas covered by montane woodlands, juniper and pinyon woodlands, chaparral and high desert vegetation. Areas in the lower elevation are covered by various lowland desert vegetation types, with the most abundant species being creosote bush (\textit{Larrea tridentata}). A variety of cactus species are present, and some areas are dominated by mesquite (\textit{Prosopis sp.}).

### 2.2. Remote Sensing Data Processing

We analyzed the historical Landsat archive across our study domain from Landsat 4, 5, 7, and 8 over the 34-year time period from 1984 to 2017, processing 2101 Level-2 surface reflectance Landsat scenes (Claverie et al., 2015; Vermote et al., 2016) were downloaded from USGS archives using the EarthExplorer interface (https://earthexplorer.usgs.gov). Clouds, cloud shadows, radiometric anomalies and missing data were masked (Foga et al., 2017). Landsat satellites provide imagery at 30-m spatial resolution in the optical spectrum since Landsat-5 with a 16-day return interval. Because of the radiometric differences between the Landsat 8 OLI detector and the previous Landsat detectors, we performed a bias correction on Landsat 8 imagery using a linear regression between the reflectance values of each band between Landsat 7 and Landsat 8 (Roy et al., 2016). This regression was developed using data from 30 pairs of images that were sampled within 10 days of each other. The resulting normalizations applied to the Landsat 8 imagery were 1.0257 × red band and 0.96349 × near infrared (NIR) band. This step normalized the reflectance values in the red and NIR band and reduced the difference in normalized difference vegetation index (NDVI) between Landsat 7 and Landsat 8, resulting in limited differences between the different sensors throughout the time period (Figure S1), except for a deviation in the red band of Landsat 5 at the end of the sensor’s lifetime from about 2008-2011, especially for bright surfaces. We did not correct for potential biases between Landsat 4, 5, and 7 as radiometric differences between these sensors are relatively small (Chander et al., 2009).

Changes in vegetation cover were assessed by analyzing changes in NDVI time series (Tucker, 1979). NDVI represents the relative difference in reflectance between the NIR and red bands, normalized by the sum of reflectance in the two bands. High NDVI values are found in regions with dense vegetation (and high levels of leaf area index), as a consequence of high levels of light absorption in the red from the presence of chlorophyll and high levels of reflectance in the NIR from scattering off mesophyll leaf cells. As such, NDVI is sensitive to changes in vegetation cover and characteristics (Carlson & Ripley, 1997; Zhang et al., 2016). Other spectral indexes which are sensitive to vegetation dynamics include enhanced vegetation index (EVI), which differs from NDVI by means of the use of an additional blue band in the denominator to correct for aerosol impacts on the red band. EVI was calculated as $EVI = 2.5 \times ((NIR−Red)/(NIR + 6 \times Red−7.5 \times Blue + 1))$.

While the overall trend patterns derived from NDVI and EVI were similar (see Figure S2 for EVI analysis), we focused our analysis in the main text on NDVI in order to simplify the presentation. Likewise, additional analyses are possible, such as ones based on satellite-derived data products for vegetation class or plant functional type. We did not perform analysis on such data products as the underlaying classification algorithm can introduce arbitrary breakpoints in the data, especially when data density evolves over time, as it does here from Landsat 4 to Landsat 8.

The median NDVI over a monthly or seasonal time period was used to increase the robustness of the time series analysis and minimize the impact of possible coregistration errors of individual satellite images. We used summer NDVI (median NDVI during the period from 1 June through 30 September) for analysis (except if indicated otherwise), as this interval provides a quantification of perennial vegetation cover and excludes the significant variation that occurs due to annual plants contributing to springtime NDVI measurements as shown for an example pixel in Figure S3. We focused on changes in perennial vegetation because these plants play a key role in maintaining the stability and functioning of the ecosystem (Berg & Steinberger, 2012). Analysis of trends in peak spring growth from NDVI is more challenging (and not undertaken here) because satellite overpass frequencies are not daily, leading to the potential for aliasing when
sampling the narrow spring peak. Further complications are introduced by a changing sampling frequency over time, which would complicate trend detection.

