The Interactive Effects of Precipitation and Disturbance on the Functioning of Dryland Ecosystems as Modulated by Mean Annual Precipitation

by

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ABSTRACT

Terrestrial ecosystems are critical to human welfare and regulating Earth's life support systems but many gaps in our knowledge remain regarding how terrestrial plant communities respond to changes in climate or human actions. I used field experiments distributed across three dryland ecosystems in North America to evaluate the consequences of changing precipitation and physical disturbance on plant community structure and function. Evidence from experiments and observational work exploring both plant community composition and ecological processes suggest that physical disturbance and precipitation reductions can reduce the diversity and function of these dryland ecosystems. Specifically, I found that aboveground net primary productivity could be reduced in an interactive manner when precipitation reductions and physical disturbance co-occur, and that within sites, this reduction in productivity was greater when growing-season precipitation was low. Further, I found that these dryland plant communities, commonly dominated by highly drought-resistant shrubs and perennial grasses, were not capable of compensating for the absence of these dominant shrubs and perennial grasses when they were removed by disturbance, and that precipitation reductions (as predicted to occur from anthropogenic climate change) exacerbate these gaps. Collectively, the results of the field experiment suggest that current management paradigms of maintaining cover and structure of native perennial plants in dryland systems are well founded and may be especially important as climate variability increases over time. Evaluating how these best management practices take place in the real world is an important extension of fundamental ecological research. To address the research-management gap in the context of dryland ecosystems in the western US, I used a set of environmental management plans and remotely sensed data to investigate how ecosystem services in drylands are accounted for, both as a supply from the land base and as a demand from stakeholders. Focusing on a less-investigated land base in the United States–areas owned and managed by the Department of Defense–I explored how ecosystem services are produced by this unique land management arrangement even if they are not explicitly managed for under current management schemes. My findings support a growing body of evidence that Department of Defense lands represent a valuable conservation opportunity, both for biodiversity and ecosystem services, if management regimes fully integrate the ecosystem services concept.

DEDICATION

To those who have struggled.

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CHAPTER 1

INTRODUCTION

Chapter 1: Theoretical background

The study of how interacting global change drivers affect ecosystem processes is a well-established field but has its roots in classic studies of single drivers. Examples include assessments of precipitation effects on aboveground net primary productivity (Noy-Meir 1973) and disturbance effects on community composition (Sousa 1979). Despite this rich history in ecological research, there is uncertainty of the specific nature of the relationships between single global change drivers and key ecosystem response variables. For example, in plant communities, the precipitation–productivity relationship continues to see refinement and additional research (Knapp et al. 2017, Carroll et al. 2021), as does the precipitation–diversity relationship (Willig et al. 2003, Adler et al. 2011, Donoghue and Edwards 2014). The disturbance–productivity and disturbance–diversity relationships have seemingly countless research articles published about them over the past decades (Huston 1979, White 1979, Sousa 1984, Collins 1987, Pickett et al. 1989), and these relationships continue to be written about in more recent decades (Mackey and Currie 2000, 2001, Peters et al. 2011, Fox 2013, Jentsch and White 2019). This effort from the ecological research community reflects the importance of understanding of disturbance effects on ecosystem and biodiversity outcomes: global change forces are in motion across the surface of the planet and are an increasing concern for humanity (Vitousek et al. 1997b, Kareiva et al. 2007).

Observing how natural systems undergo and respond to disturbances has always been a major part of our use of natural resources and was one of the oldest foci of research in the field of ecology. Disturbances can be powerful: they can destroy resources and habitats and alter the abundance and diversity of species, as well as influence nutrient cycling and energy flow, biomass accumulation, primary production, hydrological regimes and other key ecosystem processes (Sousa, 1984, White and Jentsch 2001). Though often perceived as destructive by humans, disturbances also may increase biodiversity by creating new habitats and making new resources available (Connell, 1978). Human actions are a large and common source of disturbances in natural systems worldwide and understanding how ecosystems are affected by disturbances remains an important research front.

