

Vegetative Responses to Drought Events in California Grasslands

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ABSTRACT

I conducted analyses that related biodiversity and species composition with variation in environmental factors to understand larger vegetative trends within California grassland ecosystems in the context of climate change. I used the 2012 to 2015 California drought to observe species' responses to naturally induced, prolonged conditions of low water availability. I related biodiversity and species compositional structures to spatial and temporal variables to understand variation between sites and drought and non drought conditions. I compared bedrock composition with alpha diversity metrics and analyzed the impact on grassland vegetative communities. I studied native and nonnative species composition to understand how species' origins impact drought responses. Species distribution and abundance was strongly correlated with temporal and spatial variation within the ecosystem ($p=0.037$). Bedrock characteristics were correlated with variation between site responses to the drought events and the most variation in diversity was observed for plant communities on sandstone composites ($p=0.007$). Both nonnative and native plant species had significant reductions in cover during drought years ($p=0.002, 0.004$). Preserving grasslands that hold the greatest amounts of observed biodiversity may not actually be as beneficial for conservation efforts in the context of climate change as including more diverse types of plant communities regardless of measured diversity indexes. Factors that vary between bedrock types such as water retention capacities significantly impact plant resilience and recovery. While drought may have positive effects on reducing nonnative plants during dry periods, there are lasting implications for species composition.

KEYWORDS

climate change, bedrock, nonnative species, biodiversity, rangeland ecology

INTRODUCTION

Climate change induced drought is causing permanent changes to habitat structures and community interactions. Increasing temperatures diminishes water storage potential in snow and ice reserves, resulting in less water availability via snowmelt runoff throughout the year and greater vapor pressure deficits and dry periods (Luce et. al 2016). This trend increases drought prevalence across ecosystems- current climate models project these drought events will become more intense and frequent in many ecosystems in the future (IPCC 2014). Understanding the extreme drought that occurred within California from 2012 through 2015 provides an opportunity to analyze potential biological impacts of climatic drying since climate change is acknowledged as a leading driver impacting plant ecosystems (Piras et. al 2016). Predicting the impacts of and adapting for climate change will be a crucial element of biodiversity and ecosystem service conservation, as future management decisions will be very much grounded in these environmental constraints (Heller and Zavaleta 2009). Community responses are expected to vary significantly between ecosystems and understanding ecosystem specific responses during these extreme climatic events is a necessary component of successful impact assessment.

Grassland and rangeland ecosystems throughout California are important ecological landscapes that provide valuable ecosystem services and may be uniquely impacted by drought. Grasslands continue to be a dominant vegetation type in California, amassing more than 10% of the state's total land area. They are listed among the species-richest vegetation communities (Linnell et al., 2015) and provide a natural form of water filtration as well as habitat for wildlife. They contribute to reductions in soil erosion, maintain soil health, and are crucial for preserving biodiversity in California (Chan et al. 2006, Chaplin-Kramer et al. 2011). The resilience of grassland communities that are frequently exposed to severe weather events suggests sites within this region and climate may be less impacted by environmental changes (Copeland and Harrison 2016). However, documented trends indicating average drought periods lengthening may provide new challenges to these plant communities. Severe droughts limit grassland production (Knapp & Smith 2001), cause lasting alterations to nutrient cycles (Evans & Burke 2013) and increase vulnerability to wildfires and invasive species (Abatzoglou & Kolden 2011). The future of grasslands for grazing, conservation, and wildlife habitat is dependent on the resiliency of

ecosystems to relatively sudden changes in abiotic climatic factors. Predicting and modelling vegetative responses that relate specific environmental characteristics with community resilience is a critical component of preserving grasslands and mitigating the impacts of climate change on these communities.