Vegetation is sparse across large parts of the study domain, leading to an important soil signal in the satellite observed reflectance. While NDVI largely separates out the vegetation signal from the spectral signature, absolute values of NDVI are still influenced by the soil characteristics, which complicates comparison of NDVI values between locations with different soils in dryland areas. Changes in vegetation were assessed by performing linear regression between NDVI and year, to avoid the impact of the soil signal to a large extent. We used the slope of the regression to estimate the rate at which the vegetation changed over the study period. As the soil within a given pixel stays the same over the study period, the observed trends in NDVI are almost exclusively vegetation related and these trends can hence be compared between different areas. This analysis and all posterior analysis were performed at the native 30-m Landsat pixel resolution.

2.3. Climate and Burned Area Data

Daily climate data used to examine relationships with the NDVI time series was extracted from the gridded interpolated climate data produced by the Parameter-elevation Relationships on Independent Slopes Model (PRISM; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, last accessed 01/03/2019; Daley et al., 2002) at 4 km spatial resolution. Climate data was bilinearly interpolated to the spatial resolution of the Landsat data. Annual climate data for precipitation was calculated over the hydrologic year (1 October–30 September) and mean summer temperature was used. Using winter precipitation or mean annual temperature did not qualitatively change the outcomes of our attribution analysis. We analyzed specifically whether summer precipitation explained some of the pattern in summer NDVI across the lowland desert area but found no significant relationship.

Fires have influenced many parts of the study domain, and have occurred more frequently across the wetter, western half of the domain (Figure S4). As vegetation disturbance from fire and post-fire vegetation recovery strongly influence temporal trends in NDVI, we accounted for fire disturbance in our analysis. Fire perimeters for 1950–2017 were obtained from California’s Fire and Resource Assessment Program (https://frap.fire.ca.gov/frap-projects/fire-perimeters/, last accessed 01/03/2019). We used the last date of fire disturbance for each 30 m pixel individually (Figure S4) to assess the impact of fire disturbance on the observed trends in NDVI.

2.4. Data Analysis

The role of different environmental and climate drivers in explaining the observed NDVI trends was assessed both spatially and temporally. The large-scale spatial pattern of the trend in NDVI was assessed using a Generalized Additive Model (GAM) from the “mgcv” package in R 3.6.1 software (Wood, 2011). A GAM was used because it does not have a priori determined shape of the relationship between the response variable and the covariates; it is derived purely from the data (Guisan et al., 2002). We used spatial estimates of the linear trend in annual precipitation and summer temperature, as well as mean annual precipitation and time since last fire (Figure S4) as covariates to explain the observed spatial pattern in NDVI trends. Due to computational constraints a random sample of 20,000 30 × 30 m points (0.14% of the domain) was extracted to build the GAM model. Results of the GAM model might be impacted by unaccounted spatial autocorrelation. To assess the robustness of the results from the GAM models, and further explore in-depth the drivers of NDVI change we performed a set of additional a set of analyses as described below.

In a separate analysis, linear regression models were developed for each individual Landsat pixel to assess which variables explained the interannual variability in the NDVI time series and its long-term trend. This analysis was also performed using the mean NDVI time series constructed from the entire mountain area in the western part of the study domain and the lowland desert area in the eastern part of the study domain, to better understand the response of these contrasting ecosystems to environmental drivers. The two regions were separated along a 500-m elevation contour shown in Figure 1. We used annual precipitation, mean summer surface air temperature, and previous 1-, 2-, and 3-year integrated precipitation as variables to explain the summer NDVI time series. We also explored whether interactions between precipitation and temperature could explain part of the temporal variance. We estimated the relative contribution of each
variable within the linear model by decomposing the linear model using the Lindeman, Merenda and Gold ("lmg") method as implemented in the "relaimpo" R package (Gromping, 2006; Lindeman et al., 1980). All analyses were performed using R 3.6.1 software (R Core Team, 2019).