In dryland ecosystems, the effects of disturbance can persist for years or decades (Belnap and Warren 2002, Rottler et al. 2017), and the specific mechanisms of disturbance affects systems at scales ranging from individuals to ecosystems (Jentsch and White 2019). Disturbance negatively affects individual organisms by damaging the structure and removing biomass (Pickett et al. 1989). For plants, this reduction in photosynthetic area causes lower productivity (White 1979). Changes in plant architecture, phenology, and resource efficiency can reduce individual plant productivity after a disturbance (Whitford and Duval 2019, Blumenthal et al. 2020). On the patch scale, disturbances may eliminate key species and their contribution to primary production (Coffin and Lauenroth 1989) lowering total productivity from the entire plant community (Koerner and Collins 2014). Increased abiotic stress from disturbance can cause species turnover, with negative effects on productivity (Smith et al. 2009). The presence or absence of shrubs can change the microsite conditions for subordinate plants, creating more stressful conditions and decreasing productivity (Gómez-Aparicio et al.

2004). Further, damage to canopy architecture of the dominant shrubs may greatly reduce stemflow, subsequently reducing plant available water and productivity (Whitford and Duval 2020).

In addition to physical disturbances in drylands, large changes in available water due to climate change can be considered a disturbance in its own right: the water balance of dryland systems is an incredibly powerful driver of ecosystem processes. Indeed, the relationship between precipitation and ecosystem productivity has received special attention in drylands since the foundations of dryland ecosystem science (Noy-Meir 1973). Early work established that water availability is the primary limiting factor of productivity in drylands (Lauenroth 1979, Sala et al. 1988). These systems have dynamic water use efficiency across space and time (Noy-Meir 1973, Huxman et al. 2004, Hsu et al. 2012, Maurer et al. 2020), and refining the precipitation–productivity relationship continues to be an active research front (Knapp et al. 2017, Carroll et al. 2021, Felton et al. 2021). As with disturbance, the mechanisms by which precipitation controls productivity scale from the individual to the ecosystem. Across growth forms over short time scales, water deficits cause plants to close stomata, inhibit growth, and reduce carbon assimilation and longer-term drought can cause plants to reduce shoot growth, increase root:shoot ratio, and decrease transpiration area (Chaves et al. 2003). These physiological reactions to water limitation can ultimately lead to insufficient carbon assimilation and/or loss of hydraulic conductivity and mortality (Chaves et al. 2003). Within communities, species turnover can amplify of precipitation effects on composition (Smith et al. 2009). Species richness covaries positively with soil water availability in dryland plant communities (Jordan et al. 2020), suggesting that decreased water availability can lead to decreased richness. In contrast to richness, evenness in dryland plant communities can show opposite or unrelated patterns to soil moisture, suggesting that species evenness of plant communities may have different drivers (Dorji et al. 2014, Jordan et al. 2020, Ma et al. 2020).

The mechanisms by which precipitation amount modulates the effects of disturbance across dryland ecosystems operate at multiple scales, from the ecosystem to the individual. Understanding how interactions between these drivers occur will help develop more specific theoretical frameworks of global change in drylands. The magnitude of the productivity response to disturbance can be modulated by synergistic or antagonistic interactions between disturbance and precipitation amount (Folt et al. 1999, Brook et al. 2008, Côté et al. 2016). This interaction is mechanistically controlled as a function of total energy flux and trait diversity within a system: a higher diversity of traits can reduce the impacts of potentially interacting drivers through asynchrony, functional redundancy, and the ability to recover (Jentsch and White 2019). Disturbances alter the fluxes and pools of both water and critical limiting nutrients, and these changes may result in positive synergisms that modulate the precipitation–productivity relationship within a site (Turner 2010, Buma 2015). Changes to ecosystem structure from a disturbance that alters rainfall infiltration (canopy roughness, litter abundance, soil porosity, etc.) may affect soil water dynamics, directly affecting the slope of the precipitation–productivity relationship as well as community composition (Smith et al. 2009, Whitford and Duval 2020).

Physical disturbances and changes in precipitation are two common and impactful drivers of dryland ecosystems worldwide, and where they are occurring simultaneously, their total effect on ecosystem structure and function may be amplified. Studies suggest that the effects of multiple global change drivers that occur concurrently might not be predictable from research of single global change drivers. Specifically, the effects of these drivers when occurring in concert could be synergistic or antagonistic and not simply additive (Buma, 2015). Studying one driver at a time may not accomplish our needs of understanding how and where global change is occurring. Society demands ecosystem services, and land managers must reconcile shifting climate patterns with standing policy decisions to maintain the supply of ecosystem services. Thus, ecologists have an ongoing research objective to understand how key ecosystem processes will be affected by interacting and overlapping global change drivers and synthesize our understanding at scales and with language that is useful for environmental stewardship.