Analyzing environmental variables pertaining to vegetative structure and growth increases understanding of larger ecological trends and transformations that are a result of environmental changes. Site responses to temperature and precipitation is likely to be largely related to the species composition present. The vegetative structures of grasslands is often the primary determining factor for fire hazard, erosion capacity, as well as for which wildlife and browsing species may be supported by these grasslands (Huntsinger and Oviedo 2014). Species composition influences water tables and availability in the region as well as the resiliency of the area to environmental disturbances (Frank and McNaughton 1991). Present day California grasslands are characterized by non-native, annual grasses which dominate slower growing, perennial grasses and flowering plants. This reduces ecosystem biodiversity and causes increased fire hazards due to the large amounts of dead biomass that accumulates with seasonal annual grass dieback. Extreme weather events such as drought can cause legacy effects in soil biota populations, promoting exotics and suppressing natives in plant communities that have already been invaded by nonnative vegetative species (Meisner et al. 2013). A more biodiverse plant population in which different species occupy different niches may allow for diminished resource depletion and lessen vegetation dieback (Wagg et al. 2017). While community structures are essential in the assessment of a landscape's resilience to climate change, geological site characteristics are another important consideration that influences plant community resiliency.

Relationships between bedrock and soil composition and vegetative responses to drought may also provide important insights into predicting and characterizing future ecological responses based on geological characteristics. Soil and bedrock attributes influence water tables within bedrock, as well as soil erosion and runoff capacity. The impact of soil biota on carbon and nitrogen availability suggests soil properties play a significant role in affecting vegetative responses to drought (De Vries et al. 2012). Bedrock geochemistry is also likely to have an impact on vegetation growth limitations on primary productivity (Halm et. al 2014) and regulation of water holding capacity. Bedrocks with higher concentrations of minerals such as calcium and silicon have been evidenced to have higher levels of regolith water loss rates (Jiang

2020). Bedrock chemistry is capable of producing quantitative measurements of the ecosystem's ability to retain water which is necessary for vegetative growth during drought periods (Quine 2020). There are currently limited publications regarding the resiliency of California grasslands to naturally induced, prolonged drought conditions. This research informs predictions on possible outcomes of future drought events through the analysis of a four year, natural drought event. Its purpose is to further determine how specific environmental factors impact community response to drought.

My study focuses on how grassland plant communities respond to extended drought conditions in Tejon Ranch. I address plant community structure and resilience by asking (I) What are the relationships between temporal and spatial variation and species composition and abundance? (II) How does soil type and bedrock composition influence plant community drought resilience? (III) How do native and nonnative species respond differently to drought? Some predictions regarding the outcome of this analysis include that plots with higher initial biodiversity and richness will experience less total diversity loss due to species occupation of differing ecological niches as well as increased likelihood of some of the species present having better adaptations for these environmental changes. Different types of bedrock are expected to host plant communities which respond differently to drought due to influences from environmental factors such as microbiota, erosion, and runoff. Water retention rates within the soil are expected to be influenced by bedrock mineral composition, impacting water availability for the vegetative communities present. Invasive species are expected to increase in proportion to their native counterparts, especially in locations that have already been heavily occupied by nonnative plant species. Data collection objectives include the documentation of average precipitation and temperature obtained from the PRISM Climate Database. Vegetative data includes transect data recording plant species identification, the frequency of species occurrences, and the number of species documented per plot. Bedrock and soil characteristics were recorded annually for each plot, and study sites were stratified by bedrock classifications.

METHODS

Study site

My study site is Tejon Ranch, a 270,000 acre property owned by the Tejon Ranch Company and located approximately 60 miles north of Los Angeles. It is situated within two major land resource areas (MRLA), MRLA 17 (Sacramento and San Joaquin Valleys) and MRLA 18 (Sierra Nevada foothills). Grasslands within the ranch are largely composed of nonnative annual grasses from Europe and the Middle East. The introduction of grazing ungulates such as cattle and sheep in the 1840s had significant impacts on vegetative structures and compositions. Situated within four different ecoregions including the Great Central Valley, Sierra Nevada, Mojave Desert, and Southwestern California (Figure 1), it is incredibly diverse ecologically. The ranch contains over 900 native plant species- 14 percent of the native flora that occur in California can be found within the region. Ninety percent of the area is preserved by the Tejon Ranch conservancy, which allows for research and study sites to remain largely undisturbed by anthropogenic influences such as urban development. Due to its unique size and location, analyzing the impacts of naturally induced, extreme climatic events within the region contributes to greater scientific understanding of how California Mediterranean grasslands will respond to climate change.



