Spring 5-14-2022

Biodiversity and global change in terrestrial ecosystems

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Recommended Citation

Ohlert, Timothy J.. "Biodiversity and global change in terrestrial ecosystems." (2022). https://digitalrepository.unm.edu/biol_etds/422

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BIODIVERSITY AND GLOBAL CHANGE IN TERRESTRIAL ECOSYSTEMS

by

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Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

July, 2022

ACKNOWLEDGMENTS

This dissertation was made possible by the contributions of hundreds of people over many decades. A comprehensive list of contributions would be cumbersome for both writer and reader, so a subset of contributors are highlighted here.

Foremost, thank you to my advisor, Scott Collins, for taking a chance on me as a naïve field tech and providing the knowledge, mentorship, and opportunities to make my graduate experience successful. Thank you also to my committee members, Jennifer Rudgers, Marcy Litvak, and Benjamin Wong Blonder, for their constant support of my studies. In addition, thank you to Kimberly Komatsu for her mentorship during my fellowship at the Smithsonian Environmental Research Center which, with her guidance, developed into my final chapter.

At the University of New Mexico, I was relentlessly supported by the community of scholars, not least of which were the members of the Collins Lab during my tenure. I am particularly grateful to Alesia Hallmark and Mariah Patton for their endless generosity as both colleagues and friends.

The last two years of the covid-19 pandemic made things a little weird for the ole dissertation, but my roommates, Joseph Barnett and Jonathan Keller, made it not only weatherable, but fun. Both have contributed to my dissertation and life in so many ways. I am grateful.

Many folks contributed to make the field work for this dissertation a success, particularly in the construction of the field experiment distributed across the southwestern U.S. These helpers include Stephanie Baker and Ben Specter of the Sevilleta, Sally Wittlinger, Quincy Stewart, and Shero Holland of the CAP LTER, Jim Andre and Tasha La Doux of the Granite Mountains Desert Research Center, and many friends that

traveled with me across the southwest including Gregor Hamilton, Jade McLaughlin, and Azad Vojdani. Furthermore, countless lab members, undergrads, graduate students, field technicians, and people off the street helped in ways big and small. I am in your debt.

My family went above and beyond their familial duty to contribute their time and labor. Thank you to Julie and Janet Ohlert for their help installing drought shelters, and to Mark Ohlert for help with drought shelter installation, maintenance, data collection, and being a good car buddy.

Many funding sources contributed to the work in this dissertation including Sevilleta Long Term Ecological Research (SEV LTER), Central Arizona-Phoenix Long Term Ecological Research (CAP LTER), the Smithsonian Institution, German Centre for Integrative Biodiversity Research (iDiv), UNM’s Department of Biology, UNM’s Biology Graduate Student Association (BGSA), and UNM’s Graduate and Professional Student Association (GPSA).

Finally, thanks go to my pre-graduate school mentors, Kaitlin Kimmel, Rebecca Montgomery, Emma Goldberg, and Kally Worm, without which I might be doing something else right now and having less fun.

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ABSTRACT

Terrestrial ecosystems are critical to human and ecological processes but many gaps in our knowledge remain regarding how terrestrial plant communities assemble and respond to global change. I used field experiments distributed around the world, including long-term experiments from the Sevilleta National Wildlife Refuge (SNWR) in New Mexico and deserts of the southwestern U.S., to evaluate the consequences of drought and other abiotic stressors on plant communities. Dominant grasses were particularly important for the productivity and structure of grasslands at SNWR. In general, the structure of desert plant communities had high resistance to extreme drought, though grasses and other perennial species were most negatively impacted. Global change drivers altered the beta diversity of plant communities both locally and among sites. Continued study of how communities respond to abiotic disturbances is of increasing importance as we try to conserve modern ecosystems and predict the consequences of anthropogenic global change.

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INTRODUCTION

Many important questions remain unanswered in the field of community ecology such as the importance of dominant species community assembly and how species assemble in a community following disturbance. These questions are of growing importance in our modern age of global change and climate extremes. Droughts are increasingly common, atmospheric deposition is changing soil resources, and climate variability is destabilizing biodiversity in terrestrial ecosystems around the world (Clark et al. 2001, Ellis et al. 2013, Franklin et al. 2016).

Ecological communities are the constituent parts of ecosystems, made up of assemblages of species interacting with each other (Fukami 2010). The unique role of communities in the study of ecology provides an important framework for conservation and management of ecosystems (Balvanera et al. 2014). The study of ecological communities is situated at the intersection of species' interactions with the environment, and species' interactions with each other. This dissertation contributes to decades of ecological research through an emphasis on the community structure of dryland ecosystems, comparison of drought impacts across the hot deserts of the U.S. southwest, and using trait-based techniques to study determinism in community assembly across spatial scales.

Despite evidence that diversity increases functions and services within ecosystems, outsized importance of dominant species, known as mass-ratio effects, are regularly observed in natural communities (Tilman et al. 2014, Smith et al. 2020). This discrepancy not only fuels academic debate, but the relative importance of diversity and dominant species in plant communities has consequences for conservation and restoration policy (Balvanera et al. 2014, Mace 2014). In Chapter 1, I use a 23-year species removal experiment from the Sevilleta National Wildlife Refuge to determine the role of dominant species in semiarid grassland communities. Removal experiments provide an opportunity to assess the impact of non-random species loss on natural plant communities at a local scale. With these data, I was able to determine both the strength of interactions between dominant and subordinate species and the importance of dominant species to net primary production. The two ecosystems studied in this chapter represent much of the grassland ecosystems of the southwest and the species removed in this experiment, *Bouteloua gracilis* (blue grama) and *B. eriopoda* (black grama), are two of the most important rangeland species in this region. With this study, I provide evidence of interactive effects between dominant species and subordinate species within communities as well as the unique influence that dominant species can have on the species richness-productivity relationships.

Over the past century, mean precipitation has decreased while precipitation variability has increased globally and in the southwestern U.S. (Cook et al. 2004). The combination of reduced annual precipitation and increased variability of precipitation implies increasing frequency of severe multiyear drought. Recent studies suggest that sensitivity of both biodiversity and productivity to precipitation change is greatest in drylands (Korell et al. 2021, Maurer et al. 2020, Wilcox et al. 2017). Since drylands account for 40% of the Earth's terrestrial surface, it is crucial that we understand the mechanisms by which drought affects dryland ecosystems. In Chapter 2, I use a drought experiment distributed across the Chihuahuan, Sonoran, and Mojave deserts to compare the impacts of a two-year extreme drought treatment on vegetative cover and five facets of community structure. This experiment, the first coordinated effort of its kind in the hot deserts of the U.S., provides an understanding of which aspects of desert plant communities are most vulnerable to projected increases in drought frequency and severity.

Environmental stochasticity and environmental filtering are both important mechanisms of community assembly in response to disturbances. In theory, environmental stochasticity will generate less similar, or divergent, communities as the result of disturbance, while environmental filtering will result in convergence to a common community (Grime 2006, Houseman et al. 2008, Fukami 2010). Whether disturbances due to global change drivers (GCDs) create divergent or convergent community assembly is consequential for beta diversity at local scales and for maintenance of biodiversity at global scales. Though the effects of GCDs on community similarity have been assessed within sites using traditional species-based methods (Chase 2007, Houseman et al. 2008), incorporating trait-based methods allows for assessment of biodiversity across both local and global scales (Suding et al. 2005). In Chapter 3, I use modern, trait-based methods (Blonder 2018, Mammola and Cardoso 2020) to quantify divergent and convergent effects of global change drivers on plant communities. With a global database of experiments, I test the influence of environmental stochasticity and environmental filtering on community assembly in response to five global change treatments using both species-based and trait-based methods in the first study of its kind. I determine which global change drivers have the greatest impact on the determinism of community assembly and demonstrate that the mechanisms of community convergence and divergence change across spatial scales.

These three chapters are organized iteratively from local to regional to global spatial scales. Combining both long-term and globally distributed experiments provides comprehensive insight into the consequences of global change on community assembly. Together, these chapters tell a story of the volatility and predictability of plant communities, while demonstrating their vulnerability to global change.

CHAPTER 1

THE ROLE OF DOMINANT SPECIES IN COMMUNITY ASSEMBLY AND PRODUCTIVITY IN SEMIARID GRASSLANDS

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Abstract

Determining the mechanisms by which biodiversity influences ecosystem processes is critical to a comprehensive understanding of human impacts on ecosystems. Biodiversity has positive impacts on many ecosystem functions, yet debate remains as to the role of dominant species in community assembly and ecosystem function. We used a dominant species removal experiment to test the influence of dominance in community assembly and productivity in two semiarid grasslands with different dominant species. Removal of dominant species led to increases in species richness and concurrent decreases in productivity. Compensation by subordinate species was incomplete, but attributable to different functional groups over time. Species richness and dominance were both poor predictors of productivity across ecosystems and treatments. In general, we found that the dominant species of these grasslands played a key role that no subordinate species filled across 23 years in absence of dominant species.

Introduction

Considerable empirical and experimental evidence demonstrates that biodiversity has positive impacts on many ecosystem functions, including aboveground net primary production (NPP), resistance to invasion, resilience to disturbance, and resource use (Tilman et al. 2014). Human activities are causing changes to many facets of biodiversity through both biotic and abiotic disturbance (Avolio et al. 2021). Therefore, determining how the assembly of biodiversity in ecological communities influences ecosystem processes is critical for providing a comprehensive understanding of human impacts on ecosystems.

Biodiversity can be measured as species richness (an inventory of species present) or dominance (the relative disparity between abundance among species, and the inverse of evenness). Despite evidence of positive effects of species richness on ecosystem processes, including NPP (Tilman et al. 2014, Hector et al. 1999), dominant species may play the leading role in the productivity of natural communities (Gaston 2011, Genung et al 2020). Indeed, some studies have shown that NPP is controlled more by dominant species, known as mass-ratio effects, than species richness, *per se* (Grime 1998, Smith and Knapp 2003, Smith et al. 2020). Reconciling how dominant species control NPP is an important next step to determine how ecosystems will respond to human-caused environmental change.

In most natural communities, a small number of species exist in high abundance (Gaston 2011, Avolio et al. 2019). Due to their commonness on the landscape, this small number of dominant species account for a substantial proportion of NPP (Grime, 1998, Dee et al. 2019). Mass-ratio effects on productivity are most pronounced in communities with highly productive, dominant species because the relative abundance of the dominant species directly relates to overall productivity (van der Plas 2019). When highly abundant, dominant species have additional impacts on community structure and species richness. For example, tall dominant species increase light limitation, thus reducing establishment of short-statured species (Hautier et al. 2009, Grman et al. 2021). In stressful environments, however, dominant species can facilitate growth of subdominants by decreasing heat stress and altering soil moisture and nutrient levels (Bertness and

Callaway 1994, Lortie and Callaway 2005). Dominant species also impact the structure and composition of communities through competitive or synergistic interactions with other species (Ellison et al. 2005, Gaston 2011). In contrast, loss of subordinate species may have no effect on NPP. For example, production was maintained in a tallgrass prairie ecosystem upon removal of subordinate species, but production decreased when dominant species were removed from the community (Smith and Knapp 2003). When a dominant species is removed, the resulting release in available resources can be used by a diverse species mixture to compensate for loss of production (Allan et al. 2011, Wilcox et al. 2017, Zuppinger-Dingley et al. 2014). For example, subordinate species provided complete compensation in a South African savanna grassland after the dominant grasses declined following a severe drought (Wilcox et al. 2020). Removal experiments, however, demonstrate that some dominant species play a unique role in ecosystem function as their absence results in incomplete compensation by the subordinate species in the community.

Removal experiments are a useful tool for investigating the influence of dominant species on subordinate species by directly testing the ability of subordinate species to compensate for the loss of the dominant species and revealing the extent to which dominant species affect community composition. For example, one-time removal of the dominant species in a shortgrass-steppe grassland, *Bouteloua gracilis* (blue grama), resulted in less than half of ambient vegetative cover for five years, and increased bare ground cover for ten years (Munson and Lauenroth 2009). In a wet meadow, removal of the dominant resulted in a positive effect on species richness due to the absence of competition with the dominant species (Leps 2014). However, numerous other studies reported little or no effects of dominant species removal on diversity, despite impacts to NPP (Roth et al. 2008, Rixen and Mulder 2009, Li et al. 2015). Further research is necessary to reconcile the discrepancies and clarify the impacts of dominant species removal on species richness-productivity and mass-ratio effects.

The effects of dominant species on community structure are particularly important in dryland ecosystems, where dominance is high, species richness is low, and many mechanisms linking the two (such as light limitation) are less important (Korell et al. 2021, Thomey et al. 2014, Gherardi and Sala 2019). In semiarid grassland ecosystems of central New Mexico, dominant perennial grass species make up around 80% of plant community cover and determine ecosystem sensitivity of NPP to climate (Rudgers et al. 2018). The perennial bunchgrass *Bouteloua gracilis* and stoloniferous *B. eriopoda* dominate the Great Plains and Chihuahuan Desert grasslands, respectively, and they co-occur across a grassland ecotone in central New Mexico, USA. *B. eriopoda* is better adapted for warmer, drier environments than *B. gracilis* due to its greater water use efficiency and higher optimal temperature, while *B. gracilis* has a slightly deeper root system and is longer lived than *B. eriopoda* (Peters and Yao 2012). Given differences in traits, these dominant species may have different interactions with subordinate species where they dominate, despite identical climate conditions, similar soils, and regional species pools. Furthermore, the abundance of both dominants declines dramatically during drought while forbs persist (Lagueux et al. 2021, Loydi and Collins 2021). Previously, a removal experiment comparing these two grasslands found a strong negative effect of *B. eriopoda* removal on total vegetative cover which persisted for all 16 years of the study. On the other hand, subordinate species compensated for *B. gracilis* removal after just six years of treatment (Peters and Yao 2012). This study system provides a novel opportunity to compare the role of dominant species in mass-ratio effects and species richness-productivity relationships without confounding effects of climate and regional species pools.

We used a long-term (1995-2018) species removal experiment in two comparable semiarid grasslands to assess the capacity of plant communities to compensate for dominant species loss, as well as the importance of dominant species to annual productivity. Our goal was to directly address the role of dominance and diversity in dryland ecosystem functioning. The co-occurrence of these two grasslands with different dominant species under comparable environmental constraints creates ideal conditions for studying patterns that determine the relative importance of species richness and dominance to ecosystem function. We asked the following questions: (1) *How do dominant species affect diversity and productivity in these grasslands?* (2) *Which plant functional groups benefit when dominant species are removed?* and (3) *Do mass-ratio effects or species richness predict productivity in these semiarid grasslands?*

Methods

Study site

Experiments were conducted at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA (34°20′ N, 106°43′ W). The SNWR is located at the transition zone between two grassland ecosystems, the Chihuahuan Desert, which extends south into Mexico, and Great Plains, which extends north into Colorado and east into Texas. The site receives an average of ~240 mm of precipitation per year, 60% of which occurs in July, August, and September during the summer monsoon (Pennington and Collins 2007, Petrie et al. 2014). Mean monthly temperature ranges from 2.6 C in January to 24.6 C in July (Peters and Yao 2012). At the study sites, NPP typically ranges from 100 g/m^2 in the Greats Plains to 150 g/m^2 in the desert grassland (Table 2). Soils are a sandy loam mixture including clay and calcium carbonate classified as Typic Haplargids (Kurc and Small, 2007, Peters and Yao 2012).

The Chihuahuan Desert grassland is dominated by *Bouteloua eriopoda* (black grama), a stoloniferous, C4 perennial grass whose range extends southward through the arid regions of the Chihuahuan Desert in the U.S. and Mexico (Kröhl-Dulay et al. 2004). The Great Plains grassland is dominated by *B. gracilis* (blue grama), a long-lived, caespitose, C4 perennial grass. Both grasslands feature several subdominant C4 grasses including *Sporobolis spp.* and *Pleuraphis jamesii*. A mixture of shrubs and subshrubs can be found across the landscape including *Yucca elata* and *Guteriezia sarothrae.* Common forb species include the perennial *Machaeranthera pinnatifida* and the nonnative *Salsola tragus* (Mulhouse et al. 2017). Legumes are very rare in these grasslands and are not functionally distinct from forbs regarding their role in the community, therefore, we grouped legumes with forbs for analyses (Collins and Xia 2015).

Previous studies have compared long-term trends and vegetation dynamics of these grasslands specifically in regard to climate. The Chihuahuan Desert grassland exhibits constrained production under wet conditions while the Great Plains grassland is capable of large production increases in wet years (Rudgers et al. 2018). Both grasslands perform poorly under sustained drought, with Chihuahuan Desert grassland exhibiting high sensitivity to interannual variation in precipitation (Knapp et al. 2015). Likewise, Collins et al. (2020) found that these grasslands are sensitive to long-term changes in climate, particularly the warm and cool phases of the pacific decadal oscillation, and that *B. gracilis* recovers faster from fire than *B. eriopoda*. The dominant grasses account for over 80% of total plant cover in their respective ecosystems (Collins and Xia 2015).

Dominant species removal experiment

To determine the role of dominant species in the structure and functioning of these grasslands, we used a species removal experiment at the ecotone from Chihuahuan Desert to Great Plains grassland. The dominant species removal treatment involved removing the dominant species from its respective grassland: *B. gracilis* in the Great Plains grassland and *B. eriopoda* in the Chihuahuan Desert grassland. Removal treatments were accomplished by manually clipping or scraping grasses along the soil surface while minimizing soil disturbance and grasses were removed as needed in subsequent years (Peters and Yao 2012). *B. gracilis* and *B. eriopoda* accounted for 25% and 22% of absolute cover, respectively in their grasslands. In 2018 after 23 treatment years, *B. gracilis* and *B. eriopoda* accounted for only 1.6% and 3.1% absolute cover in treatment plots in their respective grasslands. Each site includes five replicate removal treatment plots and five control plots; each plot is 3x4 m. Percent cover data were collected at the species level and converted into biomass through allometric equations based on cover and derived from destructive biomass harvesting (Muldavin et al 2008, Rudgers et al. 2019). Data were collected from 1995-2018 at the end of the monsoon growing season (September-October). We used current year biomass as our measure of NPP for herbaceous species, including grasses and forbs which senesce each winter. NPP for shrubs and other woody species was calculated as current year standing biomass minus previous year standing biomass. In 1995 and 2001, plants were not identified to species so species richness and dominance metrics were not attainable. Additionally, no data were collected in 2013 which prevented calculation of 2014 NPP for shrubs and woody species.