Much of our understanding of global change is theory-driven, and robust theory helps ecology advance as a scientific discipline. Indeed, the search for generality in ecological theory continues to be a central focus of ecological research across fields (White and Jentsch 2001, Foster et al. 2016, Jentsch and White 2019). Opportunities for discovery lie in the co-occurrence of drivers that influence key ecosystem processes. By examining co-occurring global change drivers, researchers can both study the potential for interactions as well as the effects of single phenomena and explore mechanisms. Climate change, anthropogenic disturbances, natural disasters, nutrient pollution, species invasions, and land use change have each been shown to influence key ecosystem processes across continents (Vitousek et al. 1996, 1997a, Kareiva et al. 2007, Gaiser et al. 2020, Berdugo et al. 2020, Knapp et al. 2020). When these drivers inevitably overlap in space and time, the potential magnitude and direction of their interaction is determined by the specific mechanisms through which the individual drivers influence ecosystem processes. Where possible, disaggregating global change drivers into their individual constituent effects and legacies could facilitate analysis of their mechanistic control over and impact on productivity, composition, and/or the resilience of the system (Peters et al. 2011).

Clearly, there are simultaneous and widespread alterations of key ecosystem processes from multiple global change drivers. Understanding how land management decisions incorporate dynamic responses to global change could greatly improve landscape-level sustainability of the supply of ecosystem services. By also addressing the demands for ecosystem services at large scales, managers can improve decisions about what to do with land to meet these demands and adapt to the changes already occurring across the planet. Therefore, a useful approach to improving environmental stewardship is understanding both the dynamics of ecosystem services at the landscape scale, and how policy decisions incorporate key scientific concepts that explain how the environment supports human populations and biodiversity (Cortinovis and Geneletti 2018).

By using a supply and demand framework, researchers can better identify how ecosystem services are provided from dryland systems as well evaluate how equitably services are able to be provided to stakeholder groups (Cavender-Bares et al. 2015, Yahdjian et al. 2015). Ecological research has identified the need to safeguard ecosystem services for future use (Isbell et al. 2011, Tilman et al. 2014), but restoration or conservation targets often fall short of stated objectives (Perrings et al. 2011). Evaluating ecosystem services with a supply and demand perspective allows clear analysis of where supply exceeds demand and can be used to determine where management changes are necessary to bring demand back to meet available supply (Yahdjian et al. 2015).

Thesis objectives

The overall objective of my thesis is to assess the effects of physical disturbance, precipitation, and their interactions on dryland ecosystem plant community composition, diversity, and productivity. I have three specific objectives:

Specific objective 1: assess the effects and interactions of precipitation and physical disturbance on plant community composition, diversity, and productivity.

Specific objective 2: assess how the effects and interactions of precipitation and physical disturbance vary along a gradient of aridity.

Specific objective 3: assess the effect of management decisions on the supply of ecosystem services from military lands.

Approach

In order to assess the effects of interannual precipitation variation on ecosystem functioning, I combine the use of experimentation and analyses of existing remotely sensed data and policy documents. The experimental part consisted of a well replicated rainfall manipulation + disturbance experiment located in three locations: the Nevada National Security Site in southern Nevada, USA, the Orchard Combat Training Center in central Idaho, USA, and the Jornada Basin Long-Term Ecological Research site (LTER) in southern New Mexico, USA. This experiment allowed me to investigate ecosystem responses and to test for causality, as well as assessing the mechanisms explaining observed responses. The analysis of remotely sensed data and policy documents consisted of the collection and analysis of 40 policy documents concerning environmental management, and remotely sensed data from two unique satellite platforms (Moderate Resolution Imaging Spectroradiometer (MODIS), and Landsat Thematic Mapper). This approach explored the supply and demand outcomes of policy decisions and compared a unique public land type, the US military's land estate, with other publicly held lands across the western US. These approaches complement each other. While field experimentation provides controlled conditions that allow testing for mechanisms behind ecosystem responses, they can fail to capture pertinent dimensions and interactive controls from environmental management. Remote sensing and policy analysis can provide understanding of our land use decisions but have limited capacity to infer causality at the ecosystem scale. Using these complementary approaches, this thesis explores the causes, consequences, and implications of how we manage water-limited landscapes.

Thesis structure

This dissertation is organized into three chapters addressing my objectives followed by a general conclusion chapter.