Figure 1. Map of Tejon Ranch. Topographic map displaying Tejon Ranch and its location upon four distinct ecoregions.

Vegetative data

I used vegetative data collected by Peter Hopinkson's Rangeland Ecology lab to determine vegetation patterns from 2010 to 2016. This data was collected as part of a larger ecological survey requested by the Tejon Ranch Conservancy soon after its formation in 2008. The survey was conducted with the intention of providing the conservancy a better understanding of the vegetative and community composition within the area delineated for conservation. Site locations were designated using random sampling and stratified based on bedrock composition. All sites were within 500 meters of the road. Sites within 10 meters of the road or that were located in non-grassland sites such as riparian and shrub areas were excluded based on these parameters. Sites were surveyed annually during the spring months of march and april. They used 25 m long line point transects and releve surveys taken within 100 m² releves. They listed and identified all the plants within the releve, and recorded ocular estimates of cover. Line transects were taken at the 4 corners of the releve, with each one heading in a different cardinal direction. They recorded transect hits at every meter.

Climatic data

To understand how climatic factors related to vegetative changes in my study site, I obtained climate data including mean monthly precipitation and average temperatures from the PRISM Climate Database and interpreted them using the Palmer Drought Severity Index. This method uses temperature data, precipitation data, and water balancing models to generate estimates of relative dryness and calculate changes in evapotranspiration. The interpolation method used by PRISM calculated relationships between climate and elevation using a regression model for each 800 m grid cell. The model uses point data, spatial data, and a digital elevation model to estimate climatic parameters over a specified period of time. Points within the regression are weighed and compared to the physiographic similarity of the grid cell. These physiographic indicators included location, elevation, coastal proximity, vertical atmospheric

layering, topographic positioning, as well as topographic facet orientation and orographic effectiveness of the landscape.

Analysis

Biodiversity

NMDS and Shannon Diversity. To understand the dominant vegetative communities present in my study sites and how they were impacted by the drought event, I used non geometric multidimensional scaling in R. I used the Ecology package and the metaMDS and permanova functions to analyze relationships between PRISM Climate Data and plant community surveys. This indirect gradient analysis approach produces ordinations that are based on a dissimilarity matrix. I related these vegetation data points to the data collected from PRISM that was interpreted using the Palmer Drought Severity Index. This correlated the relative importance of the gradients and provided an interpretation of species and environmental relationships. To compare diversity and environmental variables I quantified alpha diversity within each plot. I used the Shannon Diversity Index to characterize community species abundance, evenness, and richness. I arrayed site years across ordination space and categorized sites based on species composition elements and clustered plot years based on similarity. R squared correlation coefficients suggested how much variation between the sites can be explained by ordination. I derived new axes and maximized variance within the dataset with axes rotation.

Bedrock

Repeated measures ANOVA test. I analyzed differences in biodiversity between bedrock types to understand if certain bedrock types hosted vegetative communities with significant differences in drought resiliency. Sites were stratified by geological differences between bedrock types, and I grouped sites based on bedrock and soil composition using the observations recorded by Hopinkson's research team for each plot. I compared alpha diversity within bedrock types between drought and non drought years to observe differences in responses

to drought between vegetative communities based on bedrock characteristics. I used a one way repeated measures ANOVA test in conjunction with a Post Tukey HSD (mean was considered significant at P 0.05) conducted on each bedrock classification type to quantify the impact of bedrock and soil characteristics on diversity metrics.

Native and Nonnative Species

Differences in native and nonnative species. To understand the difference in reactions between nonnative and native plant species to drought conditions, I used a one sided repeated measures ANOVA test in conjunction with a Post Tukey HSD (mean was considered significant at P 0.05) and compared vegetative differences in percent cover. I used binary classifications that regarded each year in the study period as either a drought year or a non drought year and conducted tests respectively for native and nonnative percent cover.