3. Results

3.1. Vegetation Trends

Large declines in NDVI and apparent losses in vegetation cover occurred over the last 34 years (1984–2017) across the study region (Figure 2). The long-term NDVI decline was most widespread in the July-September summer period, with 87.1% of the study domain showing a downward trend. The observed negative trends in NDVI were highly significant in most 30 m pixels, with the exception of areas within recent fire scars (Figures S4 and S5). The most striking change was the strong reduction in NDVI across the lowland desert area in the eastern part of the study domain (Figure 2, Table S1). Mean summer NDVI across the lowland deserts decreased by 1.11 ± 0.26% yr⁻¹ (Figure 3; Table S1). In accordance with the change in NDVI, we observed significant increases in the red reflectance (p < 0.01; Table S2). NDVI declines were apparent throughout the year in lowland deserts (Figure 2), which suggests they were associated with a structural change in perennial vegetation.

A widespread decrease in NDVI was observed in the mountains during the summer months with a mean reduction of −0.37 ± 0.18% yr⁻¹. The relative decrease was less extreme in the mountains than the lowland desert area, while the opposite was true for the absolute change (−0.049 NDVI vs. −0.029 NDVI), as a
consequence of the higher NDVIs in the mountains (0.241 NDVI) than deserts (0.067 NDVI). Most of the mountain region showed a decline in NDVI, with isolated areas showing a slight increase. The NDVI trends were variable during autumn and winter (October–March), showing a mixture of areas with increasing, decreasing, or no trend.

### 3.2. Drivers of the Spatial Pattern of Vegetation Trends

Climate and fire occurrence explained part of the spatial pattern of the observed trends in summer NDVI (median June–September NDVI). Precipitation was highly variable from year to year, exhibiting a weak, nonsignificant decline by approximately $-17 \pm 11$ mm per decade in this lowland desert area and by $-37 \pm 27$ mm per decade in the adjacent mountain areas over the 1984–2017 study period (Figure 3, Figure S4, Table S1). Summer temperatures increased significantly by $0.5^\circ C \pm 0.1^\circ C$ per decade in the low

![Figure 3](image-url)
elevation desert and in the mountains. Wildland fires occurred frequently and were especially prevalent in the wester, higher elevation part of the study domain (Figure S4).

A GAM model incorporating temperature and precipitation trends, mean annual precipitation, and time-since-fire explained about 37% of the spatial variability in the summer NDVI trend. Regions that experienced more substantial declines in precipitation had larger decreases in summer NDVI (Figure 4a). Similarly, regions with larger more pronounced temperature increases also had stronger summer NDVI decreases (Figure 4b).

Wildland fires are an important driver of spatial patterns of NDVI change. Areas that recently burned had strong negative NDVI trends as at least part of the vegetation was killed and removed by the fire. Areas that burned around the start of our study period showed an increase in NDVI related to vegetation recovery after fires, while later-occurring fires did not demonstrate such recovery. The response to fire yielded a hump-shaped response in which positive NDVI trends were largest for fires that burned during the 1980s and 1990s, and most strongly negative for recent fires (Figure 4c). Considering these drivers together, there is still a large part of the observed variance in NDVI change which remains unexplained across the precipitation gradient in our study domain (Figure 4d), with drier areas showing a much stronger decrease than expected when compared to wet areas.

3.3. Can We Explain the Observed Trends?

A simple linear regression model using annual precipitation was able to capture part of the variance in summer NDVI time series (Figure 5; Table S1) for both the lowland desert (34%) and mountain areas (61%). Another simple model with only summer air temperature explained 32% of the variance in the lowland
desert and 24% in the mountain region. In the case of the lowland desert temperature explained more of the variance than precipitation.

A full linear model, including precipitation, temperature and summed precipitation during the previous 3 years, explained 58% and 79% of the variance in annual summer NDVI for lowland desert and mountain areas respectively (Figure 5). This means that changes in NDVI in the higher elevation region were better explained by the variables included in the model than changes in NDVI across the lowland desert. This was especially evident toward the end of the desert time series, when the linear models were unable to represent the strong decrease in NDVI during the 2012–2016 period. A relative importance variable analysis revealed summer temperature and annual precipitation contributed about equally as drivers in the lowland desert region, and that annual precipitation was more important in the mountain region (Figure S6). Precipitation of the previous year did explain a small amount of variance, with precipitation 2 and 3 years before increasing in importance the longer the time lag considered, and they seem slightly more important for drier areas (Figure S6). Including an interactive term of precipitation and temperature within the linear regression to explain the temporal trend in mean summer NDVI was not significant for both the lowland desert and the mountain region and not further included in the analysis.