Chapter 2 explores the landscape-scale implications of management for ecosystem services on military-managed land in the western United States (US). I collected over 40 environmental management documents from military installations across the drylands of the western US and analyzed their text to determine the degree to which they embodied the ecosystem services concept, and I used remotely sensed data to determine the supply of ecosystem services from military-managed lands. Three questions guided this work (1) What ecosystem services do dryland DoD-managed lands supply?, (2) What are the demands for ecosystem services of these DoD-managed lands from different stakeholders?, and (3) How do DoD management plans adopt ecosystem services principles and consider supply and demand of ecosystem services?

Chapter 3 tests hypotheses related to the disturbance and precipitation effects on aboveground net primary productivity and its consequences for ecosystem functioning. I measured plant productivity one year prior and for three years following an experimental disturbance treatment and rainfall manipulations. I explore how these drivers interact to affect aboveground net primary productivity for each ecosystem and for specific plant functional types.

Chapter 4 tests hypotheses related to key plant community responses to the interactive effects of disturbance and precipitation amount across three dryland ecosystems. I recorded plant species composition and abundance across four growing seasons in these three ecosystems and analyzed the effect of disturbance and precipitation amount on plant communities. I address how total richness and evenness are affected by these drivers individually and in combination, and explore changes in composition, dominance, and functional type abundance from experimental treatments.

Chapter 5 integrates findings from all chapters resulting in general discussion and conclusions of my dissertation.

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CHAPTER 2

ECOSYSTEM SERVICE INDICATORS ON MILITARY-MANAGED DRYLANDS IN THE WESTERN UNITED STATES

Abstract

Lands devoted to military use are globally important for the production of ecosystem services and for the conservation of biodiversity. The United States has one of the largest military land estates in the world, and most of these areas occur in water-limited landscapes. Despite many of these areas receiving intense or sustained disturbance from military training activities, the structure and function of ecosystems contained within their boundaries continue to provide critical benefits to stakeholders across spatial scales. Unique to other public lands, the land owned and managed by the Department of Defense is subject to regulation from local, state, and federal governing bodies, constraining and shaping both how land management is conducted and how ecosystem services are prioritized. Here, I explored the supply of ecosystem services from military lands in dryland areas of the United States using key indicators of ecosystem services: biodiversity estimates derived from range maps, ecosystem productivity estimates from satellite observations, and spatially explicit, hierarchical ecosystem classifications. Additionally, I utilized content analysis of the environmental management plans of these areas to describe the unique set of demands and regulatory constraints on these areas. I found that the US military land estate in drylands contains many types of ecosystems and provides a large and diverse supply of ecosystem services, comparable to the sum of services from public lands in these areas. Additionally, the degree to which the ecosystem services concept is captured in environmental

management plans is strongly shaped by the language of the governing legislation that mandated the use of environmental management plans in these areas, although these plans do not address land management using the concept of ecosystem services. Collectively, my findings suggest that military use and management of land represents an important source of ecosystem services, that military land use can be considered a cultural ecosystem service unto itself, and that top-down regulation can affect how these services are identified and valued.

Introduction

Military training areas occupy at least 1% of the Earth's surface, and may occupy up to 5%, but the true value is unknown due to non-verifiable data for many countries (Zentelis and Lindenmayer, 2015). In North America, US Department of Defense (DoD) lands across dryland regions cover ~ 6.2 million hectares (Figure 2.1), the largest biome by area within the DoD land base. By area, most of the lands managed by DoD occur in arid or semi-arid ecosystems such as the Mojave or Sonoran Deserts (Figure 2.1, Table 2.1). Many of these areas in the Southwest have seen widespread, prolonged disturbance, and the ecosystems occupying these lands are in various states of degradation due in-part to naturally slow recovery rates (Lawrence et al., 2015). Simultaneously, DoD lands host a large number of threatened and endangered species (Stein et al., 2008), as many of these areas have been protected from drivers such as overgrazing that so commonly impact dryland ecosystem structure and functioning.

Table 2.1. Aridity index values per pixel across all dryland, arid, and semiarid areas of major landholding groups (top portion, units = ratio between mean annual precipitation and mean annual evapotranspiration); net primary productivity values per four square kilometer pixel across all dryland, arid, and semiarid areas of major landholding groups (middle portion, units = grams C/m^2/year); standardized richness values per pixel across

all dryland, arid, and semiarid areas of major landholding groups (bottom portion, units = vertebrate species richness per pixel).