Differences in non drought years. To analyze native and nonnative species composition differences in grasslands between conditions preceding and following the four year drought event, I conducted one sided t tests. The first one sided t test compared nonnative species cover in 2010 and 2016, while the second one test compared native species cover in the same plots during the same time period. I classified each species as nonnative or native and then summed species cover percentages based on their delineation as native or nonnative. I excluded observations unrelated to species classification, ie. the percent cover of litter, bare ground, bioturbation, etc.

RESULTS

Climatic Data

Results from the climatic data analysis conducted using Palmer Drought Indexes and PRISM climate data indicate that 2014 was the most intense year in terms of drought severity, followed by 2013 (Figure 2). 2010, 2011, and 2016 were classified as non drought years using this methodology.

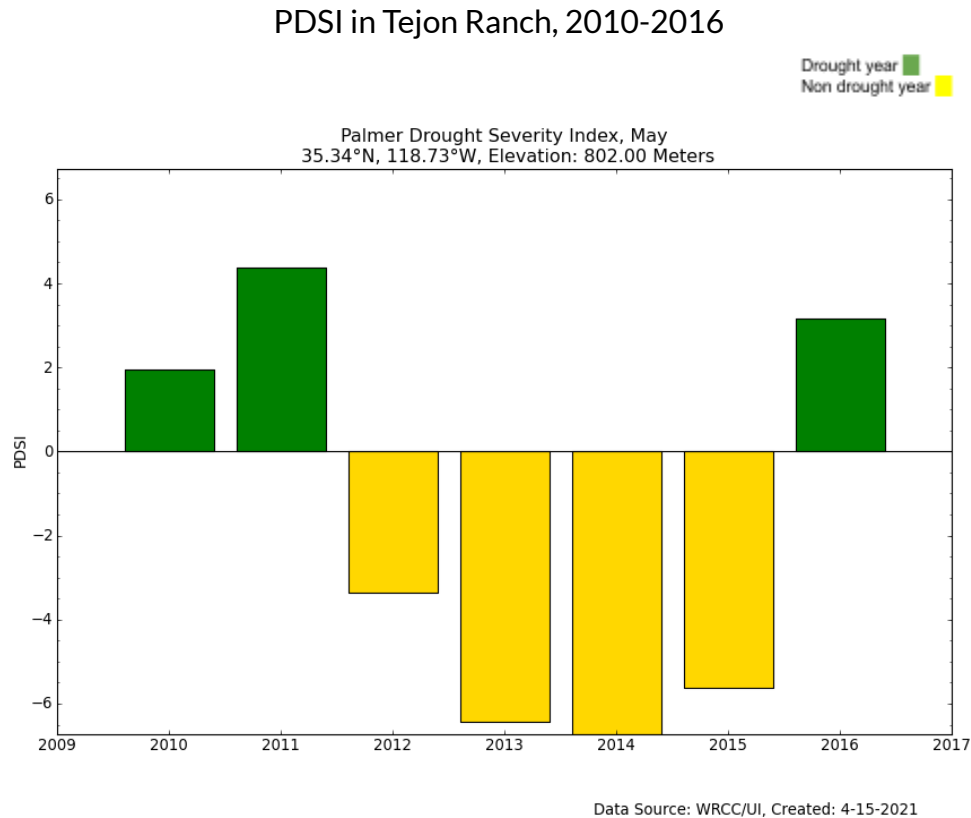


Figure 2. Palmer Drought Severity Index in Tejon Ranch, 2010-2016. Values above zero indicate a non drought year (green) and values below zero indicate a drought year (yellow)

Biodiversity

Sites showed greatest variability in biodiversity during 2014, the most severe drought year (Figure 3). The least variation in site biodiversity was observed during non drought years. In general, drought had a negative impact on biodiversity for the sites surveyed. Initial biodiversity indexes recorded prior to the drought event reveal that site responses to drought in this ecosystem are likely more dependent on factors pertaining to species composition and abiotic factors than to previous levels of diversity. Trends in biodiversity across the study period reveal more diverse sites were not more resilient to drought than less diverse sites.