When fitting linear regression models for each pixel individually we found that the per pixel model using precipitation alone was largely unable to reproduce the observed long-term trend in summer NDVI across most of the study domain, while the model that included only temperature explained considerably more of the overall spatial pattern (Figure 6). Much of the total variance in the annual summer NDVI time series across the lowland desert region was explained by temperature alone (Figure 5, Figure S7). The full model, including precipitation, temperature, and the previous 3 years of precipitation, explained a large portion of the variance across the entire study region (Figure S7). Exceptions for this general pattern are recently burned areas ($R^2 = 0.44$ for areas burned after 2000 and $R^2 = 0.53$ for areas not burned are burnt before the year 2000). There was also heterogeneity in the eastern, lower elevation region, with some areas showing relatively low $R^2$ values. The full regression model predicted the magnitude of the decrease in summer NDVI for the higher elevation areas but underestimated the magnitude of the decline in lowland desert areas (Figure 6).

To investigate whether the relationship between annual precipitation and annual NDVI changed over time, as might be expected for a structural change in vegetation composition, we separately computed regression relationships for the first half and second half of the time series. For the higher elevation areas, there was a consistent positive linear relationship between annual precipitation and annual summer NDVI, with almost identical relationships between early and late periods in the 34-year time series (Figure 7). However, for the lowland desert region the intercept of the precipitation-NDVI relationship shifted downwards after the start of the drought in 1999. This means that for the same precipitation input amount there was higher mean NDVI prior to 1999 as compared to after, which is consistent with a structural change in ecosystem functioning over the study period and a loss of canopy cover (Ehleringer, 2001).

4. Discussion

4.1. Large-Scale Vegetation Loss

Here we provide evidence for a widespread decline in perennial vegetation cover in lowland deserts of southern California over the past four decades (Figure 2). Vegetation cover also declined in surrounding
higher elevation areas, but to a lesser extent. The observed trends are consistent with the hypothesis that warming temperatures have caused a long-term increase in water limitation. This is especially clear across the lowland deserts, which are the driest areas of the study domain, and is superimposed against high levels of interannual variability in precipitation. Previous findings by Williams et al. (2020) indicate how warming increases drought severity, and here we show that this may result in a loss of vegetation cover.

Although we observed widespread decreases in vegetation cover throughout our study domain, the responses of the lowland desert and higher elevation mountain areas to climate warming and precipitation variability had different magnitudes and were likely modulated by different processes. The more mesic higher elevation areas experienced smaller relative decreases in NDVI and the relationship between mean annual precipitation and NDVI did not appear to appreciably change over time (Figure 7). Hence, this is a straightforward way to predict the potential changes in vegetation for these systems, at least within the range of climate variability observed for the study period.

In contrast, the lowland desert areas experienced a stronger relative decline in vegetation cover (Figure 2) in line with large-scale mortality events that have taken place over the last 2 decades (McAuliffe & Hamerlynck, 2010; Miriti et al., 2007). Precipitation is an important driver of vegetation patterns and trends in dryland ecosystems (Goldberg & Turner, 1986; Hereford et al., 2006; Knapp et al., 2015; Miriti et al., 2007; Poulter et al., 2014; Tucker et al., 1991; Weltzin et al., 2003). Our attribution analysis is consistent with this past body of work, but also shows that temperature is as important as precipitation in explaining interannual variability in vegetation cover and is even more important for explaining multidecadal trends (Figure 6). Many plant species in desert ecosystems have adaptations that allow them to withstand high
temperatures, making this observation somewhat unexpected. Previous research has indicated some temperature sensitivity of certain perennial desert plant species (Munson et al., 2012, 2013). However, these findings are in line with observations of photosynthetic productivity in drylands, with lower gross ecosystem productivity under higher temperatures, both interannually and spatially (Biederman et al., 2017). Higher temperatures can increase evapotranspiration, which in turn, may lead to a reduced water availability and greater moisture stress for perennial plants during dry summer months. An important challenge in future work is to further assess whether the link between surface air temperature increases and vegetation decline operates through a water stress mechanism as described above, or by means of the direct effects of heat stress on plant physiology and mortality. In this context, it is also important to recognize that some of the temperature stress may arise by means of biophysical feedbacks with variability in the hydrological cycle (Humphrey et al., 2021).