Data analysis

Species richness was calculated as the number of unique species present in a 3x4 m plot during the sampling period. We calculated dominance using the Berger-Parker dominance index: $\frac{Max\ cover\ of\ most\ abundant\ species}{Sum\ cover\ of\ all\ species}$ (Berger & Parker 1970). This metric measures the proportion of the most-dominant species relative to the abundance of the entire community (Sasaki and Lauenroth 2011, Koerner et al. 2018). Although other metrics of dominance are more closely related to community evenness, this metric is directly related to the abundance of the most abundant species, which is appropriate for our study because we experimentally removed the most abundant species (Collins et al 2020, Rudgers et al 2019). The removal experiment allowed us to determine the degree to which subordinate species compensated for loss of the dominant. Analyses with subdominant species in the control plots include every species except *B. gracilis* in the Great Plains grassland and *B. eriopoda* in the Chihuahuan Desert grassland.

How do dominant species affect diversity and productivity?

We created mixed-effects models testing the effect of dominant species removal on the species richness of subordinate species between control and treatment plots, as well as comparing NPP between treatments, controls, and the subordinate species of controls. Plot was used as a random effect to control for repeated measures and year was used as a random effect in an autocorrelation structure using the ‘nlme’ R package (v3.1-152, Pinheiro et al. 2007).

Which plant functional groups benefit when dominant species are removed?

We created mixed-effects models to compare percent cover of grasses, shrubs, and forbs between control and removal treatments. Plot was used as a random effect to control for repeated measures and year was used as a random effect in an autocorrelation structure using the ‘nlme’ R package (v3.1-152, Pinheiro et al. 2007).

Do mass-ratio effects or species richness predict productivity in these semiarid grasslands?

We created mixed-effects models to test relationships between both dominance and diversity to NPP. Within each model, we compared control and removal to each other. Plot was used as a random effect to control for repeated measures and year was used as a random effect in an autocorrelation structure using the ‘nlme’ R package (v3.1-152, Pinheiro et al. 2007). To test for nonlinear relationships, we tested linear, quadratic, cubic, and quartic model fits and then compared AIC scores of models, favoring the model with the lowest AIC score. Models were considered equivalent when $\Delta AIC < 2$, in which case the simpler model was favored. In each case, the linear model was favored.

We used R Statistical Software (v4.1.2; R Core Team 2021) for all analyses. The ‘tidyverse’ (v1.3.1; Wickham et al. 2019) and ‘plyr’ (v1.8.6; Wickham et al. 2011) R packages were used for data manipulation and data visualization. We used the ‘mumin’ package (v1.43.17; Barton 2020) to summarize the coefficients of mixed-effects models.

Results

How do dominant species affect diversity and productivity?

In the Great Plains grassland, species richness of subordinate species averaged 7.1 in control plots and 11.5 in plots with *B. gracilis* removal across all years ($p < 0.001$, Table 1, Figure S1). Subordinate species richness of annuals increased from 2.4 to 3.6, and subordinate species richness of perennials increased from 4.9 to 8.3. Subordinate species richness from grasses increased from 1.8 to 3.8, subordinate species richness from forbs increased from 4.5 to 6.1, and subordinate species richness of shrubs increased from 1.1 to 1.6. In the Chihuahuan Desert grassland, species richness of subordinate species averaged 8.0 in control plots, and 12.3 in plots with *B. eriopoda* removal across all years ($p < 0.001$, Table 1, Figure S1). Subordinate species richness of annuals increased from 2.5 to 4.0, and subordinate species richness of perennials increased from 5.4 to 8.5. Subordinate species richness of grasses increased from 2.7 to 4.8, subordinate species richness of forbs increased from 4.5 to 6.5, and subordinate species richness of shrubs increased from 1.1 to 1.3.

NPP in control plots in the Great Plains grassland averaged 97 g/m^2 (range 61 - 175 g/ m^2) from 1995-2018, whereas control plots in the Chihuahuan Desert grassland averaged 151 g/m^2 (range 68-209 g/m^2) (Table 2). Of the total NPP, subordinate species accounted for an average of 10 g/m^2 (range 0-29 g/m^2) in Great Plains and an average of 25 g/m^2 (range 0-120 g/ m^2) in Chihuahuan Desert grassland. Thus, on average, the dominant grass *B. gracilis* accounted for 90% of NPP in Great Plains grassland and *B. eriopoda* accounted for 84% of NPP in the Chihuahuan Desert grassland (Table 2, Figure 2). When dominant species were removed, subordinate species only partially compensated for the loss of NPP from dominant species. In Great Plains grassland, NPP of subordinate species increased to 59 g/m^2 (range 0-134 g/ m^2) when *B. gracilis* was removed, which is nearly five times subordinate NPP in control plots, yet still only 65% of the NPP produced by *B. gracilis* in control plots (Table 2, Figure S1). In Chihuahuan Desert grassland, NPP of subordinate species increased to 55 g/m^2 (range 0-146 g/ m^2) when *B. eriopoda* was removed, approximately twice as much NPP as subordinate species in control plots (Table 2, Figure 2). In Chihuahuan Desert grassland, subordinate species compensated for only 24% of the NPP by *B. eriopoda* (Table 2, Figure 2). Proportionally, NPP in Chihuahuan Desert grassland declined by 63% when *B. eriopoda* was removed, compared to only a 40% decrease in the Great Plains grassland with *B. gracilis* removal.

Which plant functional groups benefit when dominant species are removed?

When dominant grasses were removed, shrub and forb cover increased across all years in both grasslands (supplemental Table 1, supplemental Figure 2). In the Great Plains grassland, shrub cover increased eight-fold across all years, from 0.7% to 6.4% and forb cover more than tripled from 1.5% to 5.3% with removal of *B. gracilis* (Figure S2). In the Chihuahuan Desert grassland, forb cover nearly doubled from 4.4% to 7.6%, but there was no significant response by shrubs across all years. In both grasslands, total grass cover was lower following removal of the dominant grass species. Across all years, cover of non-dominant grasses increased from 2.2% to 21.4% in Great Plains grassland, and from 5.3% to 15.8% in Chihuahuan Desert grassland.

The effects of dominant species removal on functional groups varied over time. In Great Plains grassland, relative cover of forbs was higher in removal than control plots for the first seven years of the experiment, after which the relative cover of shrubs increased in the removal treatment relative to control plots over the next seven years (Figure 3). By year 14, the relative cover of shrubs in removal plots declined in concurrence with an increase in the relative cover of grasses (Figure 3). High grass abundance in Great Plains grassland from 2012 to 2018 is attributable to an increase in a mixture of *B. eriopoda*, *Pleuraphis jamesii*, and *Sporobolus spp*. In Chihuahuan Desert grassland, relative cover of forbs in treatment plots increased during the first seven years of study, whereas shrub cover increased from 2004 to 2007, primarily driven by increased abundance of *Gutierrezia sarothrae*. Marked increase in relative grass cover began in 2009 and was sustained through 2018 (Figure 3), attributable to increased abundance of *Pleuraphis jamesii* and other perennial grasses.

Do dominance or species richness predict productivity in these semiarid grasslands?

Under control conditions, the Great Plains grassland had a non-significant relationship between species richness and NPP ($p = 0.17$, slope = 2.3). This relationship was significantly negative when *B. gracilis* was removed from the Great Plains grassland ($p = 0.02$, slope = -4.5) (Table 3, Figure 4). There was no relationship between total NPP and species richness in control plots in the Chihuahuan Desert grassland (p = 0.14, slope = 2.2), but after removal of *B. eriopoda*, this relationship was significantly negative (p = 0.02 slope = -4.9) (Table 3, Figure 4).

The Great Plains grassland has a marginally significant correlation between dominance and NPP in control plots (p = 0.08, slope = 92.2), however, the Chihuahuan Desert grassland had no correlation (p = 0.68, slope = -15.4). When dominant species were removed, the relationship was unchanged in both Great Plains and Chihuahuan Desert grasslands (Great Plains p=0.21, slope = -81.2; Chihuahuan Desert p=0.39, slope = -47.0) (Table 3, Figure 4).

Discussion

Using a 23-year dominant species removal experiment in two semiarid grasslands, we found suppression of subordinate species by dominant grasses and that subordinate species provided only partial compensation for the loss of the dominant species. Throughout the study, forb, shrub, and grass functional groups each had phases in time in which their abundances increased in removal plots to provide partial compensation for dominant species. We found that neither species richness nor dominance was a good predictor of NPP and that the removal of dominant species resulted in increasingly negative species richness-NPP relationships. In general, *B. eriopoda* was more essential to the NPP and cover of the Chihuahuan Desert grassland than *B. gracilis* in the Great Plains grassland.

Direct effects of dominant species on diversity and productivity

Both *B. gracilis* and *B. eriopoda* suppressed establishment and abundance of subordinate species. Previous studies have shown that removing dominant species can increase local species richness (Collins et al. 2002, Suding et al. 2006), yet numerous other removal experiments have reported no diversity effect of dominant removal (e.g., Roth et al. 2008, Raffaele and Ruggiero 1995, Souza et al. 2011). Disturbances in grasslands tend to promote greater species richness when they disproportionately reduce the abundance of dominant species (Grime 2006, Leps 2014, Koerner et al. 2018). Griffin-Nolan et al. (2019) reported greater species richness and functional trait diversity in these grasslands when the abundances of the dominant species were reduced by experimental drought treatments. Other disturbances, such as grazing, fire, or increased precipitation variability, could lead to similar selection against dominant species resulting in greater species richness in these grasslands (Ladwig et al. 2014, Collins et al. 2020).

In both grasslands, removal of dominant species led to substantial NPP declines even as species richness increased. The Great Plains grassland experienced relatively more NPP compensation than the Chihuahuan Desert grassland, but neither site achieved full compensation across 23 years of dominant removal. In the Great Plains grassland, *B. gracilis* removal led to increases in the subshrub *Gutierrezia sarothrae* as well as the perennial grasses *B. eriopoda*, *Pleuraphis jamesii*, and *Sporobolus cryptandrus*. Similarly, *G. sarothrae* and *P. jamesii* increased in abundance in the Chihuahuan Desert grassland upon *B. eriopoda* removal. Disparity between species richness and NPP responses to removal of dominant species demonstrates a decoupling of the typically positive species richness-NPP relationship, in our case more species generated less productivity. Removal experiments in grasslands and tundra similarly find that species-rich communities are unable to compensate for removal of dominants (Smith and Knapp 2003, Rixen and Mulder 2009, Pinder 1975). However, some ecosystems report few impacts of dominant removal on either species richness or productivity (Roth et al. 2008, Li et al. 2015, Souza et al. 2011). Previous studies at SNWR found *B. gracilis* to be a better competitor than *B. eriopoda* (Thomey et al. 2014, Chung and Rudgers 2016). Therefore, removal of *B. gracilis* should make more resources available for subordinate species relative to removal of *B. eriopoda*. Indeed, we found greater compensation by subordinate species in Great Plains grassland than Chihuahuan Desert grassland.

Lack of compensation in the Chihuahuan Desert grassland upon *B. eriopoda* removal may also be attributable to facilitation. Especially in stressful environments, dominant species can have mutualistic interactions with subordinates (Maestre et al. 2009). In particular, *B. eriopoda* is known to alter soil resources and increase colonization of subordinates in intershrub zones (Schlesinger et al. 1999, Stewart et al. 2014, Zhang 2021). *B. eriopoda* primarily spreads through stolons and leaves a substantial amount of standing litter once senesced. Combined, the standing litter and stolons of *B. eriopoda* contribute to seed trapping and alter soil resources in Chihuahuan Desert ecosystems (Stewart et al. 2014, Peters et al. 2020). In contrast, *B. gracilis* is a more typical perennial bunchgrass, with much smaller basal cover than crown cover (Coffin and Lauenroth 1991, Peters 2002). Therefore, growth of *B. gracilis* is less likely to facilitate establishment and growth of surrounding plants than an equivalent abundance of *B. eriopoda*.

Successional pattern of functional groups

In both grasslands, dominant species removal led first to an increase in forb abundance, followed by an increase in shrubs. Counterintuitively, compensation often occurs among functional groups different than the removed species (Bret-Harte et al. 2008). Peters and Yao (2012) reported similar findings over a shorter time scale in this experiment. An initial increase in annual plant cover was most apparent in the first ten years of removal treatments, but was more sporadic for the following six years of their study (Peters and Yao 2012). A removal experiment in a similar Chihuahuan Desert ecosystem found that short-lived annual species were most responsive to functional group removal treatments (Buonopane et al. 2005). We found that annuals and other forbs remained in similar abundance to control plots for an additional decade of the experiment. Annual and short-lived forbs utilize resources made available by dominant species removal more quickly than other functional groups (Buonopane et al. 2005). A similar increase in forb abundance occurred two years after removal of the dominant perennial grass from an alpine meadow (Li et al. 2015). Upon removal of *B. gracilis* in the Colorado shortgrass steppe ecosystem, forb abundance immediately increased and persisted over ten years while abundance of graminoids lagged, particularly perennial graminoids (Munson and Lauenroth 2009).

Peters and Yao (2012) reported a steadily increasing abundance of shrubs in the Great Plains grassland through the first 16 years of this dominant species removal experiment. We found that immediately following their study period (1994-2010), shrub abundance in the Great Plains experienced a considerable decline down to levels observed in control plots. Indeed, previous study in these semiarid grasslands found that shrub encroachment often occurs when shrubs replace *B. eriopoda* as opposed to *B.*

gracilis (Peters et al. 2006). The waning of shrubs 16 years after removal treatment contradicts previous work which suggests shrubs maintain dominance in these grasslands once established (Turnbull et al. 2010, Li et al. 2008, Sankey et al. 2012). Decreased shrub abundance might have been caused by abiotic disturbance during a severe freezing event in 2011 which resulted in immediate damage to *Larrea tridentata* (creosote bush) throughout SNWR (Ladwig et al. 2019). Though *L. tridentata* was not found in any of our experimental plots, other shrub species in Chihuahuan Desert ecosystems, such as *Gutierrezia saraothrae*, are likely limited by freezing as well (Smith et al. 1997).

Following the decline of shrubs in treatment plots of both grasslands, perennial grasses exhibit the greatest increased abundance in dominant species removal plots for the last ten years of our study. Other studies of the perennial grasses in SNWR find that abundances of dominant grasses tend to increase over time, but are reduced to very low abundance by pulse disturbance events such as fire or extreme drought (Báez et al. 2012, Ladwig et al. 2014, Collins et al. 2020). Therefore, we expect that abundance of perennial grasses, especially *B. eriopoda*, should continue to increase in the absence of another disturbance (Rudgers et al. 2018, Collins et al. 2020). The temporal layering of functional group abundance that we found suggests that multi-decadal removal experiments are necessary in these grasslands to capture the totality of vegetation change.

Natural disturbances of these ecosystems often mimic the effects of the removal treatment. Drought has a negative effect on grass cover, but a neutral or positive effect on shrub and forb cover in these grassland (Báez et al. 2013, see next chapter). Though grasses dominate under average conditions, shrubs and forbs perform well in the absence of grasses regardless of environmental conditions. Therefore, interactions between dominant grasses and other grass species are likely net facilitative, while their interactions with shrubs and forbs are net competitive. Indeed, coexistence of species and functional groups over time occurs when interactions change with the variability in abiotic conditions (Chesson 2000, Soliveres and Allen 2018).

Species richness and mass-ratio effects

Removal of *B. gracilis* from Great Plains and *B. eriopoda* from Chihuahuan Desert grasslands resulted in a negative species richness-NPP relationship. In the absence of dominant species, communities incurred neither synergistic interactions that may lead to complementarity effects of species richness, nor the emergence of a new dominant species capable of producing selection effects of species richness (Fargione et al. 2007). Main effects of dominant species removal created a far greater effect on NPP than either species richness or dominance. Recent studies show that mass-ratio effects are more important than species loss in determining ecosystem responses to disturbance (Smith 2011, Winfree et al. 2015, Smith et al. 2020). Since common and abundant species are particularly vulnerable to environmental stressors (Wilfahrt et al. 2021), projected increases in climate variability and frequency of drought in these grasslands could have a considerable impact on their productivity through impacts on the dominant species, as opposed to impacts on species richness or other measures of diversity (Rudgers et al. 2018). Biodiversity is implicated as an important feature for the stability of ecosystems facing climate extremes (Isbell et al. 2015). However, biodiversity effects are less important for stability in highly asynchronous communities (Valencia et al. 2020, Hallett et al. 2014) including those at SNWR.

Through this long-term experiment, we demonstrated the existence and importance of mass-ratio effects in these grasslands exposed to stressful environmental conditions. The dominant species of these grasslands play unique roles in productivity that no other species were able to fill even after 23 years. Overall, dominant species can inhibit the diversity of communities while being critical to productivity. Compensation by subordinates was only partial and occurred in a successional pattern among functional groups which unfolded over two decades of the experiment. Disturbances to these ecosystems, including drought, fire, and grazing, are likely to disproportionately affect the abundances of dominant grass species. Thus, bolstering diversity in these communities and mitigating the impact of disturbances will result in more predictable and stable ecosystems.