Biodiversity Across Study Sites

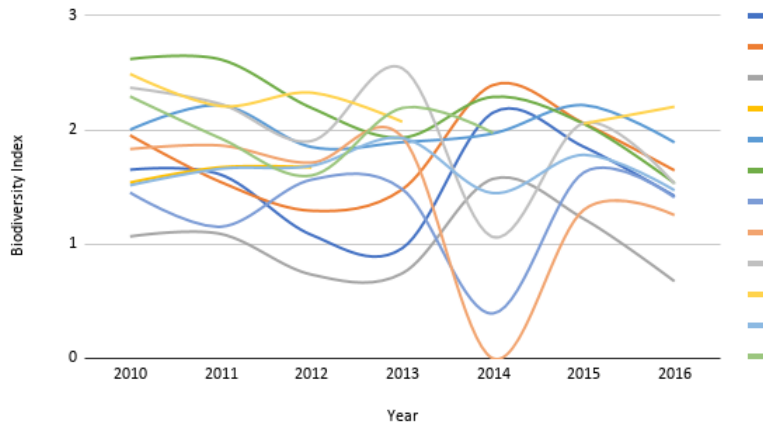


Figure 3. Biodiversity Across Study Sites. This graph shows average Shannon diversity indexes for all plots for the study period

Results from the NMDS suggest that variation within spatial and temporal characteristics within study sites had significant impacts on species abundance and diversity metrics. Two axes were extracted as independent variables, including site locations and the year during which the species composition observations were made. I observed a significant correlation between species distributions and abundances and environmental variations in drought and geographical positioning ($p=0.037$). I observed two distinct vegetative communities within the sites and years surveyed, with some overlap of the most abundant species documented within all sites studied (Figure 4). The first vegetative community exhibited less variation related to abiotic factors, while the second vegetative community had a significantly larger range across sites and years.

Results of NMDS Across all Sites 2010-2016

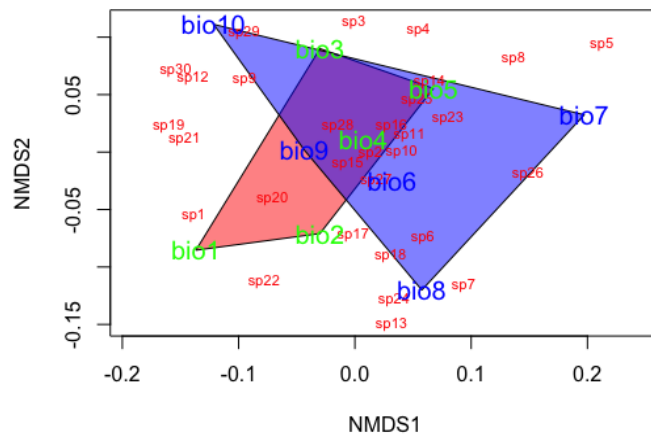


Figure 4: Results of NMDS Across all Sites 2010-2016. Results of NMDS of biodiversity and community structure. Axes are representative of spatial and temporal variation within the dataset as they relate to species abundance. The two distinct vegetative communities observed between all site types are evidenced in red and blue.

Bedrock

I used a one way repeated measures ANOVA on biodiversity by bedrock classification. The differences in biodiversity between drought and non drought years were significant for vegetation located upon sandstone composites ($p=0.007$). Sites located upon sandstone composites exhibited significant declines in Shannon diversity metrics during drought years, but quickly exhibited signs of recovering once precipitation and water availability factors returned to normal averages. Sites that were located upon alluvium and grandlorite hosted plant communities that sustained biodiversity indexes similar to non drought years during dry periods. Biodiversity indexes on alluvium substrates were actually observed to increase slightly during dry periods, and returned to slightly lower levels of diversity that were evidenced prior to the drought event (Figure 5). I observed these sites to have the lowest average biodiversity (1.542). Sites located on grandlorite bedrock had the highest average biodiversity (2.002), and experienced only minor declines in diversity metrics during the drought years that were not observed to recover in the year subsequent to the drought.