		Drylands (AI <= 0.50)			Arid (AI <= 0.2)			Semi-Arid (0.2 < AI <= 0.5)		
		Area (Mha)	Mean	SD	Area	Mean	SD	Area	Mean	SD
Aridity	DOD	6.72	0.12	0.07	6.02	0.1	0.04	0.7	0.26	0.06
	Tribal	20.34	0.24	0.1	9.38	0.15	0.03	10.97	0.31	0.08
	NPS	6.06	0.16	0.12	4.35	0.09	0.05	1.71	0.33	0.09
	BLM	68.81	0.19	0.08	39.24	0.13	0.05	29.57	0.26	0.06
	USFS	37.71	0.35	0.09	1.85	0.16	0.03	35.86	0.36	0.08
NPP	DOD	6.72	65.5	113.7	6.02	39.6	58	0.7	279	201.7
	Tribal	20.34	183.5	164	9.38	63.1	69.7	10.97	278.6	154.3
	NPS	6.06	118.6	182	4.35	34.2	44.2	1.71	326.8	221.5
	BLM	68.81	98.4	92.6	39.24	54.9	54.6	29.57	152.8	101.2
	USFS	37.71	375.9	173.9	1.85	153.4	111.6	35.86	386.8	169
Richness	DOD	6.72	0.37	0.1	6.02	0.37	0.1	0.7	0.4	0.1
	Tribal	20.34	0.31	0.07	9.38	0.33	0.06	10.97	0.3	0.08
	NPS	6.06	0.32	0.06	4.35	0.32	0.05	1.71	0.31	0.08
	BLM	68.81	0.3	0.07	39.24	0.32	0.08	29.57	0.28	0.06
	USFS	37.71	0.33	0.09	1.85	0.33	0.09	35.86	0.33	0.09

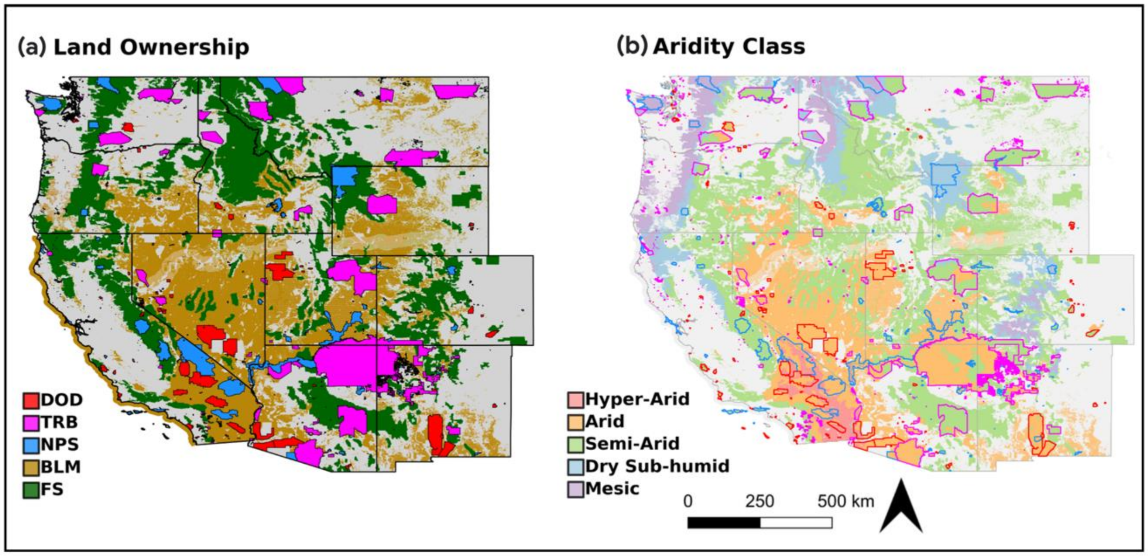

Figure 2.1. Major landholdings in the western United States (a). US Department of Defense installations (DOD; red) in the western United States. Other large land-holding organizations shown are Tribal lands (TRB; pink), National Park Service (NPS; blue), Bureau of Land Management (BLM; brown), and the US Forest Service (FS; green). Aridity values in the western United States (b). Hyper-arid (red), arid (orange), semi-arid (green), dry sub-humid (blue), and mesic (purple) lands for the landholders displayed in figure A are shown.