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Figures

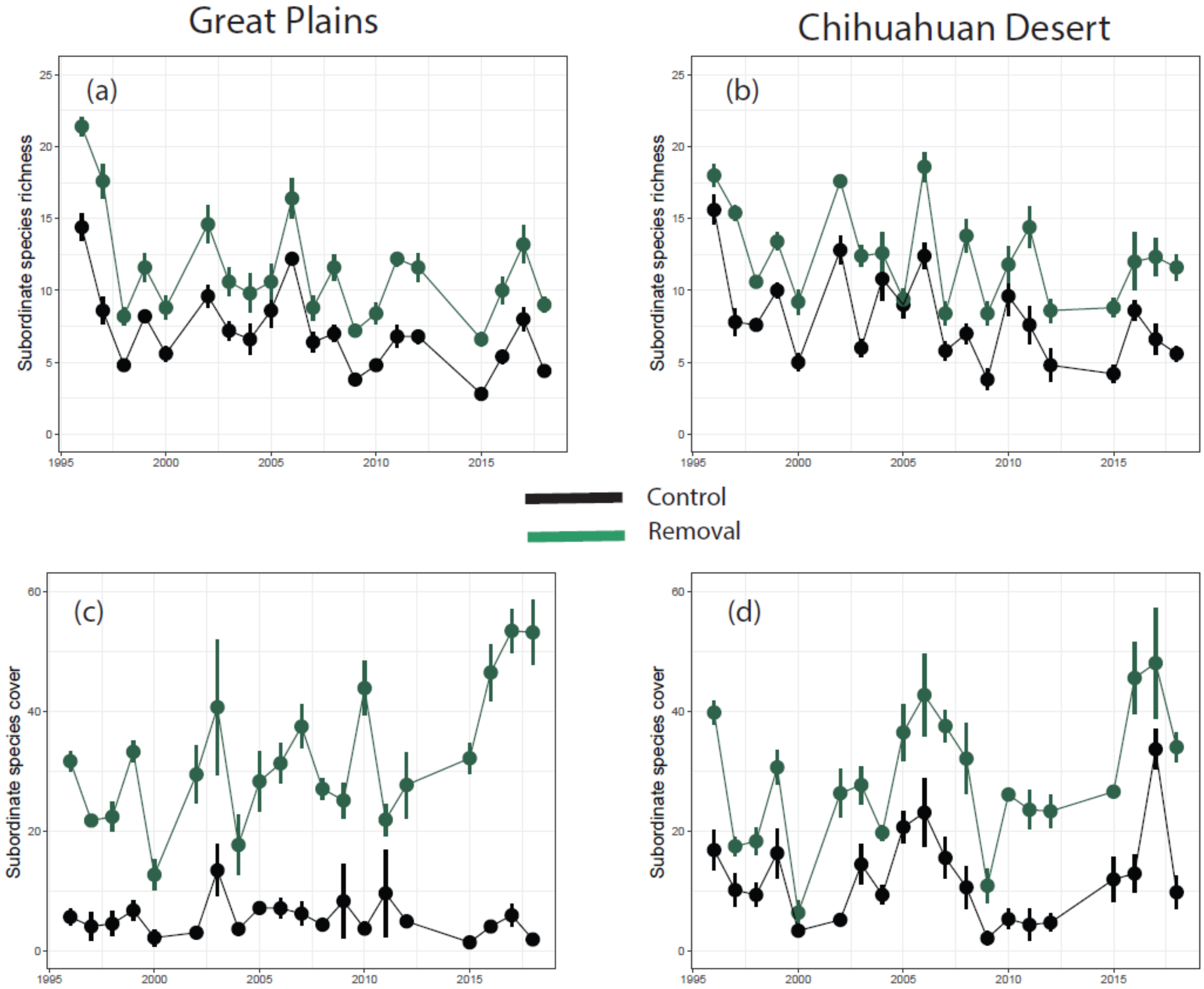


Figure 1. Comparison of a,b) subordinate species richness and c,d) subordinate species cover in control plots (black), and of all species in plots where the dominant species was removed (green) from 1995 to 2018 in a,c) Great Plains dominated by *Bouteloua gracilis* and b,d) Chihuahuan Desert dominated by *B. eriopoda* at the Sevilleta National Wildlife Refuge, New Mexico, USA. Removal of dominant species increases both richness and cover subordinate species. Colored points depict means and standard error shown with lines around the means.

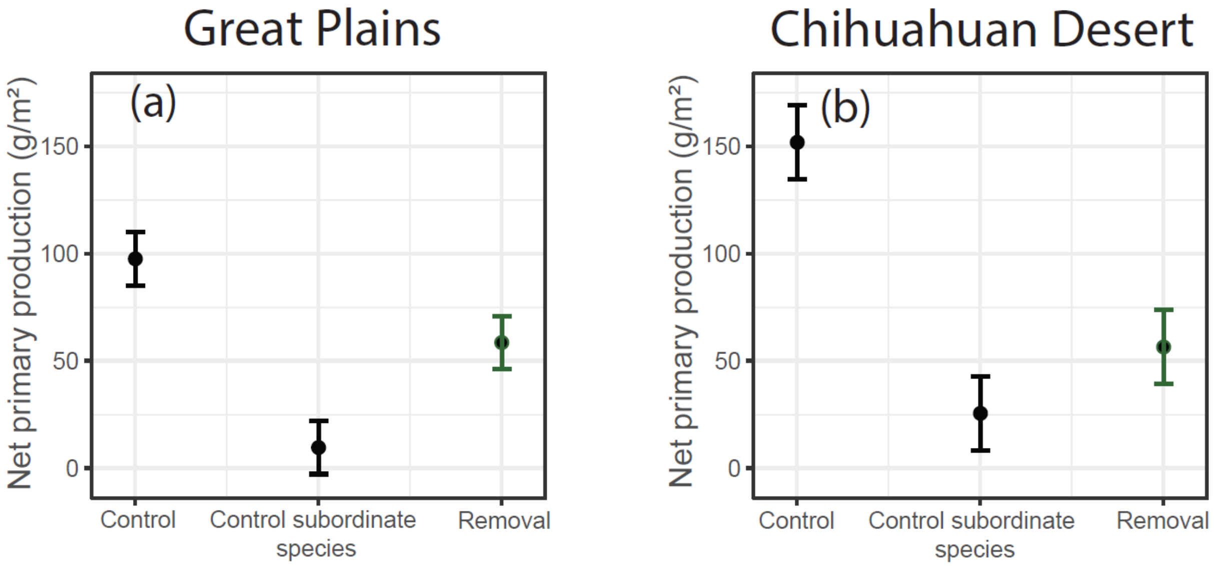


Figure 2. Results of regression models showing the mean (circle point) value of net primary production in a) Great Plains grass and b) Chihuahuan Desert grassland for all species in control, subordinate species in control, and all species in removal treatments. Error bars show standard error of the model (Table 2) and asterisks denote significant difference from the control NPP (subordinate species and removal only).

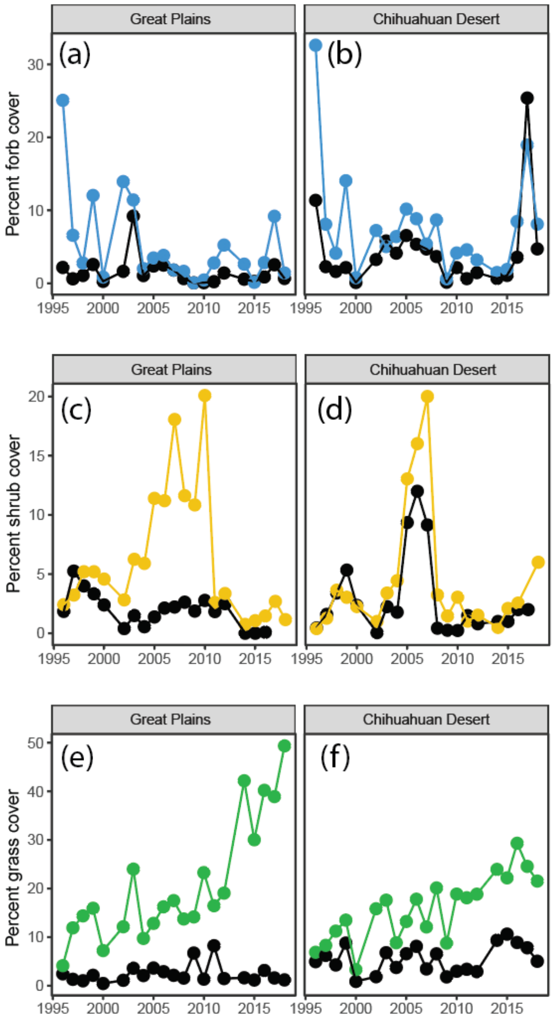


Figure 3. Percent cover of subordinate species for a,b) forbs c,d) shrubs and e,f) grasses over the 23-year time series (1995-2018). Black points indicate average values from control plots containing *B. gracilis* in the Great Plains grassland and *B. eriopoda* in the Chihuahuan Desert grassland. Colored points indicate average values from treatment plots with *B. gracilis* removed from the Great Plains and *B. eriopoda* removed from the Chihuahuan Desert grassland. Forb cover in treatment plots is initially greater than cover in control plots in both grasslands. Shrub cover increases in treatment relative to control plots in both grasslands around 2003.Grass cover in both grasslands steadily increases over the time series.

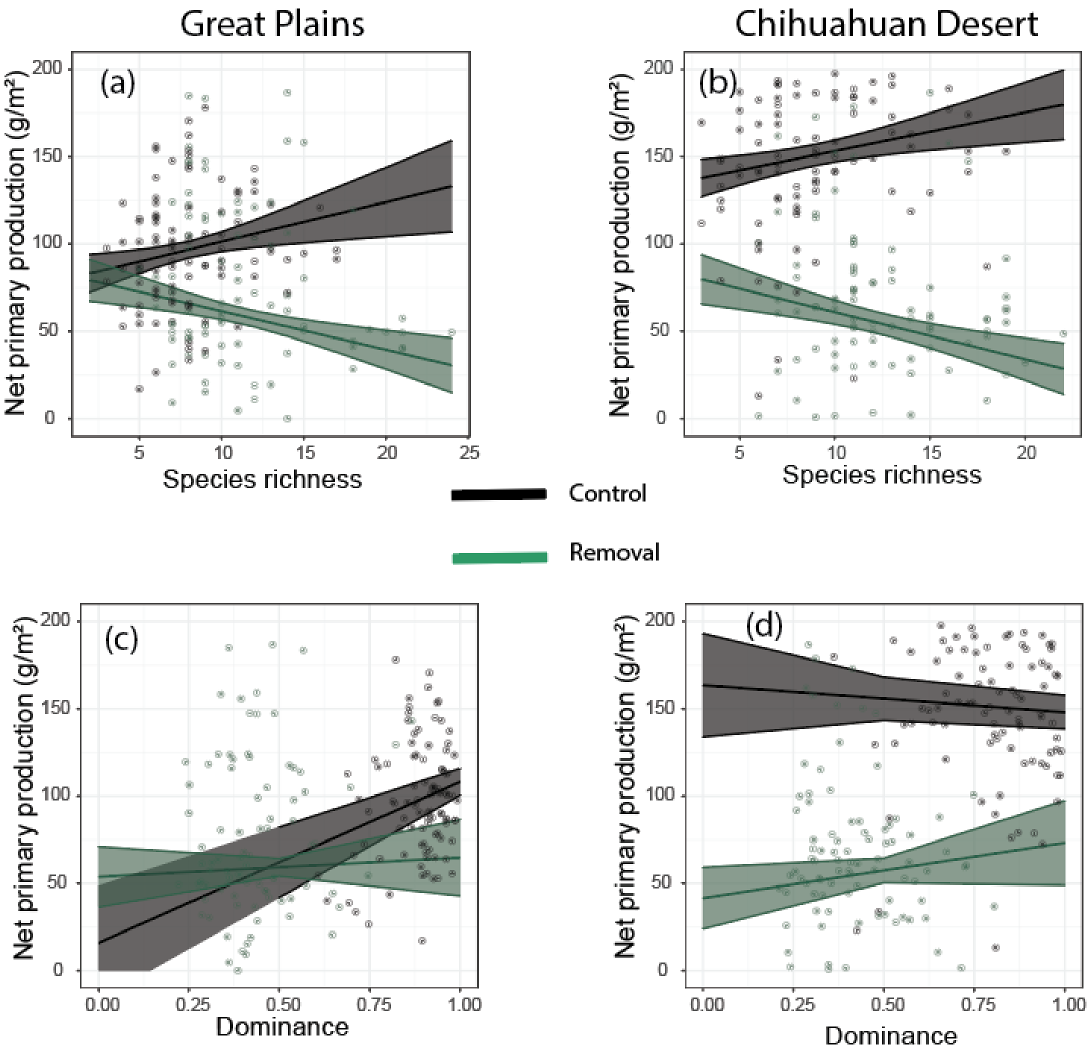
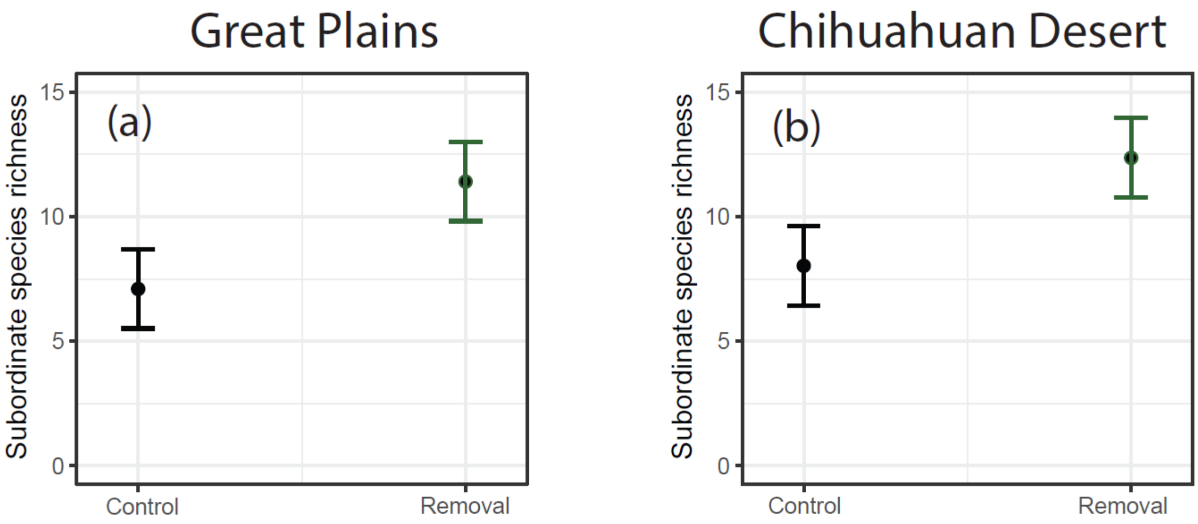
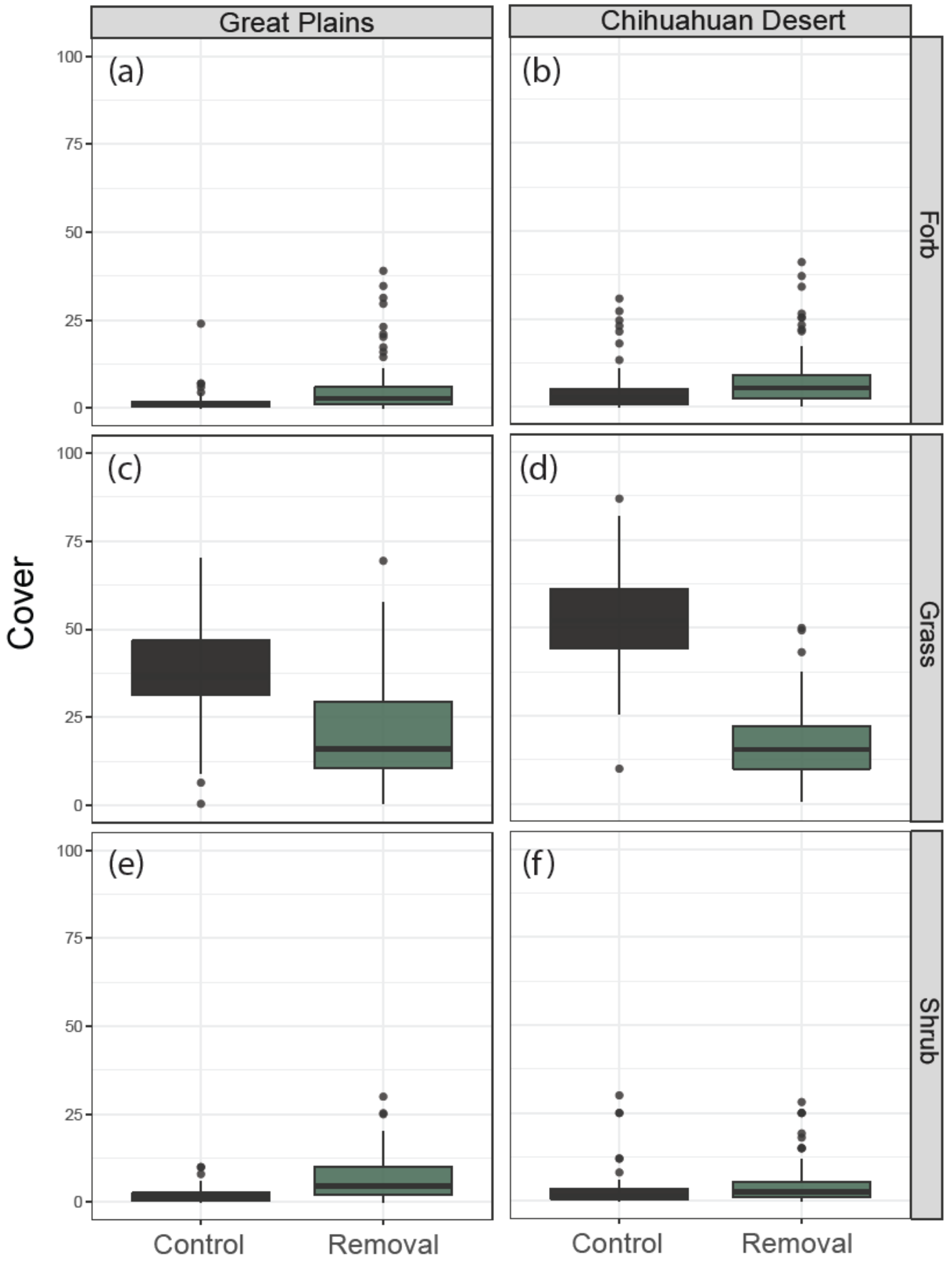


Figure 4. Relationship between a,b) species richness and net primary production and c,d) dominance and net primary production in a,c) Great Plains grassland and b,d) Chihuahuan Desert grassland for control plots (black) and plots where dominant species were removed (green) (*Bouteloua gracilis* in Great Plains and *B. eriopoda* in Chihuahuan Desert). Error bands show standard error of regression models (Table 3).



Supplemental figure 1. Comparison of subordinate species richness in control vs. dominant species removal treatment plots across the 23-year study period. In both grasslands, dominant species removal resulted in increased species richness. Model results can be found in Table 1, see the methods section for details.



Supplemental Figure 2. Percent cover of subordinate species for a,b) forbs c,d) grasses and e,f) shrubs by functional groups aggregated across the 23-year time series with and without *B. gracilis* removed from the Great Plains and *B. eriopoda* removed from the Chihuahuan Desert grassland. Model results can be found in Table S1 and year to year comparisons can be seen in Figure 3.

Tables

	Control Estimate	**Removal Estimate**	**p-value**
Great Plains	**7.1**	**11.5**	**< 0.001**
Chihuahuan Desert	**8.0**	**12.3**	**< 0.001**

Table 1. Changes to subordinate species richness in response to removal of *B. gracilis* in the Great Plains grassland and *B. eriopoda* in the Chihuahuan Desert grassland across 23 years of removal treatments. Year and plot were used as random effects in these models. See methods section for details. Visualized in Figure S1.