Biodiversity Across Bedrock Classifications 2010-2016

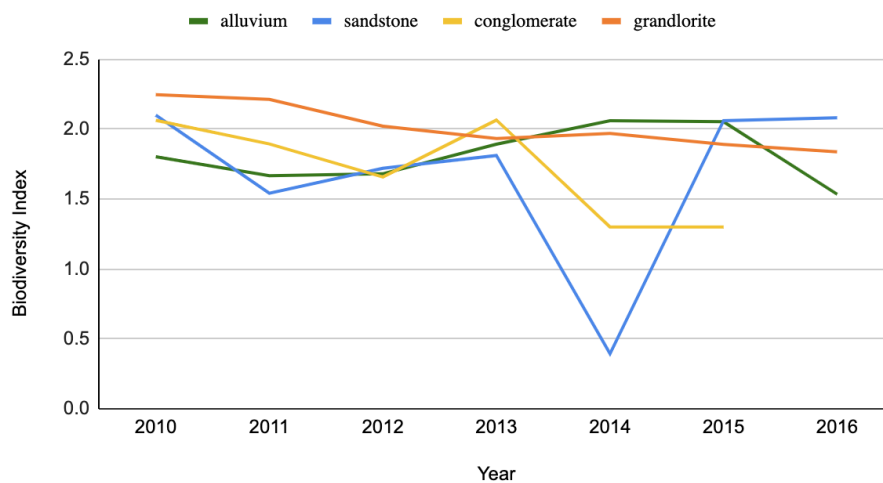


Figure 5: Biodiversity Across Bedrock Classifications. Differences between mean biodiversity indexes in sites distinguished by bedrock composition is illustrated. Biodiversity indexes are displayed for each year of the study.

There was a significant difference in biodiversity between sites located on sandstone and grandlorite, and sites located on grandlorite and alluvium ($p= 0.00162$). Despite the absence of data for conglomerate substrates subsequent to the drought, I observed that communities located upon this composite slightly increased in the initial phase of the prolonged drought before experiencing rapid declines in biodiversity as the drought conditions were extended into 2014 and 2015. Vegetative communities on alluvium and grandlorite displayed the least variability in terms of alpha biodiversity throughout all years surveyed, while sites located on sandstone and conglomerate substrates experienced the most variation in community biodiversity as a result of the drought.

Native and Nonnative Species

The difference between species cover between drought and non drought years was significant for both nonnative and native plant species ($p=0.002, 0.004$). Mean species cover was significantly greater for nonnative species than native species (0.47,0.18). The F ratios for nonnative and native species (23.82, 9.28) indicates greater variability for invasive species response to drought than for native species in terms of percent cover. Percent cover for native species was impacted by drought at much lower proportions than it was for nonnatives (Figure 6). Indeed, despite a general lessening in native species cover throughout the drought, native species cover experienced much gradual declines that were considerably less variable in terms of species composition. While native species initially covered approximately 20% of sites, they declined to averages around 10-15% cover during dry years before their cover increased back to comparable levels of coverage they had occupied prior to the drought event. Nonnative species percent cover decreased at a larger proportion than native species cover when comparing means between drought and non drought years.