Lands devoted to military activities are a large portion of the total area of federal lands in the United States (Figure 2.1). The DoD acquired a large and diverse land base to develop military readiness through built infrastructure and personnel training, with the land provided to the DoD by the federal government expressly devoted to the achievement of military goals (Lillie and Fittipaldi, 2010). The purpose of DoD land contrasts with other US federal agencies such as the National Park Service, the Bureau of Land Management, and the US Forest Service, which are organized around land management goals. There has been a large shift in environmental management within the DoD through time, from the initial commodity-based resource management to single-species management in the more recent past, and finally on to more ecosystem-based management principles (Lillie and Fittipaldi, 2010). Despite an acknowledgement of ecosystem-based land management principles, the scale and extent of ecosystem services from DoD lands remains largely unknown. Despite the uncertainty of the net export of ecosystem services across all DoD-managed drylands, studies of individual DoD installations show the importance ecosystem type in controlling the flow of ecosystem services (Warren et al., 2007; Zentelis and Lindenmayer, 2015). Since the majority of DoD-managed lands are located in drylands, future management must address the interaction of ecosystem type, management activities, and demand for ecosystem services from dryland areas.

Ecosystem services demand and supply drive land management and are an extension of the societal norms embedded in the legislation governing them (Carpenter et al., 2009). Ecosystem services demand occurs at multiple scales from local (forage production) to global (carbon sequestration). Across scales, stakeholders are variable in both their demand for and valuation of ecosystem services. Managing for these demands can be challenging, so focusing on how specific ecosystems supply services in addition to considering demand may offer valuable management insight (Geijzendorffer et al., 2015; Yahdjian et al., 2015). As the human population continues to grow, explicitly considering the demand of ecosystem services relative to ecosystems' capacity to supply will aid in land stewardship and safeguard against unnecessary land degradation (Cowie et al., 2018).

Drylands, despite the pervasive view that they are marginal lands, are home to 30% of the human population, and provide critical ecosystem services that billions of people depend upon including 43% of global agricultural production (Pan et al., 2021;

Ramankutty et al., 2008; Reynolds et al., 2007). Even though they are water-limited, drylands supply society regulating, provisioning, and cultural ecosystem services, all three of which are underpinned by supporting services (Hoover et al., 2020; Millennium Ecosystem Assessment, 2005). These ecosystems are unique relative to more mesic ecosystems in their greater spatial and temporal heterogeneity, and this in turn affects the distribution of ecosystem services supplied from drylands. For instance, most of the interannual variability in the global carbon cycle can be attributed to semiarid systems (Ahlström et al., 2015), global livestock production is affected by precipitation variability in dryland areas (Sloat et al., 2018), and heterogeneity of dryland ecosystems complicates adequate environmental monitoring and restoration efforts in both wealthy and developing countries (Maestre et al., 2012). Yet, drylands have been historically neglected across realms of scientific research, government planning, and conservation efforts (Durant et al., 2012; Hoover et al., 2020; Okin et al., 2015). Indeed, many drylands have been degraded, defined as a loss of soil structure, fertility, and vegetation productivity. Estimates range widely, from 4-74% of drylands globally experiencing some form of degradation (Safriel, 2007). To improve how ecosystem services are accounted and managed for across the DoD land base, researchers must more fully account for variability and complexity of dryland ecosystems as well as their status and modern usage.

The global patterns of dryland degradation led the United Nations to formally adopt the Land Degradation Neutrality in 2011 in an effort to reduce the area of lands with uses that degrade their productivity (Orr et al., 2017). Land Degradation Neutrality (LDN) is a conceptual framework in which the amount and quality of land resources required to support ecosystem functions and services and enhance food security remain stable or increase within specified temporal and geographical scales and ecosystems. The distinction between two different phases of land degradation is at the heart of the LDN concept. Land can be in the process of being degraded through a use that reduces productivity with time or it can be in the state of an already degraded land, but producing a persistently low productivity relative to the land's potential (Orr et al., 2017; Safriel, 2017). This has direct application to military training areas in dryland ecosystems that often contain a matrix of degraded and intact ecosystems (Warren et al., 2007; Zentelis et al., 2017). By considering indicators of degradation at the landscape scale across military lands and considering them within the LDN framework, researchers can more robustly assess how these lands contribute to the supply and demand of ecosystem services across stakeholder groups (Orr et al., 2017). In North America, the demand for dryland ecosystem services likely exceeds the current supply, making conservation and careful management of the large dryland area within the DoD land estate crucial for providing and safeguarding ecosystem services (Bengtsson et al., 2019). Drylands that are warmer and have lower species diversity are particularly vulnerable to reductions in services due to increased disturbance, and biodiversity loss in drylands can further exacerbate the decline in ecosystem services when coupled with disturbances and land use pressures (Maestre et al., 2022). The climate-biodiversity status of DoD lands creates widespread management challenges for military training areas in drylands where the primary land use can be destructive (Warren et al., 2007; Zentelis et al., 2017).