	Treatment	**Estimate**	**p-value**
Great Plains	**Control - all species**	**97.0**	**<0.001**
	Control - subordinate species	**9.8**	**<0.001**
	***B. gracilis* removal**	**58.5**	**<0.001**
Chihuahuan Desert	**Control - all species**	**151.2**	**<0.001**
	Control - subordinate species	**24.9**	**<0.001**
	B. eriopoda removal	**54.69**	**<0.001**

Table 2. Comparison of NPP of full communities in control conditions, subordinate species in controls, and subordinate species after removal of the dominant species in Great Plains and Chihuahuan Desert grasslands. Year and plot were used as random effects in these models, see methods section for details. Visualized in Figure 2.

Productivity ~ Species richness	**Model term**	**Estimate**	**p-value**
Great Plains	**Intercept**	**78.7**	**< 0.001**
	Species richness	2.3	0.17
	B. gracilis removal	5.0	0.81
	Species richness x *B. gracilis* removal	**-4.5**	**0.02**
Chihuahuan Desert	**Intercept**	**131.2**	**< 0.001**
	Species richness	2.2	0.14
	B. eriopoda removal	-43.2	0.10
	Species richness x *B. eriopoda* removal	**-4.9**	**0.017**

Productivity ~ Dominance	**Model Term**	**Estimate**	**p-value**
Great Plains	Intercept	16.0	0.73
	Dominance	92.2	0.078
	B. gracilis removal	37.8	0.46
	Dominance x *B. gracilis* removal	-81.2	0.21
Chihuahuan Desert	**Intercept**	**163.4**	**<0.001**
	Dominance	-15.4	0.68
	***B. eriopoda* removal**	**-121.8**	**< 0.01**
	Dominance x *B. eriopoda* removal	47.0	0.39

Table 3. Relationships between species richness and NPP as well as dominance and NPP in Great Plains and Chihuahuan Desert grasslands with and without removal of the dominant species. In both grasslands, species richness has only weak correlation with NPP, but dominance correlations with NPP are strong in both grasslands. See methods for model details. Also visualized in Figure 4.

Site	**Functional group**	**Control Estimate**	**Removal Estimate**	**p-value**
Great Plains	**Forb**	**1.5**	**5.3**	**<0.05**
	Grass	**2.2**	**21.4**	**<0.001**
	Shrub	**1.9**	**6.0**	**<0.01**
Chihuahuan Desert	**Forb**	**4.4**	**7.6**	**<0.01**
	Grass	**5.3**	**15.8**	**<0.001**
	Shrub	2.8	4.5	0.44

Table S1. Comparison of functional group cover in controls and when dominant species are removed in both Great Plains and Chihuahuan Desert grasslands. Grass functional group does not include dominant species. Year and plot were used as random effects in these models, see methods section for details. Visualized in Figure S2.

CHAPTER 2

RESISTANCE OF DESERT PLANT COMMUNITIES TO EXTREME DROUGHT IN THE HOT DESERTS OF THE U.S.

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Abstract

The hot deserts of the southwestern U.S. are experiencing increased frequency and severity of drought due to anthropogenic climate change. Plant communities in these deserts differ in dominant species and community assembly, which could lead to opposing responses to drought over time. Thus, identifying the ways in which these desert plant communities respond to drought is critical to assessing the vulnerability of these ecosystems to future change. We measured the responses of community cover and five facets of community structure for two years in response to a 66% precipitation reduction in six sites across the hot deserts of the southwestern U.S. Decreased vegetative cover in response to drought was attributable more to the sensitivity of grasses than forbs. Though site-level community structure responses were mixed, responses of increased evenness were linked to cover responses across sites. Contrary to expectations, communities made up of annual species were more resistant to drought effects than those dominated by perennial species. In general, we found that community structure, but not abundance, was resistant to severe drought in herbaceous communities of southwestern U.S. deserts.

Introduction

Drylands cover 40% of Earth’s terrestrial surface and are a critical component of human and ecological systems (Maestre et al. 2016, European Commission Joint Research Centre 2018). Drylands are more sensitive to drought and disturbance than less-arid terrestrial ecosystems, making them exceptionally vulnerable to intensifying climatic perturbations caused by anthropogenic climate change (Huxman et al. 2004, Maurer et al. 2020, Burrell et al. 2020). Climate change forecasts predict greater climate variability and increased occurence of climatic extremes, including drought (Intergovernmental Panel of Climate Change 2014, 2022, Cook et al. 2004, Dai 2013). In the hot deserts of the U.S. - Mojave, Sonoran, and Chihuahuan - increased drought frequency is likely to disrupt ecosystem processes through perturbation of plant communities (Collins et al. 2020, Munson et al. 2016, McAuliffe and Hamerlynck 2010, Gherardi and Sala 2015). Despite the vulnerability of dryland ecosystems to drought, relatively few studies to date have experimentally imposed drought conditions in the hottest and driest ecosystems of the southwestern U.S. (Yahdjian et al. 2021). Desert ecosystems, are functionally and structurally different than more temperate ecosystems since deserts are fundamentally water-limited, as opposed to limitation by light, nutrients, temperature, or other physiological factors (Wheeler et al. 2021, Berdugo et al. 2022, Hoover et al. 2020, Maestre et al. 2016). In addition, the deserts of the southwestern U.S. experience high interannual climate variability, making drought a more frequent disturbance on these landscapes, historically (Maurer et al. 2020, Gutzler and Robbins 2011). Plant communities in deserts may be tolerant of drought due to a long evolutionary history with drought, or they may be more senstive to drought due to their fundamental water limitation.

The structure of plant communities responds to disturbance across five facets of community assembly: species richness, species evenness, species gains, species losses, and reordering of rank abundance (Avolio et al. 2015, 2019, 2021, Jones et al. 2017). Species richness quantifies the diversity of species in communities and species evenness quantifies the similarity of abundances within communities. Species gains, losses, and rank abundance change all describe how the structure of communities change between timepoints by quantifying colonization, local extinction, and community reordering (Hallett et al. 2016, Avolio et al. 2019). Plant communities in dryland ecosystems respond to drought across these axes of community structure. For example, Korell et al. (2021) showed that drought decreases species richness at local scales in drylands. In addition, extreme drought can alter rank abundances (Batbaatar et al. 2021) and increase evenness (Castillioni et al. 2020) without any effect on species richness in the North American Great Plains. In dryland annual communities, drought can also increase evenness as a consequence of reduced competition (Alon and Sternberg 2019).

Ecosystems comprised of long-lived species, such as perennial grasses or shrubs, are more resistent to stressors and are thus expected to be relatively slow to respond to disturbance (Chapin et al. 2004, Greaver et al. 2012). In contrast, the same stressor applied to ecosystems dominated by short-lived species should elicit a more rapid response (Morris et al. 2008, Collins et al. 2008). Plant communities in the hot deserts of the U.S. include both long-lived perennial species and short-lived ephemerals. The intershrub zones of the Mojave and Sonoran Deserts are comprised of winter annual species with life spans of just a few months (Brooks 2000, Venable and Kimball 2012). Species of these annual communities can lay dormant in the seedbank for many years and only germinate when environmental conditions are favorable (Gremer and Venable 2014, Clauss and Venable 2000). Grasslands of the Chihuahuan Desert are dominated by perennial grasses which make up over 80% of aboveground production (see previous chapter, Muldavin et al. 2008, Rudgers et al. 2018). Due to the abundance of perennial grasses, responses of Chihuahuan Desert grasslands to disturbance are tightly tied to the sensitivity of perennial grasses (Collins et al. 2020, Báez et al. 2013, Munson et al. 2013). Thus, drought should have a more immediate impact on both the community structure and ecosystem processes of annual communities of the intershrub zones in the Mojave and Sonoran Deserts than perennial grasslands of the Chihuahuan Desert.

In this study, we used a coordinated drought experiment in Mojave, Sonoran, and Chihuahuan Desert plant communities to assess the effects of extreme drought on vegetative cover and community structure over time. Regional distribution of this experiment provided distinct community assemblages, and we used two sites in each desert to capture a range of grass cover, forb cover, and species pools. Our study addressed three questions: (1) *Do annual-dominated communities respond more rapidly to drought than perennial-dominated communities?* (2) *Which facets of community structure change in response to drought?* and (3) *Are changes to communitiy structure correlated with cover responses over time?*

Methods

Site details

We established drought experiments at six sites, two each in Mojave, Sonoran, and Chihuahuan deserts (Figure 1, Table 1). Both Mojave Desert sites, Granite Cove and Molar Junction, were located at the Granite Mountains Desert Research Center, near Kelso, CA. Granite Cove was established within a *Larrea tridentata* (creosote) shrubland with an herbaceous community dominated by *Schismus barbatus*, while Molar Junction was established 0.6 km away in a mixed-species shrubland. Abundant species included the annual plants *Erodium cicutarium*, *Acmispon strigosus*, and *Pectocarya heterocarpa* (Ohlert et al. 2021). The Sonoran Desert sites, White Tank and McDowell, were located at White Tank Mountain and McDowell Mountain regional parks 72 km apart on the west and east edges of the Phoenix, AZ metro area, respectively (Wheeler et al. 2021). Herbaceous communities at both Sonoran sites were dominated by annual plants including *Plantago ovata*, *Pectocarya recurvata*, and *Schismus arabicus*. Two Chihuahuan Desert sites, Sevilleta Black and Sevilleta Mixed, were located 4.3 km apart at the Sevilleta National Wildlife Refuge north of Socorro, NM. Both are in arid grasslands; the Sevilleta Black site is dominated by *Bouteloua eriopoda*, and the Sevilleta Mixed site is co-dominated by *B. eriopoda* and *B. gracilis* with a mixture of other C4 perennial grasses including *Pleuraphis jamesii* and *Sporobolus spp.*

Experimental design

Each site contains 14 2.5x2.5 m plots with a permanent 1x1 m vegetation sampling quadrat in the center. With a focus on herbaceous plant communities, we chose plot locations in intershrub zones, defined as an area not included within the dripline of a shrub canopy. A few plots subsequently included small amounts of woody vegetation due to colonization and proliferation of seedlings after plots were established. Each site included seven unmanipulated control plots and seven plots were located under rainout shelters. Treatment and control plots were spatially paired in the Chihuahuan Desert sites and were randomly assigned in the Sonoran and Mojave Desert sites. Rainout shelters were constructed of 1-5/8 in. hollow galvanized steel ranging from three to five feet in height, sloped from south to north to allow water to run down gutters while minimizing shadows on the plot. Gutters were made of clear acrylic sheets that allow photosynthetically active radiation to pass through (Yahdjian & Sala 2002). Triangular gutters with width of 4-1/3 in. were made by bending acrylic sheets, 15 of which were fastened to the top of each frame in order to reduce rainfall by 66% of ambient year-round. This 66% rainfall reduction was designed to achieve a target 1 in 100-year drought event in coordination with the International Drought Experiment (Lemoine et al. 2016, Knapp et al. 2017). Rainout shelters were erected within a week following pretreatment data collection to ensure consistent year-round drought treatments. In the first treatment year, five of the six sites experienced ambient precipitation close to the 30-year average precipitation and one site, White Tank, received approximately 160% of average precipitation (Table 1). In the second treatment year, a regional drought led to ambient rainfall of about half of the long-term average at McDowell and approximately a quarter of the average at both Granite Cove and Molar Junction (Table 1).

Data collection

We identified each species rooted within each quadrat and visually estimated abundance as the percent of ground covered by each species. All data were collected by or with supervision of the lead author to ensure measurement consistency. We chose data collection dates to coincide with peak biomass of these ecosystems. Typically, peak biomass occurs in winter and spring in the Mojave and Sonoran Deserts following winter rains and favorable temperatures. In the Chihuahuan Desert, the annual monsoon season during July and August results in a peak biomass season in the fall. We therefore collected pretreatment community composition data in March 2019 at the Sonoran

Desert, April 2019 at the Mojave Desert, and October 2018 at the Chihuahuan Desert sites. Vegetation composition was sampled annually for the next two years of drought treatments.

Community structure

Cover of each species within each quadrat was summed to yield a measure of total cover. Species were sorted into three functional groups: grass, forb, and shrub. We included legumes with forbs because few herbaceous legumes occur at any of the study sites, and their abundance was < 1% cover when they did occur. Shrubs accounted for minimal vegetative cover and only occurred at two of six sites. We calculated percent grass and percent forb as the summed cover of each functional group in a plot divided by the summed cover of all functional groups (Table 1). Therefore, percent grass and percent forb added up to 100% except when shrubs were present. Species were also classified as either annual or perennial based on local knowledge of each species' life history. Species richness was defined as the number of unique species identified in each 1x1 m quadrat. We calculated evenness using the EQ index which accounts for the similarity of abundances between species based upon a rank-abundance curve and is independent of species richness (Smith and Wilson 1996). We used the 'codyn' package in R (v2.0.5; Hallett et al. 2016, Avolio et al. 2019) to quantify species gains as the number of new species in a plot from the previous year divided by the total number of unique species in both current and previous year. Similarly, we quantified species losses as the number of species present in the previous year, but not present during the current year, divided by the number of unique species in both years (Hallett et al. 2016, Avolio et al. 2019). We again used the ‘codyn’ package in R to calculate rank change as the absolute value of the average change in species ranks between the current year and previous year for each replicate divided by the total number of unique species in both time periods (Hallett et al. 2016, Avolio et al. 2019).

Response ratios

We measured effect size using the Relative Interaction Intensity index (RII):

$$\frac{t-c}{t+c}$$

where *t* equals the value of a community property in a drought treatment plot and *c* equals the value of that community property in a control plot (Armas et al. 2004). RII was calculated using the paired treatment and control plots of the Sevilleta sites, and paired to neighboring pairs of treatment and control plots at the other sites. RII is bound between -1 and 1 and can incorporate situations in which the community values are 0, unlike other indices such as log response ratio. The latter property of RII is especially important in the low-productivity desert plant communities which often have no seasonal growth, especially when subjected to drought. We calculated an RII value for pairs of treatment and control plots. Pairs were determined by geographic proximity of treatment and control plots to minimize the effect of spatial variability. This resulted in seven RII values per site with which we used the qt function in the R ‘stats’ package (v4.1.2; R core team 2021) to generate 95% confidence intervals for RIIs and we considered responses to treatment as significant when the 95% confidence interval did not overlap 0.

In order to assess the impacts of species richness, evenness, species gains, species losses, and rank change on vegetative cover over time, we used mixed regression models comparing RII of those five metrics to the RII of cover. For each year, we created linear models to test correlation between the RII of cover and the RII of each community metric using site as a random effect.

We used R Statistical Software (v4.1.2; R Core Team 2021) for all analyses and we used the 'tidyverse' (v1.3.1; Wickham et al. 2019) and 'plyr' (v1.8.6; Wickham et al. 2011) packages for data manipulation and visualization. Data are available at Ohlert and Collins (2021).

Results

Within-site responses

Total vegetative cover decreased in response to drought at five of six sites in either the first or second years of treatment. In the first treatment year, vegetative cover decreased at three sites: White Tank, Sevilleta Black, and Sevilleta Mixed (Figure 2a, Table 2). At White Tank, cover fell from 44.2% in control plots to 16.7% in treatment plots, at Sevilleta Black, cover decreased from 28.6% in controls to 11.5% in treatment plots, and at Sevilleta Mixed, cover fell from 20.3% in controls to 9.6% in treatment plots. In the second treatment year, cover decreased at four sites: Granite Cove, Molar Junction, White Tank, and Sevilleta Mixed (Figure 2a, Table 2). Due to a severe regional drought during the second treatment year, absolute values of cover were particularly low at Mojave and Sonoran sites. At Granite Cove, cover was 0.5% in control plots and 0.2% in treatment plots, and similarly, cover was reduced from 0.5% in controls to 0.3% in treatment plots at Molar Junction. At White Tank, cover was 4.6% in control plots and 1.9% in treatment plots, and at Sevilleta Mixed, cover fell from 28.5% in controls to

19.5% in treatment plots. McDowell was the only site where cover was unaffected by the drought treatment in either year.

Cover changes across years were attributable more to changes in grass cover than forb cover. Grass cover significantly decreased in the first year at three sites: White Tank, McDowell, and Sevilleta Mixed (Figure 2b, Table 2). At White Tank, grass cover decreased from 35.7% in controls to 7.7% in treatment plots, at McDowell, grass cover decreased from 33.9% in control plots to 25.2% in treatment plots, and at Sevilleta Mixed, grass cover decreased from 18.9% in control plots to 9.3% in treatment plots. In the second year, grass cover decreased at just two sites: White Tank and Sevilleta Black (Figure 2b, Table 2). At White Tank, grass cover decreased from 2.6% to 0.6% in treatment plots. At Sevilleta Black, grass cover fell from 6.8% in control plots to 4.2% in treatment plots. Forb cover did not change in the first year at any sites, and in the second year, decreased at only Granite Cove from 0.23% in control plots to 0.1% in treatment plots (Figure 2c, Table 2).

Cover of annual species declined at only White Tank in the first year of treatment from 44.2% in control plots to 16.7% in treatment plots (Figure 2d, Table 2). There were not enough annual species at Sevilleta Mixed in the first treatment year for analysis as only a single control plot had annuals and no treatment plots had annuals. In the second treatment year, cover of annual species significantly decreased at three sites: White Tank, Molar Junction, and Granite Cove (Figure 2d, Table 2). At White Tank, cover decreased from 3.9% in controls to 1.6% in treatment plots. At Molar Junction, cover decreased from 0.5% in controls to 0.3% in treatment plots. At Granite Cove, cover of annuals decreased from 0.5% in control plots to 0.2% in treatment plots. Cover of annuals was greater in treatment than control plots in the second year at the Sevilleta Mixed site, though there were not enough annuals in the first year for this site to be analyzed.

Perennial species were only found in the Chihuahuan Desert sites with the exception of a single individual found within a drought treatment plot at Molar Junction in the first treatment year. Therefore, responses of perennials were only recorded for Sevilleta Black and Sevilleta Mixed. In the first treatment year, cover of perennials decreased at both Chihuahuan Desert sites dominated by perennial grasses (Figure 2e, Table 2). At Sevilleta Black, cover of perennials decreased from 23.7% in controls to 10.9% in treatment plots and at Sevilleta Mixed, cover of perennials decreased from 19.9% in control plots to 9.6% in treatment plots. In the second treatment year, perennial cover decreased at Sevilleta Mixed from 28.1% in control plots to 16.9% in treatment plots (Figure 2e, Table 2).