Percent Cover of Native and Nonnative Species 2010-2016

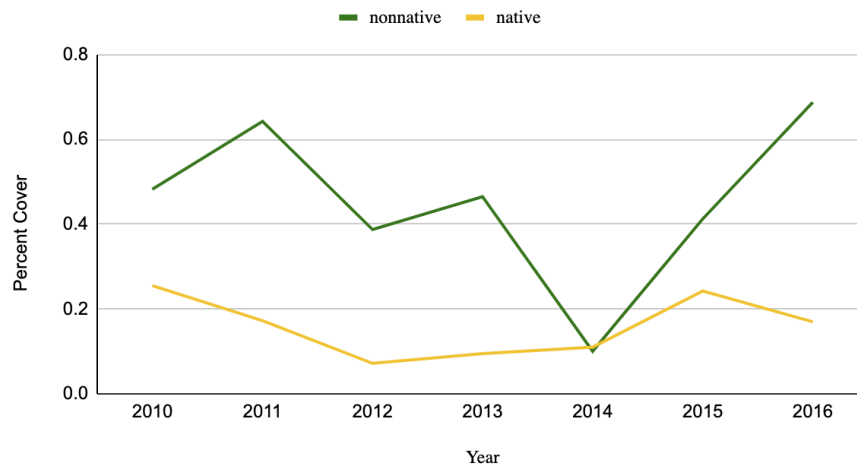


Figure 6: Percent Cover of Native and Nonnative Species 2010-2016. Differences in mean percent cover between native species and nonnative species are indicated for each year in the study period. Observations made of the percent cover of bare ground, gravel, bioturbation, etc. are excluded.

Nonnative species that used to occupy approximately a mean of 40-60% of total cover dropped to species cover percentages as low as 20% during the most severe dry period, and quickly recovered to 60% cover in 2016. Mean differences between species cover during wet and dry years was larger for non native species than for native species. Species cover was significantly different in wet years preceding and subsequent to the four year drought for both nonnative and native plant populations ($p=0.0122$, $p=0.0467$). Nonnative species had higher mean percent cover in 2016 than in 2010 (0.665, 0.497), while native species had lower mean cover in 2016 than in 2010 (0.159, 0.238).

DISCUSSION

The main objective of this project was understanding how environmental and plant community structures impacted vegetative responses to a prolonged, naturally occurring drought event within a Californian grassland ecosystem. There were significant differences observed between species composition and distribution as functions of site location and drought prevalence. While native plants fared better during the duration of the drought, community structures favored nonnative species following periods of intense dryness. Bedrock composites hosted plant communities with significantly different biodiversity indexes during drought years. I

observed complex relationships between both abiotic and biotic factors and subsequent responses to drought, indicating that existing grassland dynamics and functions are highly linked to a plant community's resilience to drought severity.

Biodiversity

Documented biodiversity and observed species distributions were highly dependent upon both drought conditions and environmental variation. R square values derived from the NMDS analysis indicate high correlations between species abundance and spatial distribution. Models of vegetative distributions across California affirm that climatic variables considered simultaneously were the strongest predictors of biodiversity (Richardson et. al. 1980). In conjunction with this finding, the distinctive plant communities observed I also underwent changes to species distribution throughout the study period. I observed abiotic variation between the location and point of time during the study at which the data samples were collected. Intensity, duration, and timing of the extremity of the drought event had implications for ecosystem resilience to the drought (Hoover et. al 2014). However, I did not observe correlation between the level of biodiversity observed at the beginning of the study and the resilience of these more diverse communities to drought. Some diverse plots appeared to retain diversity indexes during drought years that were comparable to documented indexes in non drought years, while other diverse plots experienced either sharp declines or slight increases in diversity. I observed a general trend of overall decline in diversity indexes after the drought event which points to droughts' long term impact on plant communities.

Grassland communities may be more impacted by legacy effects of climate change and less impacted during the actual drought events themselves (Hahn et. al. 2020). All sites displayed the most variation within biodiversity during the most intense period of drought in 2014, and more intense drought conditions yielded more variable alpha diversity. This conclusion is in conjunction with similar findings on the relationship between biodiversity and ecosystem functioning as being systematically altered by abiotic factors relating to drought severity as they departed from ambient conditions (Garcia et al. 2018). The incredible variation between site responses to drought years indicates the importance of preserving diverse types of grasslands as opposed to focusing on conserving distinct, diverse plant communities. Bedrock and water

holding capacities and complex interactions between native and nonnative species competing for the same resources may be more important factors in determining an ecosystem's resilience to drought (Cartwright et al. 2020).