The DoD manages a large land estate in dryland ecosystems in the US, and here I consider the supply, demand, management, and future of critical ecosystem services explicitly across these water-limited landscapes. I specifically analyze spatial patterns of ecosystem productivity, e.g., net primary productivity (NPP; Robinson et al. 2018), and higher-order biodiversity, e.g., total species richness of terrestrial vertebrate functional groups mammals, birds, and reptiles (Jenkins et al., 2015), which represent integrated measures of ecosystem functioning and a suite of ecosystem processes. Changes in NPP and vertebrate diversity are tightly linked to land degradation and decreased ecosystem functioning in drylands (Bengtsson et al., 2019; Monk and Schmitz, 2022; Orr et al., 2017; Sinclair and Byrom, 2006).

Critically, ecosystem processes and attributes do not equate to ecosystem services (Haines-Young et al. 2012). Ecosystem services can be most precisely defined as 'what ecosystems do for people' (Haines-Young and Potschin 2018). A key aspect of accounting for ecosystem services to consider separately the goods and benefits people derive from ecosystems services and the contributions to human well-being that ecosystems make, i.e. ecosystem services. While ecosystem functions are inherently tied to ecosystem services, they are not services themselves unless these benefits are realized by people (Olander et al. 2018). Many analyses of ecosystem services do not explicitly link services to ecosystem health (Hernández-Blanco et al., 2022). However, metrics of ecosystem health provide a useful proxy for ecosystem services, especially in dryland systems (Hummel et al. 2019, Lu et al. 2018). Here I consider NPP and vertebrate biodiversity as measures of ecosystem function and ecosystem properties, respectively (Hummel et al. 2019). I selected these ecological metrics for these analyses because of their particular relevance in capturing ecosystem services in drylands. NPP is widely used as a proxy for ecosystem services with direct economic valuation (forage production), as well as ecological integrity, because NPP is both sensitive to land degradation and can capture large-scale ecosystem services like carbon sequestration and erosion prevention. My use of vertebrate diversity as an indicator of ecosystem services is less direct than NPP. Using biodiversity alone is not adequate for capturing ecosystem services, but higher-order biodiversity at large scales does provide information about aesthetic, recreational, and existence values of species (Mace et al. 2012).

Benefit relevant indicators offer a basis for economic valuation and consideration of ecosystem services beyond indicators of ecological function alone (Olander et al. 2018). The lively debate behind identifying, quantifying, and valuation of ecosystem services has expressed a clear need for articulating ecosystem service endpoints and methods for economic valuation (de Groot et al. 2010). Ecosystem service assessments in drylands have been far less comprehensive and conducted on shorter and smaller scales than more mesic systems (Lu et al. 2018). To address this knowledge gap, I quantify biome-scale indicators of ecosystem services across the DoD land base in addition to specific examples of ecosystem services and their benefit relevant indicators at the unit scale.

By evaluating the use and availability of these ecosystem services from DoD-managed drylands, researchers can better understand the value of these lands across scales and balance immediate and future demands for these areas (Figure 2.2). Military control of these lands has led to a highly unique land use: military training occurs only a portion of the land estate the DoD controls within drylands, yielding a matrix of intact, preserved areas juxtaposed with degraded lands (Warren et al., 2007). Military training areas are commonly semi-natural because of their land use history and land management regimes, and semi-natural areas are important for supplying ecosystem services but remain understudied in the ecosystem services literature (Zentelis and Lindenmayer, 2015; Zhao et al., 2020). Any land, whether used for training or not, can supply ecosystem services at large scales (Millennium Ecosystem Assessment, 2005). Popular concepts of military training areas may include decimated bombing ranges, but the modern DoD land base has thousands of hectares of natural or semi-natural ecosystems that are providing unquantified ecosystem services.