Species richness decreased in response to drought at just Granite Cove in both treatment years. In the first treatment year, species richness decreased at Granite Cove from an average of 8.1 species per m^2 in control plots to an average of 5.3 species per m^2 in treatment plots (Figure 3a, Table 2). In the second treatment year, species richness decreased at Granite Cove from 4.6 species per m^2 in control plots to an average of 2.0 species per m^2 in treatment plots (Figure 3a, Table 2). Evenness did not change within any site in the first treatment year, but in the second year, evenness increased at both Molar Junction and White Tank (Figure 3b, Table 2). Species gains decreased with drought treatment in the first year at Granite Cove and decreased in the second year at White Tank (Figure 3c, Table 2). Species losses were unchanged at all sites in the first treatment year. However, in the second treatment year, losses increased at Granite Cove and decreased at Sevilleta Mixed (Figure 3d, Table 2). We found no significant difference in rank abundance change in either the first or second treatment years at any sites (Figure 3e, Table 2).

Cross-site responses

Species richness response was not correlated with cover responses in the first treatment year ($p = 0.85$, slope = 0.04, $r^2m = 0.001$) (Figure 4a), but was correlated in the second treatment year ($p < 0.001$, slope = 0.53, $r^2m = 0.21$) (Figure 4b). Evenness response was correlated with cover responses in both treatment years, but correlation of cover responses with other facets of communities were limited. In the first year, evenness responses were negatively correlated with cover responses ($p < 0.01$, slope = -0.57, $r^2m = 0.10$) (Figure 4c). The second treatment year had a similar negative correlation ($p < 0.01$, slope = -0.57, $r^2m = 0.22$) (Figure 4d). Responses of species gains were not correlated with cover responses in the first treatment year ($p = 0.14$, slope = 0.14, $r^2m = 0.04$) (Figure 4e) and neither in the second treatment year ($p = 0.22$, slope = 0.11, $r^2m = 0.05$) (Figure 4f). Species losses were also not correlated with cover responses in year one ($p = 0.86$, slope = -0.02, $r^2m = 0.001$) (Figure 4g) though there was significant negative correlation in year two ($p < 0.01$, slope = -0.23, $r^2m = 0.16$) (Figure 4h). Rank change responses were not correlated with cover responses in the first treatment year ($p = 0.84$, slope = 0.03, $r^2m = 0.001$) (Figure 4i) nor in the second ($p = 0.97$, slope = -0.01, $r^2m = 0.00$) (Figure 4j).

Discussion

In this study, we assessed the impact of two years of drought on multiple dimensions of plant communities in the hot deserts of the southwestern U.S. Drought sensitivity of vegetative cover was linked to response of the grass functional group, while forb responses were fewer than expected. Responses of species richness, species evenness, species gains, species losses, and rank abundance change were sporadic over the two years of study, with multiple sites exhibiting no change in community structure measures despite considerable responses of functional groups and overall cover. Across sites, species evenness responses were negatively correlated with cover responses for both treatment years, and cover responses were correlated with species richness responses and species losses in the second treatment year only.

Grass sensitivity across deserts

Over two years of treatment, grasses responded more negatively to drought than forbs. Though greater sensitivity to drought of grasses than forbs has been documented in grasslands (Koerner and Collins 2014, Zhang et al. 2021, Hallett et al. 2019), the role of grasses in these desert communities differs from temperate grassland communities. Grass cover in the Sonoran and Mojave Deserts is dominated by nonnative annual grasses including *Schismus arabicus*, *S. barbatus*, and *Bromus rubens* (Wheeler et al. 2021, Ohlert et al. 2021). Though these nonnative grasses make up a small fraction of the annual flora, they comprise a large amount of the biomass of these systems (Wheeler et al. 2021, Ohlert et al. 2021). Nonnative grasses are successful invaders of Mojave and Sonoran desert ecosystems, but their origin in the Mediterranean region likely leaves them vulnerable to the driest conditions that these desert ecosystems present (Jackson 1985). Drought may be one of the few disturbances that limits the spread and abundance of these nonnative annual grasses (Brooks and Berry 2006). However, senesced grasses in the Mojave and Sonoran Deserts promote fire, which easily spreads through the intershrub zones and negatively affects cacti and shrubs (McLaughlin and Bowers 1982, Thomas 1991, Moloney et al. 2019). As climate variability increases, the Mojave and Sonoran Deserts are increasingly at risk of dominance by nonnative grasses and loss of prominent perennial flora (Brooks and Chambers 2011, Thomey et al. 2012, Aslan et al. 2021).

Similarly, grass flora in the Chihuahuan Desert is dominated by native perennial grasses that are sensitive to drought (Báez et al. 2013, Ladwig et al. 2014, Collins et al. 2020). The dominant grasses of these ecosystems are particularly important to ecosystem processes and subdominant species are unable to compensate for their loss (see previous chapter). Other studies at these sites similarly find that drought can decrease the growth of dominant species without affecting overall diversity (Báez et al. 2013). Indeed, our experiment shows a tight link between the responses of grass cover and total vegetative cover in the Chihuahuan Desert, despite no change in forb cover or community structure. As drought frequency increases in the Chihuahuan Desert, negative impacts on dominant perrennial grasses will affect vegetative abundance on the landscape, and may eventually lead to reordering of plant communities.

Which aspects of community structure changed?

Drought had relatively few effects on species richness in our study, affecting overall species richness at just one site over two years of treatment. Though Tilman and Haddi (1992) found consistent negative effects of a regional drought on the species richness of four different grassland communities, recent research in temperate grasslands of North America shows that drought manipulation can have no effect on species richness (Batbaatar et al. 2021, Castillioni et al. 2020). In contrast, a recent metanalysis found that drought effects on species richness were greatest in more-arid environments (Korell et al. 2021). Since total vegetative growth is more sensitive to precipitation change in drylands, loss of aboveground vegetation should incur a commensurate decline in richness. Indeed, we found that declines in species richness were correlated with declines in vegetative cover at the plot scale (Figure 4b). Responses of species richness to drought at the plot level, but not at the site level, suggests an additional layer of complexity to the diversity of dryland ecosystems which may not be present in temperate grasslands. A similar drought manipulation study in annual communities of Mediterranean shrublands with greater mean annual precipitation (540 mm) found that drought did not directly affect species richness, but changed the slope of the relationship between species richness and aboveground net primary production (Alon and Sternberg 2019). Further, drylands have relatively high spatial turnover which likely contributes to the variability of responses at the plot level (Noy-Meir 1973).

Previous studies of drought impacts on evenness report either no effect (Batbaatar et al. 2021) or positive effects (Alon and Sternberg 2019, Castillioni et al. 2020). Evenness increased in response to drought in annual communities of Mediterranean shrublands which was attributed to release from competition (Alon and Sternberg 2019).

At the plot level, we found evidence of linkages between changes to evenness and changes to cover. In particular, plots with greater increases in evenness, implying reduced dominance, had the greatest loss of vegetative cover. Dominant species are known to be particularly important drivers of ecosystem processes in response to drought (Smith et al. 2020, Hoover et al. 2014, Knapp et al. 2020, Báez et al. 2013). Mass-ratio effects drive vegetative abundance in the Chihuahuan Desert (see previous chapter), and recent studies at the Mojave and Sonoran Desert sites highlight the importance of mass-ratio effects with respect to the dominant grasses of those deserts (Ohlert et al. 2021, Wheeler et al. 2021). Despite increased evenness due to drought, there was no consistent change in rank abundance at any site in either treatment year. Rank change is considered an important process that restructures communities in response to disturbance (Avolio et al. 2021), and previous drought experiments in the North American Great Plains found that extreme drought induced greater rank change than ambient (Batbaatar et al. 2021). Lack of rank change, despite considerable responses to total vegetative cover, implies that species were roughly equally impacted by the drought treatment without obvious shifts to dominance or rarity.

Species turnover should be particularly responsive in communities comprised of short-lived plants with high sensitivity to environmental conditions (Collins et al. 2008). Annual forbs play a novel role in desert ecosystems through delayed germination while waiting for favorable abiotic conditions, often when seasonal rainfall is above average (Cayan et al. 1999, Venable and Pake 1999, Bowers 2005, Venable 2007, Gremer and Venable 2014). However, we found relatively low turnover even among the annual communities in our study comprised of short-lived species. Species gains and losses were highly variable and not clearly concentrated in any given community type across the six sites in our study. Negative correlation between species losses and cover response occurred only in the second year of treatment, but such correlations between turnover and cover are expected to further magnify with disturbance duration (Smith et al. 2009, Smith et al. 2015, Jones et al. 2017). Though communities are expected to continue to change over a long period of time with continued resource stress (Komatsu et al. 2019, Seabloom et al. 2021), evidence of increased turnover is mixed (Smith et al. 2015, Avolio et al. 2021, Batbaatar et al. 2021), and long-term drought studies are lacking. Extending drought experiments to incorporate multi-year drought effects is necessary to capture the full trajectory of change that drought imposes on plant communities, while also simulating the types of droughts that are expected to occur in the next century (Trenberth et al. 2014, Cook et al. 2015, Bradford et al. 2020).

Overall, the lack of community change despite considerable negative cover responses is contrary to previous studies showing linkages between community changes and ecosystem processes (Smith et al. 2015, Kimmel et al. 2019). With this distributed experiment, we demonstrated that drought impacts on the vegetative cover of desert ecosystems are immediate and concentrated in grasses. Sensitivity of vegetative cover to drought is linked to the responses of community structure, in particular, species evenness. Further study in dryland ecosystems should include longer duration of treatment and incorporate a wide range of communities in order to predict the consequences of drought across a variety of desert ecosystems. Understanding the trajectory of changes that drought imposes on plant communities will prepare human and ecological systems for extreme global change in not only deserts, but all terrestrial ecosystems.

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Figures

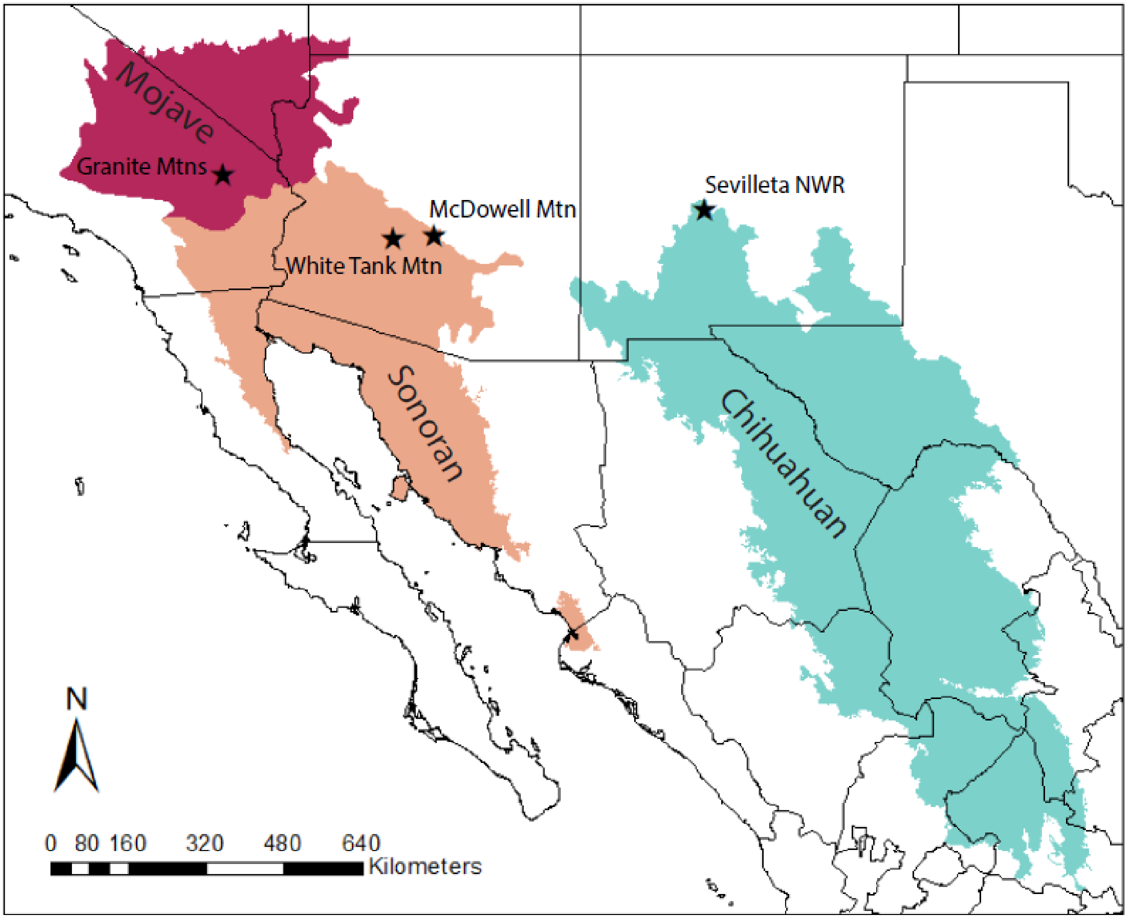

Figure 1. Map of site locations within the hot deserts of the U.S. See Table 1 for further information regarding the abiotic and biotic conditions of these sites.

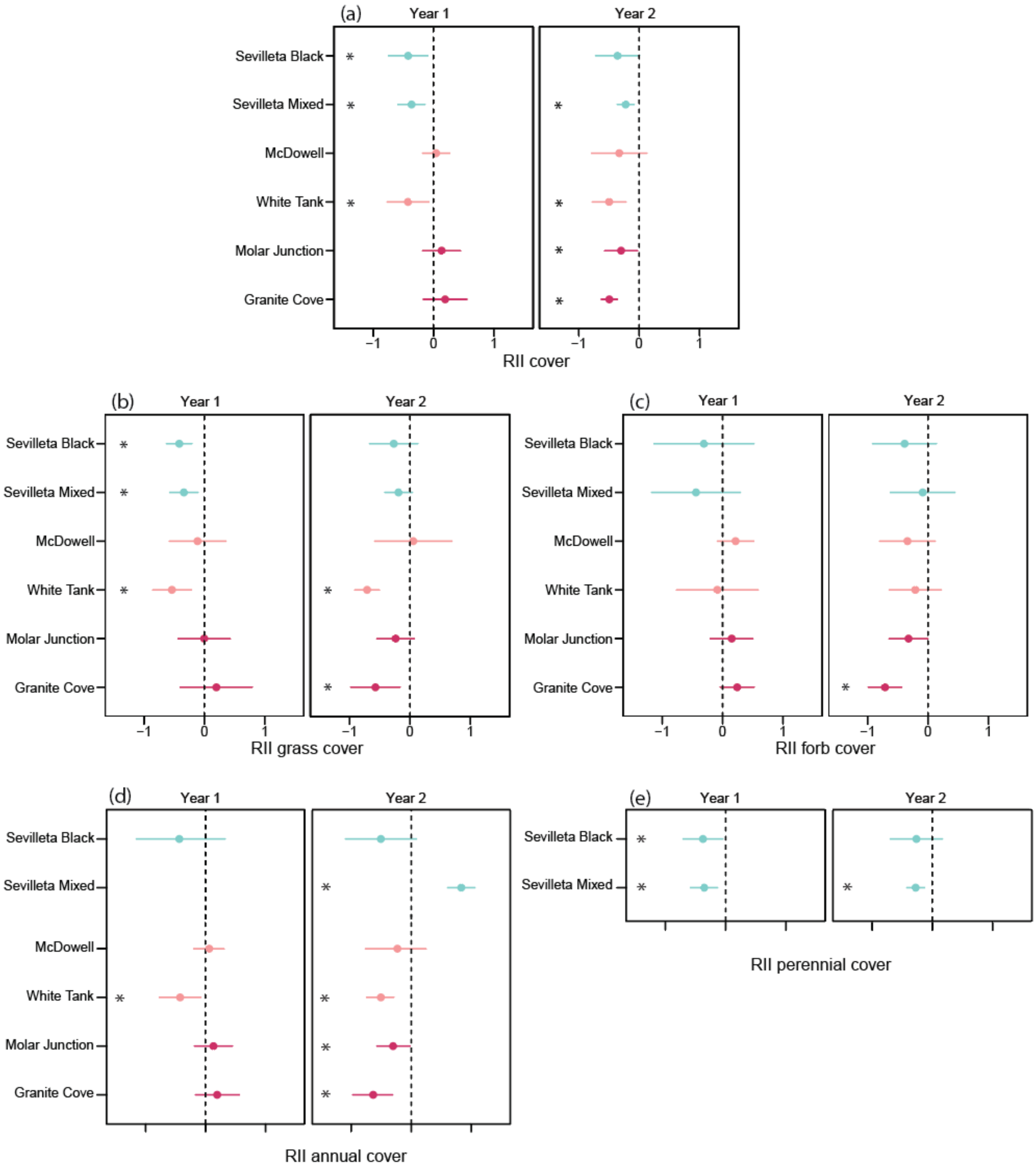

Figure 2. Relative Interaction Intensity index (RII) of a) total vegetative cover b) grass cover c) forb cover d) cover of annual species and e) cover of perennial species in six

desert plant communities in the U.S. hot deserts for two years of drought treatment. Mean responses are shown with points and error bars display the 95% confidence interval. Asterisks denote significant responses in which 95% confidence intervals do not overlap 0. RII were not calculated for annual species at Sevilleta Mixed in the first year, nor for perennial species in the Mojave and Sonoran Deserts in either treatment years due to a lack of data. RII values are shown in Table 2.