Bedrock

Bedrock composition was linked to biodiversity, species composition, and vegetative responses to climate change. The results of the repeated measure ANOVA test showed that bedrock composition was a determinant of vegetative resiliency to biodiversity indexes. Similar analyses using soil and site variables found that the strongest gradient for all vegetation layers was bedrock (Searcy 2003). Vegetative communities located upon sandstone hosted plant communities that exhibited the least resilience to drought. Plant communities above sandstone substrates may have been impacted by the diminished water retention rates of this bedrock. This is supported by findings on the role of rock moisture storage in the mediation of how water storage is initiated and the proportion at which moisture levels are retained (Rempe et al. 2018). I did not observe significant changes in alpha diversity for vegetative communities located upon alluvium and grandlorite during the study period. This indicates these bedrock composites may be more adept at retaining water during dry years. Grandlorite bedrock consistently hosted more diverse plant communities throughout both drought and non drought years, while alluvium bedrock consistently hosted the least diverse grassland communities.

Bedrock composites may significantly influence grassland resilience to drought as well as their performance during wet years. Anderson et al. reported similar results in their estimations of climate resilience for conservation across geological factors, noting the role of geophysical function on a sites' likelihood to retain species and functions under the stress of climate change (Anderson et al. 2014). Precipitation can be a leading characteristic of water tables and indirectly impact vegetation through modification of soil moisture contents available to plant species (Stephenson 1990), and bedrock characteristics were fundamental in altering levels of soil moisture content available to plants. This is especially important in California grasslands, where abiotic factors such as water continue to be a dominating limiting factor for species proliferation and growth. These findings may be useful in ecological models analyzing historical and future trends.

Native and Nonnative Species

Climate change induced drought may cause permanent changes native and nonnative species composition in grassland ecosystems, promoting increased variation within native and nonnative species cover. The relative performance of nonnative species and co-occurring natives often depends on growing conditions. Water availability is often a dominating abiotic factor that dictates vegetative trends (Daehler 2003). Evidence of greater variability in percent cover within invasive species responses to drought compared with native species suggests that there will be greater unpredictability within heavily invaded communities. Clearer trends may be observed for vegetative communities that contain higher abundances of native species. This claim is supported by related studies that made observations on how the variation in water availability has a larger impact on species cover for nonnative species than for native species (Brummer et al. 2016). Proportional decreases in invasive species cover and native species cover between drought and non drought years suggests invaded communities may be more susceptible to drought induced biodiversity loss, as supported by similar studies on nonnative species and drought (Kelso et al. 2020).

Comparisons between wet years preceding drought and wet years following the drought suggest nonnative species cover increases more rapidly than native species cover. This is supported by evidence that abiotic disturbance can enhance species abundance of nonnative species in communities (Hobbs et. al. 1992). This has important implications for Californian grasslands, many of which are characterized by large proportions of nonnative species. Nonnative species have significant advantages in dominating grassland ecosystems after severe drought conditions, and this trend may shape vegetative structures in California grasslands as droughts become more frequent and intense.

Limitations and Future Directions

One significant limitation of this study is that it is observational, not experimental, so the results indicate correlations between vegetative and environmental variables that are not necessarily indicative of causation. Additionally, this study was conducted within a unique

geographical location with distinctive historical and management trends that differ from surrounding grassland locations, and therefore the results cannot be extrapolated to other grassland ecosystems. Additionally, the limited temporal vegetative data documented following the drought indicates may not capture long term vegetative trends in wet years that occur after a long drought period. Estimates of longitudinal and latitudinal data used to develop the palmer drought indices calculations may not completely capture unique geographical and abiotic factors in each site such as slope and elevation and the influence of these respective variables.

Management Implications

Implications involved in the outcome of this analysis indicate that in some Mediterranean grasslands, this research may be useful in rangeland managers' and range ecologists' understanding of how climate change induced drought will impact species composition in the future. Additionally, it has important implications regarding how bedrock characteristics influence the biodiversity of the vegetative communities they host, and how these classifications may act as important indicators of community response and resilience to drought. This analysis may be useful in understanding how climate change induced drought will impact species composition as it relates to bedrock composition. It indicates that in some Mediterranean grasslands, researchers and rangeland scientists may be able to better understand how climate change induced drought will impact species composition as it relates to native and invasive species. It may also be useful for modeling changes in vegetative communities as related to abiotic climatic factors, and indicates that environmental managers can expect more variability and unpredictable trends in vegetative responses to climate change as droughts increase in severity, duration, and frequency.

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