For lowland desert areas, our analysis suggests these ecosystems may have crossed an ecological threshold, leading to a shift in the precipitation versus NDVI relationship over the study period (Figure 7). Although NDVI is often linearly related to precipitation, we observed that the intercept of this relationship declined after the onset of the drought period in 1999 (Dai, 2013), coincident with rising temperatures. We find a lower NDVI after the year 1999 than before for a given level of annual mean precipitation. This suggests that the vegetation is undergoing or has undergone a restructuring through large-scale mortality in response to new temperature extremes. The break in the relationship suggests climate warming has not just contributed to a reduction in overall vegetation cover but has induced a reorganization of species composition, a consequence of varying increases in plant mortality between species. McAuliffe and Hamerlynck (2010) found that Ambrosia species has experienced up to 100% mortality in desert regions around our study region, while L. Tridentata has experienced lower mortality rates. For drylands, such reductions in year-to-year rainfall-use efficiency is indicative of degradation in other settings (Ehleringer, 2001). As these systems may be governed by thresholds, one potential implication is that it will be very difficult to predict future responses to changing environmental conditions. This could pose an important limitation to our ability to understand how drylands will be affected by future climate change.

There are several processes that could reduce or slow the recovery of desert vegetation. Many perennial desert plant species are long-lived, resulting in slow plant turnover times, frequently greater than 100 years (Cody, 2000; Vasek, 1980). Shrubs that are able to survive drought do so by a combination of factors, including cavitation-resistant xylem, deciduousness, photosynthetic stems and a broad range of plant water potential, water uptake depth and gas exchange behavior (Pivovaroff et al., 2016). Many of these strategies could be impacted by high temperatures, when evaporative demand increases. This, in combination with a recruitment bottleneck (e.g., Turner, 1990) where seedling establishment only occurs during rare, multiyear wet periods, results in very slow regeneration (Shriver et al., 2019). On the other hand, desert annual plants will simply not germinate in dry years or will germinate in very low numbers and will remain very small in stature during dry years (Venable, 2007). Increased temperatures will influence the suite of species that germinate along with their ability to survive and reproduce (Kimball et al., 2010). Over time, reduced reproductive rates of desert annuals would deplete the seed bank. Once vegetation decreases, recovery is further limited because few species can colonize bare soil directly but depend on existing adults (“nurse plants”) for protection from adverse environmental conditions during the first few years following germination (McAuliffe, 1988). Vegetation recovery after disturbance can take a century in some desert ecosystems (Carpenter et al., 1986; Webb et al., 1988), and we may have entered a long-term state characterized by reduced vegetation cover for these lowland desert areas.
**4.2. Precipitation Legacy Effects**

Studies of the importance of time lags between precipitation occurrence and vegetation response have often indicated that the legacy of precipitation in prior years influences productivity and other ecosystems processes in the present (Bunting et al., 2017; Kimball et al., 2018; Ogle et al., 2015; Sala et al., 2012). We observed this type of legacy effect in the Landsat record (Figure S6), and that the importance of precipitation legacy increased at longer timesteps, underscoring the importance of long-term precipitation regime in driving vegetation trends.

Another factor that has been hypothesized to influence vegetation response to drought is the increase in atmospheric CO$_2$. While increases in atmospheric CO$_2$ have the potential to reduce the impact of temperature and drought on desert vegetation (Hamerlynck et al., 2000), our results imply that any positive effect of rising CO$_2$ over the last 30 years was overwhelmed by the competing negative effects imposed by climate variables observed here, leading to a net decrease in NDVI. This is in line with previous findings that climate drivers can overwhelm the atmospheric CO$_2$ effect (Brookshire & Weaver, 2015).