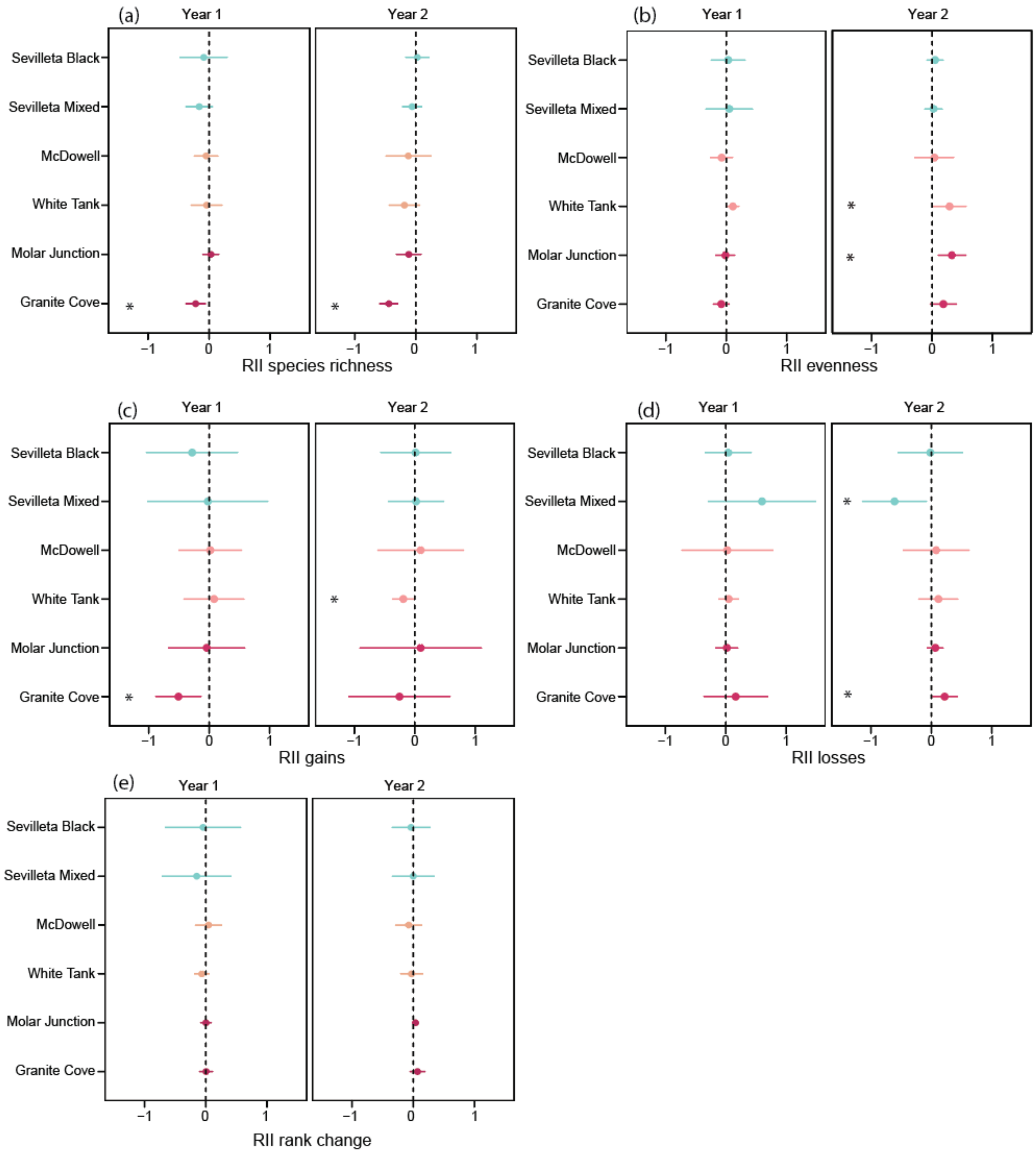

Figure 3. Relative Interaction Intensity index (RII) of a) species richness b) species evenness c) species gains d) species losses and e) rank abundance change in six desert

plant communities in the U.S. hot deserts for two years of drought treatment. Mean responses are shown with points and error bars display the 95% confidence interval. Asterisks denote significant responses in which 95% confidence intervals do not overlap 0. RII values are shown in Table 2.

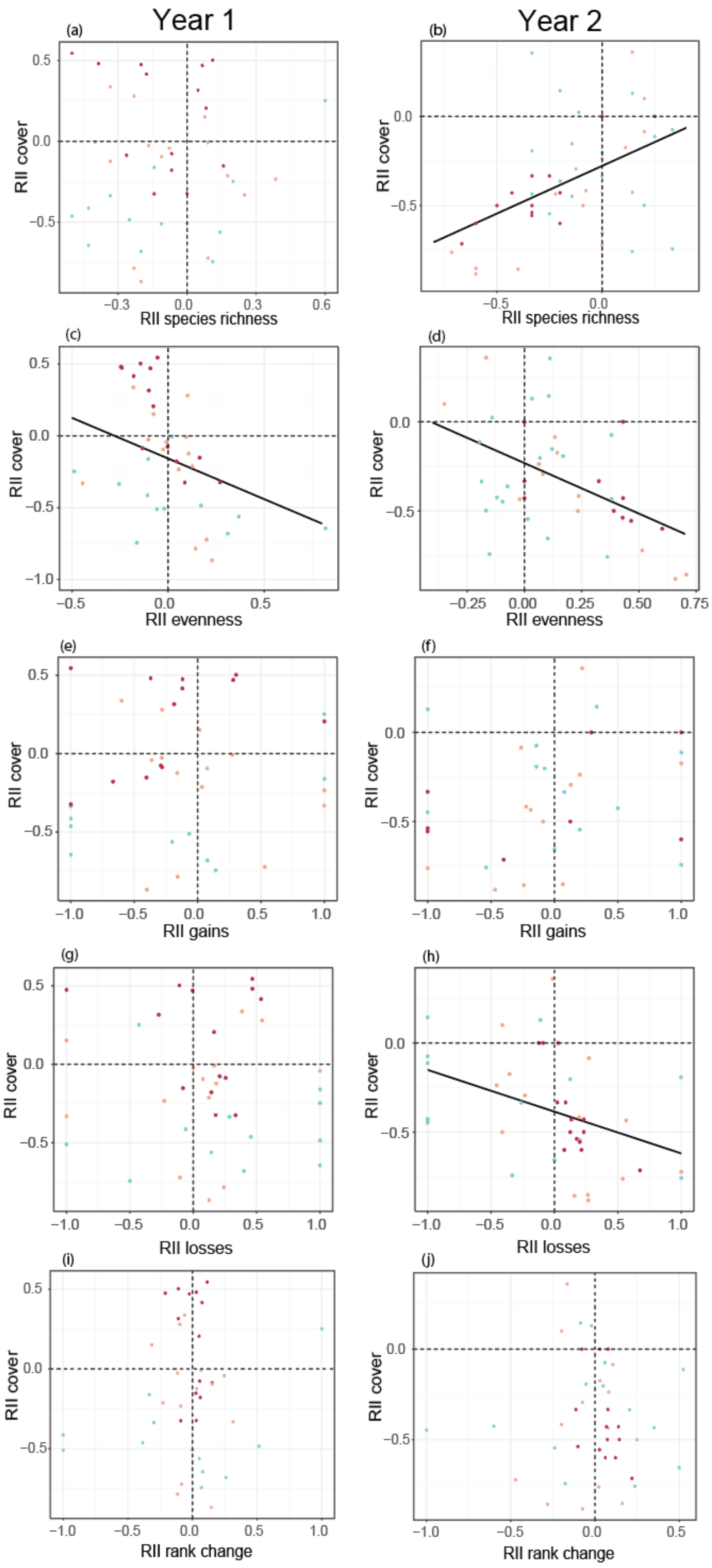
Year 1
Year 2
(a)
(b)
RII cover
RII species richness
−0.3
0.0
0.3
0.6
0.5
0.0
−0.5
−0.5
0.0
(c)
(d)
RII evenness
−1.0
−0.25
0.00
0.25
0.50
0.75
(e)
(f)
RII gains
−1.0
0.5
1.0
(g)
(h)
RII losses
(i)
(j)
RII rank change

Figure 4. Relationship between RII responses of a,b) species richness c,d) species evenness e,f) species gains g,h) species losses i,j) rank abundance change and RII responses of vegetative cover in the a,c,e,g,i) first and b,d,f,h,j) second year of drought treatment. The black line shows a significant correlation between the two responses based on regression models. See methods for details. Points show responses of paired plots: Mojave Desert in red, Sonoran Desert in tan, and Chihuahuan Desert in blue. Significant correlations are shown with a black line.

Tables

Site	Desert	MAP	MAT	Year 1 precip	Year 2 precip	Elevation	Peak season	Site species	% grass	% forb
Granite Cove	Mojave	220mm	16C	224mm	56mm	1,128m	Spring	15	29	71
Molar Junction	Mojave	220mm	16C	224mm	56mm	1,128m	Spring	34	19	81
White Tank	Sonoran	212mm	24C	345mm	241mm	400m	Spring	19	79	21
McDowell	Sonoran	295mm	24C	264mm	128mm	204m	Spring	18	63	37
Sevilleta Black	Chihuahuan	249mm	14C	243mm	216mm	1,669m	Fall	20	70	17
Sevilleta Mixed	Chihuahuan	234mm	14C	227mm	227mm	1,669m	Fall	9	96	4

Table 1. Summary of sites including their biotic and abiotic attributes including mean annual precipitation (MAP), mean annual temperature (MAT), elevation, peak growing season, the total number of unique species in all plots in the pretreatment year (site species), and the percentages of vegetative cover comprised by grasses and forbs in the pretreatment year.

Metric	Treatment year	Site	Mean RII	95% lower	95% upper
Cover	1	**Sevilleta Black**	**-0.42**	**-0.75**	**-0.09**
		Sevilleta Mixed	**-0.37**	**-0.60**	**-0.14**
		McDowell	0.04	-0.19	0.27
		White Tank	**-0.42**	**-0.78**	**-0.07**
		Molar Junction	0.13	-0.19	0.46
		Granite Cove	0.19	-0.18	0.56
	2	Sevilleta Black	-0.36	-0.73	0.02
		Sevilleta Mixed	**-0.22**	**-0.37**	**-0.07**
		McDowell	-0.33	-0.79	0.14
		White Tank	**-0.50**	**-0.78**	**-0.21**
		Molar Junction	**-0.30**	**-0.58**	**-0.01**
		Granite Cove	**-0.49**	**-0.63**	**-0.35**
Grass cover	1	**Sevilleta Black**	**-0.42**	**-0.64**	**-0.20**
		Sevilleta Mixed	**-0.34**	**-0.58**	**-0.10**
		McDowell	-0.11	-0.59	0.36
		White Tank	**-0.54**	**-0.87**	**-0.21**
		Molar Junction	-0.00	-0.44	0.44
		Granite Cove	0.20	-0.41	0.80
	2	Sevilleta Black	-0.27	-0.68	0.14
		Sevilleta Mixed	-0.19	-0.43	0.05
		McDowell	0.06	-0.59	0.70
		White Tank	**-0.71**	**-0.92**	**-0.50**
		Molar Junction	-0.24	-0.55	0.08
		Granite Cove	**-0.57**	**-0.99**	**-0.15**
Forb cover	1	Sevilleta Black	-0.31	-1.14	0.53
		Sevilleta Mixed	-0.44	-1.18	0.30
		McDowell	0.21	-0.09	0.52
		White Tank	-0.09	-0.77	0.60
		Molar Junction	0.15	-0.21	0.51
		Granite Cove	0.24	-0.05	0.53
	2	Sevilleta Black	-0.39	-0.93	0.15
		Sevilleta Mixed	-0.09	-0.63	0.45
		McDowell	-0.34	-0.81	0.13
		White Tank	-0.21	-0.65	0.23
		Molar Junction	-0.32	-0.65	0.01
		Granite Cove	**-0.47**	**-0.62**	**-0.32**
Annual cover	1	Sevilleta Black	-0.41	-1.16	0.34
		Sevilleta Mixed	NA	NA	NA
		McDowell	0.06	-0.20	0.32
		White Tank	**-0.42**	**-0.78**	**-0.07**

		Molar Junction	0.13	-0.19	0.46
		Granite Cove	0.19	-0.18	0.56
	2	Sevilleta Black	-0.51	-1.11	0.09
		Sevilleta Mixed	0.83	0.60	1.07
		McDowell	-0.26	-0.77	0.26
		White Tank	**-0.51**	**-0.75**	**-0.28**
		Molar Junction	-0.30	-0.58	-0.01
		Granite Cove	**-0.49**	**-0.63**	**-0.35**
Perennial cover	1	**Sevilleta Black**	**-0.38**	**-0.71**	**-0.04**
		Sevilleta Mixed	**-0.36**	**-0.59**	**-0.13**
		McDowell	NA	NA	NA
		White Tank	NA	NA	NA
		Molar Junction	NA	NA	NA
		Granite Cove	NA	NA	NA
	2	Sevilleta Black	-0.27	-0.71	0.17
		Sevilleta Mixed	**-0.28**	**-0.43**	**-0.13**
		McDowell	NA	NA	NA
		White Tank	NA	NA	NA
		Molar Junction	NA	NA	NA
		Granite Cove	NA	NA	NA
Species richness	1	Sevilleta Black	-0.09	-0.48	0.31
		Sevilleta Mixed	-0.16	-0.38	0.06
		McDowell	-0.05	-0.25	0.15
		White Tank	-0.04	-0.30	0.22
		Molar Junction	0.03	-0.11	0.17
		Granite Cove	**-0.22**	**-0.38**	**-0.06**
	2	Sevilleta Black	0.02	-0.18	0.22
		Sevilleta Mixed	-0.06	-0.22	0.10
		McDowell	-0.12	-0.50	0.25
		White Tank	-0.19	-0.44	0.07
		Molar Junction	-0.12	-0.33	0.10
		Granite Cove	**-0.44**	**-0.60**	**-0.29**
Species evenness	1	Sevilleta Black	0.03	-0.26	0.32
		Sevilleta Mixed	0.05	-0.35	0.44
		McDowell	-0.08	-0.27	0.11
		White Tank	0.11	-0.001	0.22
		Molar Junction	-0.02	-0.18	0.15
		Granite Cove	-0.08	-0.22	0.05
	2	Sevilleta Black	0.05	-0.09	0.19
		Sevilleta Mixed	0.03	-0.13	0.18
		McDowell	0.04	-0.29	0.37
		White Tank	**0.29**	**0.01**	**0.57**

		Molar Junction	**0.33**	**0.10**	**0.57**
		Granite Cove	0.19	-0.03	0.41
Species gains	1	Sevilleta Black	-0.28	-1.05	0.48
		Sevilleta Mixed	-0.02	-1.02	0.98
		McDowell	0.01	-0.51	0.53
		White Tank	0.08	-0.42	0.58
		Molar Junction	-0.04	-0.68	0.60
		Granite Cove	**-0.51**	**-0.89**	**-0.13**
	2	Sevilleta Black	0.01	-0.57	0.60
		Sevilleta Mixed	0.02	-0.44	0.48
		McDowell	0.10	-0.62	0.81
		White Tank	**-0.19**	**-0.37**	**-0.01**
		Molar Junction	0.10	-0.92	1.11
		Granite Cove	-0.26	-1.10	0.59
Species losses	1	Sevilleta Black	0.04	-0.34	0.43
		Sevilleta Mixed	0.6	-0.29	1.49
		McDowell	0.01	-0.75	0.77
		White Tank	0.05	-0.12	0.22
		Molar Junction	0.02	-0.17	0.21
		Granite Cove	0.16	-0.37	0.70
	2	Sevilleta Black	-0.02	-0.56	0.52
		Sevilleta Mixed	**-0.61**	**-1.15**	**-0.07**
		McDowell	0.08	-0.47	0.63
		White Tank	0.12	-0.21	0.45
		Molar Junction	0.07	-0.07	0.20
		Granite Cove	**0.22**	**0.01**	**0.43**
Rank change	1	Sevilleta Black	-0.04	-0.66	0.57
		Sevilleta Mixed	-0.15	-0.71	0.42
		McDowell	0.04	-0.17	0.26
		White Tank	-0.06	-0.19	0.06
		Molar Junction	0.00	-0.09	0.10
		Granite Cove	0.01	-0.11	0.12
	2	Sevilleta Black	-0.04	-0.35	0.28
		Sevilleta Mixed	0.00	-0.35	0.35
		McDowell	-0.08	-0.29	0.14
		White Tank	-0.03	-0.21	0.16
		Molar Junction	0.04	-0.07	0.09
		Granite Cove	0.07	-0.06	0.20

Table 2. Results of RII for total vegetative cover, grass cover, forb cover, annual species cover, perennial species cover, species richness, species evenness, species gains, species losses, and rank change. Results are considered significant when the upper and lower boundary of the 95% confidence interval does not overlap 0. Significant results are bolded. NA denotes where not enough data were available to calculate RII. These results are visualized in figures 2 and 3.

CHAPTER 3

CONVERGENCE AND DIVERGENCE IN COMMUNITIES RESPONDING TO GLOBAL CHANGE

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Abstract

Global change affects the structure and biodiversity of ecosystems by changing the availability of limiting resources such as water and nitrogen. Competing theories suggest that in response to a changed resource landscape, communities should either converge to a similar assemblage of species due to environmental filtering, or diverge to more different community types due to stochastic community assembly. We used a database of 220 global change treatments within 52 experiments in herbaceous plant communities at 42 sites to study the impact of drought, irrigation, nitrogen addition, phosphorus addition, and multiple nutrient addition on convergence and divergence of both the species and trait composition of plant communities. Within sites, drought, nitrogen addition, and multiple nutrient addition led to divergence of replicates. However, treatment communities compared across sites showed convergence of community assembly when subjected to drought and multiple nutrient addition. In general, we found that global change drivers create divergent responses of communities at local scales and convergent responses at global scales.

Introduction

Biodiversity is one of the most important drivers of ecosystem functions and services including ecosystem productivity (Tilman et al. 2014, Duffy et al. 2017), resistance to invasion (Kennedy et al. 2002), and carbon storage (Maestra et al. 2012). As threats to biodiversity have emerged over the past century, biodiversity research has become an important tool to improve conservation and land management to achieve ecological goals (Balvanera et al. 2014, Mace 2014). Changes to our climate and environment pose the greatest threat to plant communities by introducing novel environmental conditions, including changes to precipitation and soil nutrient availability (Clark et al. 2001, Ellis et al. 2013, Franklin et al. 2016). These anthropogenic environmental changes (known as global change drivers or GCDs) alter plant community structure and function by modifying available resources which can decrease both diversity and stability (Komatsu et al. 2019, Seabloom et al. 2021).

GCDs impact ecosystems through environmental filters, which may select for a subset of species adapted to the GCD. In combination with disturbances, GCDs may lead to rapid reordering and turnover in species composition (Avolio et al. 2014, Avolio et al. 2015, Smith et al. 2009). While most studies to date focus on mean differences in plant community richness and composition in response to GCDs, the variability of response is equally important for understanding whether GCD effects on biodiversity create more or less uniformity within an ecosystem (Fraterrigo and Rusak 2008, Fukami 2010, Murphy and Romanuk 2012). Compositional heterogeneity within an ecosystem is reflected in spatial beta diversity, the relative amount of dissimilarity in species composition across a landscape (Whittaker 1972, Legendre and Caceres 2013). In response to GCDs, plant community composition across a landscape can converge, resulting in lower beta diversity and species compositions more similar to each other, or diverge, resulting in greater beta diversity and species compositions that are less similar to each other (Houseman et al. 2008, Avolio et al. 2015, Koerner et al. 2016) (Figure 1). Competing theories suggest that environmental filtering and stochastic assembly following disturbance should create either convergence or divergence among plant communities (Keddy, 1992, Grime 2006).