**4.3. Spatial Heterogeneity**

While we observed a reduction in NDVI over the entire lowland desert area, there were important local differences in magnitude between nearby pixels, showing the value of performing vegetation trend analysis at relatively high resolution (30 m). This type of fine scale information may be useful to land managers, as they develop conservation and management plans. This local spatial heterogeneity within the overall large-scaled patterns also explains the relatively low explanatory power of the GAM model. As the input climate drivers have a coarse resolution (4 km) we were limited to describing large-scaled patterns of vegetation change. However, important local differences also occur, and are likely tied to fine scale differences in topography, hydrology, and species composition. Such differences between nearby pixels (30 m) are in line with previous findings that contrasting species have differential sensitivity to changing climate conditions, depending on structural, physiological, and life-history characteristics (e.g., Miriti et al., 2007; Munson et al., 2012). Other environmental factors such as slope, orientation, and soil depth and type will influence the impact of changing climate conditions on ecosystem function and vegetation dynamics (Munson et al., 2015). Unfortunately, no detailed soil maps exist for this region, and so we were unable to quantify the impact of soil characteristics on the vegetation trends we observed in the Landsat time series.

Much of our study domain is public land that is protected from development, though historical and current anthropogenic impacts nonetheless have influenced vegetation dynamics (Lovich & Bainbridge, 1999). For example, off-road recreational vehicles may disturb biological soil crusts and perennial plants (Lovich & Bainbridge, 1999). Most of these effects are local, and it is unlikely that past and present anthropogenic disturbances explain the large-scale vegetation decline described here, though they clearly drive some changes, as observed for fire (Figure 4).

**4.4. Implications for Dryland Conservation**

Desertification and the large-scale degradation of productive areas across global drylands remains a global concern (Millennium Ecosystem Assessment, 2005). Much of this attention has focused on the degradation of dryland grazing lands, where transitions from grassland to woody, less productive systems carry implications for livestock (e.g., Venter et al., 2018). Here we show that more xeric systems also have undergone large-scale vegetation changes during the satellite era. While part of this reduction may be attributed to a reduction in perennial vegetation LAI, ample field data confirms an important contribution of perennial plant mortality (e.g., McAuliffe & Hamerlynck, 2010; Miriti et al., 2007). Perennial plant species are considered more sensitive to drought than annual species (Schwinning & Ehleringer, 2001), and a shift in plant community composition toward a larger dominance of perennials compared to perennials with climate warming appears possible. This may help explain the pattern of increasing spring NDVI and decreasing summer NDVI we observed (Figure 2). Such changes would have important implications for ecosystem functioning and carbon, water, and nutrient cycling, as well as for food webs and higher trophic levels. For example, a shift from perennial to annual vegetation has been related to an acceleration of the N-cycle and increasing inorganic N availability (Booth et al., 2003). Furthermore, as the nutrient cycles in dryland systems depend
largely on precipitation, increasing drought may lead to a decoupling of C-N-P cycles (Delgado-Baquerizo et al., 2013), with subsequent impacts on ecosystem function.

Precipitation is expected to decrease in many dryland areas including Southern California (Dai, 2012), which, in combination with increasing precipitation variability (Swain et al., 2018), will likely result in more frequent droughts (Williams et al., 2020). However, we found that the desert perennial vegetation is also sensitive to temperature change, which means that dryland vegetation may be more susceptible to climate change than expected (Hoover et al., 2019). This is consistent with the findings of an experimental warming study on desert vegetation, where a 2°C increase in temperature caused significant declines in photosynthesis (Wertin et al., 2017) depending on plant functional traits (Valencia et al., 2016). While we have quantified the decrease in desert vegetation that already has taken place, our findings indicate further, potentially important restructuring of desert vegetation with future warming.

Data Availability Statement

Landsat Level-2 surface reflectance data are available at https://earthexplorer.usgs.gov. Fire perimeters are available from the California’s Fire and Resource Assessment Program (FRAP; https://frap.fire.ca.gov/frap-projects/fire-perimeters/). The climate data used is available from the PRISM Climate Group, Oregon State University (http://prism.oregonstate.edu; Daly et al., 2002).

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