Convergence could occur through environmental filter effects because only a subset of all species is adapted for the abiotic conditions of a GCD. Therefore, only species adapted for the new environment will persist through the environmental filter (Keddy 1992, Chase 2007, Houseman et al. 2011). As beta diversity is linked to variability, a change in resource availability may favor species adapted to this resource, potentially overwhelming underlying environmental variability (Tilman 1982, Harpole and Tilman 2007). For example, traits such as shorter plant height and deeper rooting depth may be more likely to persist through environmental filter effects of drought, while traits such as higher specific leaf area (SLA) and leaf dry matter content (LDMC) are favored with eutrophication of soils (Firn et al. 2019, Tatarko and Knops 2018, Barkaoui et al. 2016, Garbowski et al. 2020, Yang et al. 2018). If a GCD has a similar filtering effect on species and traits of plant communities across space, those communities will become more similar to each other, thus converging. For example, Chase (2007) found that drought induced convergence among multitrophic communities in experimental ponds by reducing species richness, thus decreasing beta diversity.

Other evidence suggests that GCDs may induce divergence among plant communities by magnifying stochastic processes of community assembly. That is, changes in resource availability can magnify processes like priority effects, historical contingency, and biological inertia and result in magnification of differences between species assemblages across space (Grime 2006, Von Holle et al. 2003). For example, continuous fertilization in a low-productivity grassland increased divergence of replicates (i.e. increased beta diversity) by magnifying priority effects (Houseman et al. 2008). When subjected to GCDs, established species are better able to utilize an influx of resources, such as additional nitrogen, or persist through resource depletion, such as drought (Evans et al. 2011, Castillioni et al. 2020, Wilfahrt et al. 2021). Therefore, GCDs can create divergence among communities, thus increasing beta diversity, by magnifying initial differences in community composition.

Trait-based studies offer an ability to test the mechanisms of convergence and divergence of communities subjected to GCDs (Pavoine et al. 2009, Sandel et al. 2010). While analyses of species composition can determine whether subsets of species are advantaged by a treatment, trait-based analyses can test whether those subsets of species are also more similar to each other functionally (Lavorel and Garnier 2002, Lavorel and Grigulis 2012). Therefore, trait-based similarity measures are likely more sensitive to environmental filtering effects than species-based similarity measures. For instance, trait-based analyses can determine whether species in communities subjected to drought have similar water use efficiency or rooting depth, whereas non-trait measures could only compare the similarity of species identity. Discrepancies between species-based and trait-based convergence or divergence have been found in studies of community succession through time. In semi-natural grasslands, beta diversity of trait composition tends to converge over time while beta diversity of species composition remains consistent even as alpha diversity changes through succession (Fukami 2005, Helson et al. 2012). Conversely, restorations of resource-rich grasslands resulted in convergence of species composition, though trait composition neither converged not diverged over time (Catano et al. 2021). Indeed, analyses based on species composition alone can lead to an incomplete view of how GCDs alter the variability of community assembly. Moreover, species-based methods are incapable of comparing the similarity of communities across sites that are responding to the same GCD simply because distant sites may have few or no species in common (Clarke et al. 2006). Trait-based analyses, however, can compare responses of communities to GCDs across sites as traits create a common currency for measuring diversity in plant communities. For example, Bjorkman et al. (2018) used community-weighted trait means to track changes in tundra plant communities as a long-term response to warming and Diaz et al. (2007) used traits to determine the types of plants promoted by grazing across sites globally.

In this study, we used a global database of 220 global change treatments within 52 experiments in herbaceous plant communities at 42 sites to study the impact of GCDs on convergence and divergence of both the species and trait composition of plant communities. We tested the impacts of GCDs on the variability of community composition within experiments and between sites. We asked the following questions: (1) *Do global change drivers create local convergence or divergence within plant communities?* (2) *Are responses of species composition analogous to responses of trait assembly within communities?* and (3) *Do GCDs cause the same directional shifts in traits among communities?*

Methods

Species composition data

We used datasets of global change experiments in herbaceous terrestrial ecosystems from the CoRRE database (corredata.weebly.com). This database includes species identity and relative abundance values for control and treatment plots in plant communities subjected to global change treatments. We used only experiments that manipulated at least one of the core resources assessed in this study: drought, irrigation, nitrogen addition, phosphorus addition, or addition of multiple nutrients (typically N and P together). We used only experiments with at least four years of treatment for drought and at least five years of treatment for all other manipulations since global change treatments can typically take multiple years before impacting plant communities (Komatsu et al. 2019, Seabloom et al. 2021). We used measurements from the final year of treatment for each experiment to maximize our ability to detect treatment effects. Given the importance of replication when studying convergence and divergence across replicates, we only used experiments with at least five replicates of each control and treatment plot. This left 220 treatments within 52 experiments at 42 sites around the world across all treatment groups: 14 drought treatments, 18 irrigation treatments, 72 N addition treatments, 9 P addition treatments, and 107 multiple nutrient addition treatments.

Trait data

We derived trait data using a combination of plant trait databases including TRY (Kattge et al. 2011) and the Fine-Root Ecology Database (FRED) (Iversen et al. 2021), in addition to categorical trait data collected for the CoRRE database. These data were then gap-filled using Bayesian hierarchical probabilistic matrix factorization (Schrodt et al. 2015). Traits were z-score transformed across all species in the database to create comparable scales for analyses. For this study, we used a subset of five continuous traits with correlation values less than 0.35, because high correlation of traits can lead to certain species overinfluencing an analysis (Ohlert and Kimmel et al. *in revision*). The traits used were plant vegetative height, leaf dry matter content (LDMC), specific leaf area (SLA), rooting depth, and stem specific density. Together, these five traits represent a range of plant functions including both above- and belowground processes as well as the leaf economic spectrum (Reich 2014, Diaz et al. 2016, Kong et al. 2019).

Distances between communities

Species composition

For each experiment, we separately created non-metric multidimensional scaling (NMDS) ordinations to quantify dissimilarity of community composition in response to global change treatments based in the Bray-Curtis dissimilarity metric. Each replicate was plotted in two-dimensional NMDS space and we calculated the distance of replicates to the centroid of treatment group replicates using the betadisper function from the 'vegan' package in R (v2.5-7; Oskanen et al. 2013). With this method, replicates with more similar species composition receive shorter distances between centroids. We repeated this process for each treatment within each experiment, including for control plots.

Trait composition

To quantify the distances in trait space between replicates within experiments, we used the 'hypervolume' package (v3.0.2; Blonder 2018) in R to create five-dimensional Gaussian hypervolumes of each replicate weighted by the relative abundance of species within the replicate. Hypervolumes were calculated using the Silverman rule of thumb estimator with a 0.95 quantile of type probability with bandwidth calculated out to three standard deviations. The five traits used were plant vegetative height, LDMC, SLA, rooting depth, and stem specific density. Next, we used the kernel.similarity function in the ‘bat’ package (v2.6.0; Mammola and Cardoso 2020) to measure the Euclidean distance between the centroids of replicates for each pair of plots within the same treatment type (including controls) for each experiment.

We quantified distances in trait space across sites using the relative abundance of species for each treatment at each site. First, we first used the ‘hypervolume’ package (v3.0.2; Blonder 2018) in R to create five-dimensional Gaussian hypervolumes of the communities for each treatment within each experiment weighted by the relative abundance of species within the treatment (Blonder 2018). Hypervolumes were calculated using the Silverman rule of thumb estimator with a 0.95 quantile of type probability with bandwidth calculated out to three standard deviations. The five traits used were plant vegetative height, LDMC, SLA, rooting depth, and stem specific density. Next, we used the kernel.similarity function in the ‘bat’ package (v2.6.0; Mammola and Cardoso 2020) in R to measure the Euclidean distance between the centroids of the hypervolumes for pairs of experiments with similar treatments (e.g. N addition experiments at different sites). This generated a measure of the distance between pairs of sites for each treatment type (including controls).

Statistical analyses

For intra-experiment analyses of both NMDS-based species composition and hypervolume-based trait composition, we used the distances between pairs of replicates to calculate log response ratios (LRR) for each experiment: ln $(\frac{treatment\ distance}{control\ distance})$. For each treatment type, we calculated 95% confidence intervals of the mean of the log response ratios using the qt function in the R ‘stats’ package (R core team 2021). We considered significance as when confidence intervals of LRRs did not overlap with zero. LRRs above zero indicate community divergence (i.e. treatments less similar than controls) and LRRs below zero equals convergence (i.e. treatments more similar than controls).

To test the correlation of species composition LRRs to trait composition LRRs, we created linear models with the form: trait composition LRR ~ species composition LRR. Models were created separately for each of the five treatment categories and each experiment contributed a single species composition LRR value and trait composition LRR value.

To compare the similarity of communities between sites in trait space, we used linear models with the form: distance in trait space ~ treatment to compare the pairwise distances between communities subjected to global change treatments to the pairwise distances of control communities in corresponding experiments.

We used R Statistical Software (v4.1.2; R Core Team 2021) for all analyses. The ‘tidyverse’ (v1.3.1; Wickham et al. 2019) and ‘plyr’ (v1.8.6; Wickham et al. 2011) R packages were used for data manipulation and data visualization.

Results

Do global change drivers create local convergence or divergence within plant communities?

Species composition diverged within experiments in response to three of the five global change treatments: drought (mean = 0.18, 95% conf int. min = 0.06, 95% conf int. max = 0.30), N addition (mean = 0.08, 95% conf int. min = 0.001, 95% conf int. max = 0.16), and multiple nutrient addition (mean = 0.24, 95% conf int. min = 0.16, 95% conf int. max = 0.32). In all three cases, 95% confidence intervals of the log response ratios were above zero (Table 1, Figure 2a). Log response ratios of irrigation (mean = 0.09, 95% conf int. min = -0.07, 95% conf int. max = 0.25) and phosphorus addition (mean = 0.06, 95% conf int. min = -0.06, 95% conf int. max = 0.18) treatments did not differ from zero across all experiments.

We observed fewer patterns of divergence in response to treatments with the trait-based analysis. Though multiple nutrient addition resulted in trait divergence (mean = 0.32, 95% conf int. min = 0.22, 95% conf int. max = 0.42), all other GCDs had no consistent effect across experiments (drought mean = 0.12, 95% conf int. min = -0.09, 95% conf int. max = 0.33; irrigation mean = 0.08, 95% conf int. min = -0.21, 95% conf int. max = 0.37; N addition mean = -0.02, 95% conf int. min = -0.11, 95% conf int. max = 0.07; P addition mean = -0.04, 95% conf int. min = -0.44, 95% conf int. max = 0.36) (Table 2, Figure 2b).

Are responses of species composition analogous to responses of trait assembly within communities?

Correlation between trait and species composition responses were significant for irrigation ($P < 0.001$, $r^2 = 0.56$) and multiple nutrient addition ($p < 0.001$, $r^2 = 0.19$), but marginally significant for P addition ($p = 0.07$, $r^2 = 0.30$) and drought ($p = 0.07$, $r^2 = 0.18$), and not significant for N addition ($p = 0.59$, $r^2 = -0.01$) (Table 3).

Do GCDs cause the same directional shifts in traits among communities?

Contrary to responses within experiments, both drought and multiple nutrient addition converged across experiments (drought $p=0.024$, multiple nutrients $p < 0.001$, Table 4). Neither irrigation nor phosphorus treatments altered the distances between communities in trait-space (irrigation $p = 0.23$, phosphorus $p = 0.65$, Table 4).

Discussion

Three of the five GCDs, drought, N addition, and multiple nutrient addition, exhibited divergence within experiments, evidence of environmental stochasticity effects. In contrast, two of the five GCDs, drought and multiple nutrient addition, exhibited convergence among experiments, evidence of environmental filtering. Importantly, effects on species composition were stronger than on trait composition within experiments, and correlations between species and trait composition responses were weaker than expected. The discrepancy between trait and species responses highlights the importance of assessing trait composition when studying community assembly as trait composition reflects environmental filtering effects at higher resolution. We suggest that the mechanisms driving convergence and divergence of communities changes across spatial scales, with environmental stochasticity a more important factor at local scales and environmental filtering more important at regional and global scales.

Species composition within experiments subjected to GCDs

When limiting resources, such as nitrogen or phosphorus, are made abundant, small differences between communities can be magnified (Fukami 2015). Greater levels of added N can lead to greater divergence among communities (Houseman et al. 2008) and addition of both N and P magnifies divergence among communities beyond N addition alone (Koerner et al. 2016). Adding N can magnify the competitiveness of dominant species, regardless of species identity (Inouye and Tilman 1988), and adding multiple nutrients in combination with N can further reduce niche dimensionality (Harpole and Tilman 2007, Carroll et al. 2021, Wilcots et al. 2021). By magnifying differences in initial composition, historical contingency and priority effects are more closely tied to species identity than species traits (Fukami et al. 2005, Fukami 2015), thus magnifying stochastic processes of community assembly. Indeed, we found that adding nitrogen magnified the differences between communities locally, and adding multiple limiting nutrients enhanced this effect.

Divergence at the local scale in response to drought treatment, however, is not a product of resource addition, but of resource subtraction. Whereas resource addition creates divergence by spurring growth and magnifying differences between communities, drought disturbance eliminates members of the community, thus making space and resources available for colonizers (Davis and Pelsor 2001, Bartha et al. 2003, Chesson et al. 2004). Though colonizers likely have similar traits following the competition-colonization tradeoff (Grime 1977, Pierce et al. 2017), colonizer identity is primarily a neutral process based on stochasticity (Hurtt and Pacala 1995, Hubbell 2001). Therefore, as drought increases the role of colonization in community composition, assemblages of species will be increasingly different despite colonizers sharing similar colonization-favorable traits. Indeed, we found a strong effect of drought on the divergence of species composition, but not trait composition at local scales. Overall, divergence appeared to be stimulated by deviation from ambient conditions, regardless of whether the treatment added or subtracted resources. Irrigation did not produce effects opposite of drought, but rather, irrigation effects were directionally similar to the effects of drought treatment.

Potential mechanisms separating species composition response and trait composition response

Both trait-based and trait-neutral mechanisms operate simultaneously on diversity, resulting in community assembly that is a combination of both mechanisms (Suding et al. 2005). In our study, responses of trait composition were only somewhat correlated with species composition responses as few treatments conveyed a close relationship between the two. This difference is particularly surprising given that both the trait composition and species composition measures were weighted by species' relative abundance. Trait composition is a better reflection of environmental filtering than species composition since processes that are more neutral in terms of species identity, such as colonization and priority effects, are often more deterministic with trait identity (Catford et al. 2020, Fargione et al. 2003). Still, discrepancies between trait responses and species responses emphasize that within experiments, increased beta diversity of species composition often occur with reduced beta diversity of trait compositions.

Discrepancies between trait responses and species responses can occur when numerous species in the local species pool share similar traits. For example, a drought experiment from the Great Plains grassland at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA exhibited divergence of species composition (LRR = 0.26), meaning that the plots subjected to drought treatment had less similar assemblages of species, while trait composition converged (LRR = -0.51). The species that persisted through the drought treatment were mostly small forbs sharing similar traits, such as small height and shallow rooting depth. In cases similar to the experiment at SNWR, focus on only the responses of species composition would overestimate the positive effects of a GCD on beta diversity. Similarly, studying only trait diversity would fail to account for other facets of diversity important to communities, such as phylogenetic diversity (Cadotte et al. 2009, Cavender-Bares et al. 2009). Thus, understanding when species composition responses and trait composition responses contrast will help to more accurately characterize GCD effects on ecological communities.

Spatial scale determines convergence/divergence dynamics

Convergence in response to GCDs at the global scale contrasts with the divergent responses at local scales. Indeed, the treatments that induced the greatest divergence at local scales incurred convergence at global scales. Further, drought and multiple nutrient addition which provoked change at local scales also provoked change at global scales.

The similarity of responses to drought and multiple nutrient treatments across spatial scales implies that these treatments created the greatest disturbance of those communities overall. Despite detecting divergent responses of communities at local scales with nitrogen addition, nitrogen effects were not great enough to induce detectable change across experiments.

The often-interacting nature of global change effects on the alpha diversity of plant communities (Zavaleta et al. 2003, Koerner and Collins 2014, Franklin et al. 2015, Harpole et al. 2016, Reich et al. 2020) likely also applies to global change effects on beta diversity, that is, simultaneous pressures may interact synergistically to create change in communities greater than additive effects. Indeed, our study found that multiple nutrient addition treatments had the largest effect sizes on community similarity both within experiments and across sites. Similar responses to drought and multiple nutrient addition suggest that both resource subtraction and resource addition produce similar change. A study of GCD effects on alpha diversity with the same dataset of experiments found that responses to treatments were common but largely independent of the identity of the GCD (Avolio et al. 2021).

Together, local divergence and global convergence suggests different mechanisms affecting community assembly at different scales. Divergent responses in both species and trait composition at local scales reflect environmental stochasticity, while convergent responses at global scales reflect environmental filtering. Priority effects and historical contingency are primarily local processes (Fukami 2015) since both are tied to the potential for colonization within the local species pool and other inherently local stochastic effects. Convergent responses of GCDs at global scales is evidence for large-scale environmental filtering effects. Though previous studies suggest that GCDs favor certain adaptive traits regionally and globally (Bjorkman et al. 2018, Yang et al. 2020), we show here that GCDs also increase the similarity of communities around the world by selective pressure for the same suites of traits everywhere. As trait convergence takes place in response to GCDs, biodiversity loss is extended beyond species extinctions to decrease variety in the types of species that persist.

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Figures

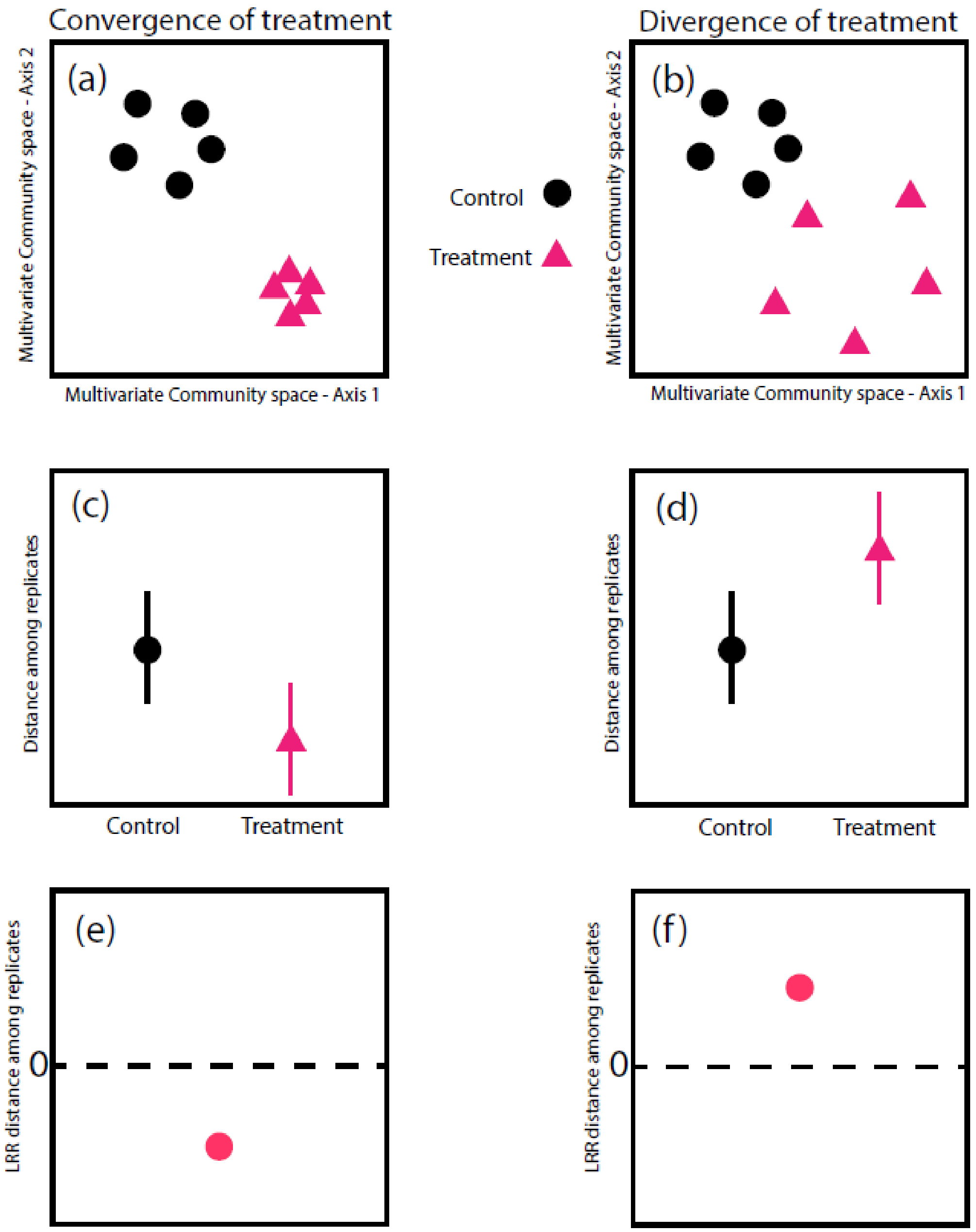

Figure 1. Conceptual figure showing a) convergence and b) divergence among replicates in multivariate community space. Panels c and d show the range of distances among replicates from panels a and b, respectively. Panels e and f show panels c and d represented as log response ratios, where values below 0 denote convergence in treatment replicates and values above 0 denote divergence in treatment replicates.

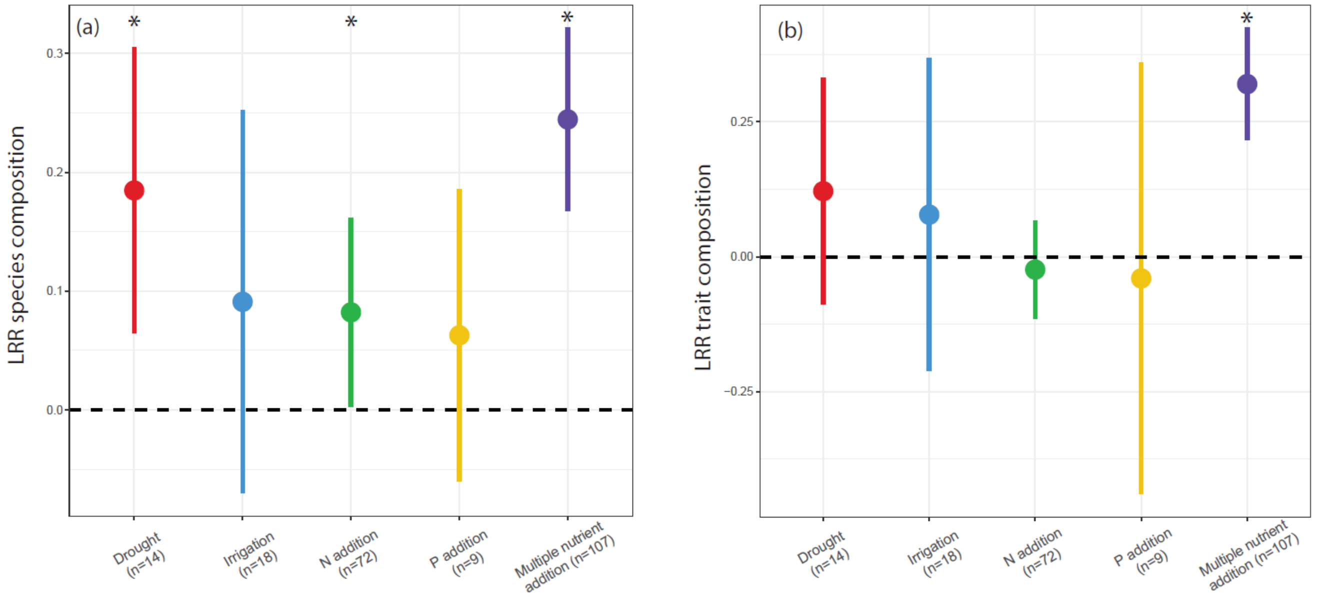

Figure 2. Log response ratios of within-experiment responses to five global change treatments for a) species composition and b) trait composition. The mean response value for each treatment is shown as a single point and error bars are 95% confidence intervals. Asterisks denote treatments for which 95% confidence intervals do not cross 0. Values above 0 signify divergence of treatment relative to control, while values below 0 signify convergence. Means and confidence interval values can be found in Tables 1 and 2.

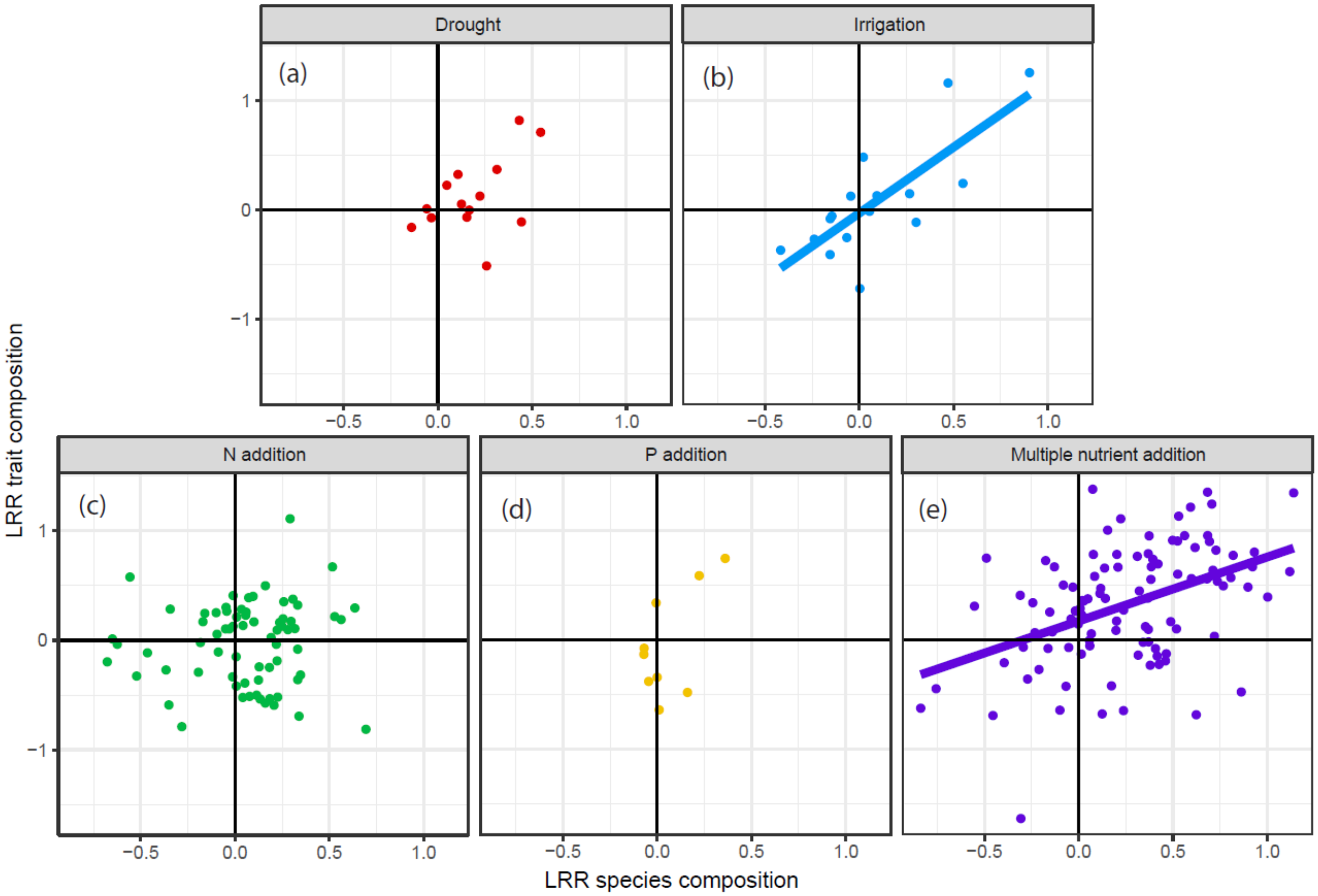

Figure 3. Relationships between log response ratios of species composition and log response ratios of trait composition for each of five global change treatments. Lines show significant regressions. See Table 3 for regression details.

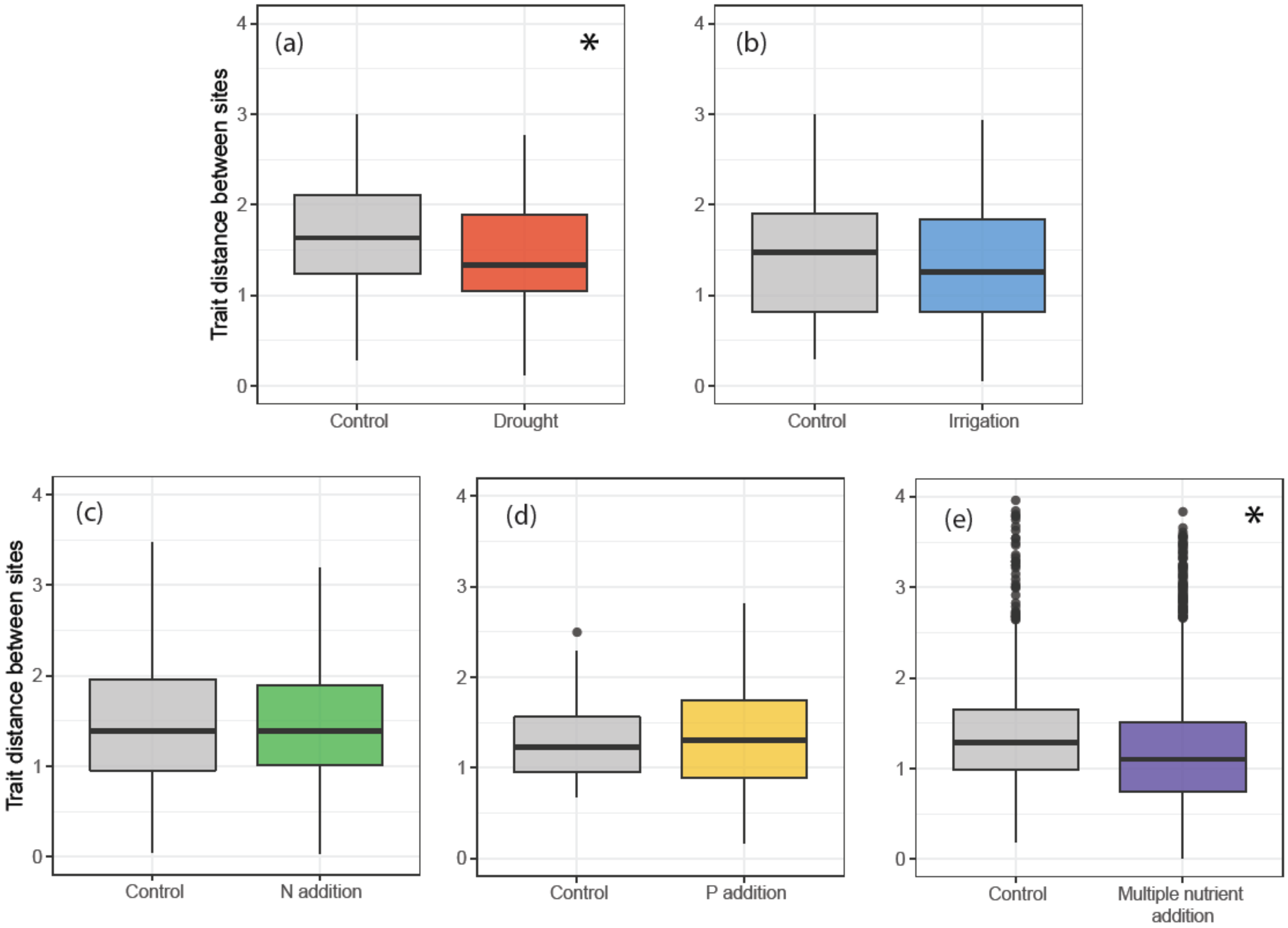

Figure 4. Comparison of the distance between pairs of experiments in control vs. treated communities. Bold black lines display the median value, the bottom and top of the box display the first and third quartiles of the data, and the whiskers extend 1.5 time the interquartile range. Data lying outside 1.5 times the interquartile range are plotted individually. Asterisks denote significant differences between control and treatment groups based on models described in the methods, the results of which are shown in Table 4.

Tables

Treatment	Mean LRR (species composition	95% conf int min	95% conf int max
Drought	**0.18**	**0.06**	**0.3**
Irrigation	0.09	-0.07	0.25
N	**0.08**	**0.001**	**0.16**
P	0.06	-0.06	0.18
Multiple nutrient	**0.24**	**0.16**	**0.32**

Table 1. Summary of 95% confidence intervals for log response ratios of species composition responses to five GCDs. These results are visualized in Figure 2a.

Treatment (traits)	Mean LRR	95% conf int min	95% conf int max
Drought	0.12	-0.09	0.33
Irrigation	0.08	-0.21	0.37
N	-0.02	-0.11	0.07
P	-0.04	-0.44	0.36
Multiple nutrient	0.32	0.22	0.42

Table 2. Summary of 95% confidence intervals for log response ratios of trait composition responses to five global change treatments. These results are visualized in Figure 2b.

Treatment	Slope	p-value	r-squared
Drought	0.86	0.07	0.18
Irrigation	**1.20**	**<0.001**	**0.56**
N	0.08	0.59	-0.01
P	2.03	0.07	0.30
Multiple nutrient	**0.59**	**<0.001**	**0.19**

Table 3. Regression results of models comparing log response ratios of species composition and log response ratios of trait composition for five global change treatments. These results are visualized in Figure 3.

Treatment	Control estimate	Treatment estimate	p-value
Drought	**1.67**	**1.18**	**0.035**
Irrigation	1.44	1.34	0.27
N	1.49	1.45	0.17
P	1.31	1.39	0.65
Multiple nutrient	**1.44**	**1.43**	**<0.001**

Table 4. Summary of models comparing the trait space distances among sites between control plots and plots treated with one of five global change treatments. These results are visualized in Figure 4.

CONCLUSION

Assembly of plant communities changes through time, across spatial scales, and is often shaped or disrupted by abiotic disturbances. In this dissertation, I used long-term experimental data to compare the influence of dominant species on community assembly in semiarid grasslands. Additionally, I established a cross-site drought experiment in the hot deserts of the U.S. to investigate the impact of drought on community structure in desert ecosystems. Finally, to assess determinism of community assembly on a global scale, I used modern, trait-based methods to compare the spatial variability of communities subjected to global change treatments.

In the first chapter, I discovered suppression of subordinate species by dominant grasses and noted that subordinate species provided only partial compensation for the loss of the dominant species. Forb, shrub, and grass functional groups each had phases in which they provided partial compensation for dominant species. I found that species richness-NPP relationships were contingent upon the presence of dominant species and their removal resulted in increasingly negative species richness-NPP relationships. The dominant species of these grasslands performed unique roles in productivity that no other species were able to fill even after 23 years. Overall, dominant species can inhibit the diversity of communities while being critical to productivity.

In the second chapter, I assessed the impact of drought on multiple dimensions of plant communities in the hot deserts of the U.S. southwest. Drought sensitivity of vegetative cover was linked to response of the grass functional group, while forb responses were rarer than expected. Changes to the evenness of species' abundances played an important role in the impacts of drought on desert ecosystem processes through heightened sensitivity of dominant species to abiotic change. Further understanding of the trajectory of change that drought imposes on plant communities will prepare human and ecological systems for extreme climate events.

In the third chapter, I found that global change drivers (GCDs) created divergence of community assembly at local scales and convergence of community assembly at regional and global scales. Therefore, I suggest that the relative effects of environmental stochasticity and environmental filtering on convergence and divergence of communities changes across spatial scales. Divergence of communities at local scales is an important process for maintaining diverse species pools amidst disturbances, while convergent responses of GCDs at global scales are consistent with large-scale environmental filtering effects. I show here that GCDs increase the similarity of communities around the world by selective pressure for the same suites of traits everywhere. As trait convergence takes place in response to GCDs, the consequences of biodiversity loss are extended beyond species extinctions by diminishing the range of species that persist through global change.

As plant communities endure shifting environmental conditions, responses to disturbances can determine the resistance, resilience, and stability of whole ecosystems. Terrestrial plant communities are vulnerable to environmental change brought about by anthropogenic influences of our modern world. Studying how communities respond to abiotic disturbance is of increasing importance as we seek to conserve modern ecosystems and predict the consequences of anthropogenic global change.