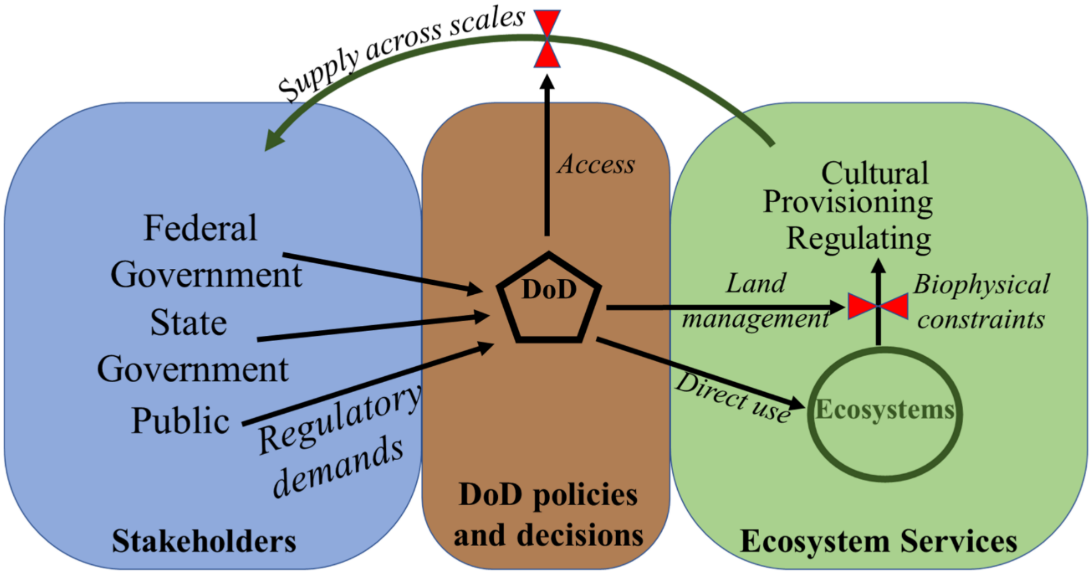

Figure 2.2. Conceptual diagram of the supply and demand of ecosystem services on Department of Defense lands. The framework highlights DoD policies and land use decisions in the brown polygon in the center, influencing both supply and demand. Stakeholders across spatial scales are shown in the blue polygon, and the potential ecosystem services from the DoD land base are shown in the green polygon. Demands for ecosystem services are expressed via regulations and direct administrative linkages are shown as black arrows, where supply is shown with a green arrow. Demands originate on multiple levels of organization through federal, state, and public institutions, including demands from within the Department of Defense for direct use of lands for military training and other uses. The supply of ecosystem services from DoD lands is provided by different types of ecosystems contained in the land estate but is modulated through both land management decisions and controlled and restricted access to the public on DoD lands: environmental management and limited accessibility are controls of the flow of ecosystem services to stakeholders.

Stakeholders can create additional ecosystem service demands at large and small scales through regulation, influencing how the DoD is able to use lands (Figure 2.2). DoD policies and land use decisions are filtered through regulatory demands, land management activities, and their land use needs. Climate and biodiversity interact with land management decisions to modulate the potential ecosystem services that are produced. A key difference in DoD lands and other broad-scale landholders is that the DoD often restricts access, further modulating which services can be accessed by stakeholders (Figure 2.2).

With this conceptual framework, I addressed three overarching research questions:

1) What ecosystem services do DoD-managed drylands supply across their spatial extent, and how does the supply of ecosystem services compare to other land management regimes?

2) How are demands for ecosystem services from DoD-managed lands as reflected in the governing legislation across scales of government?

3) How explicitly do DoD management plans adopt the ecosystem services concept?

To address these questions, I took a paired geospatial and content analysis approach to both capture the degree of ecosystem services supplied by the DoD land base as well as evaluate the degree to which DoD environmental management plans embody the ecosystem services concept and capture demands of stakeholders.

Methods

To determine the ecosystem services supplied by DoD-managed lands in drylands (hereafter DoD drylands), I first reviewed what ecosystem services are supplied across dryland ecosystem types. Then I applied a spatial filter to capture the unique locations and ecosystems DoD manages in the western US to understand the scale and extent of ecosystem services from these lands. Further, I spatially filtered lands managed by the National Park Service (NPS) and the Bureau of Land Management (BLM) to capture the breadth of federal land management, with a preservation ethos within the NPS and a combined conservation-utilitarian ethos within the BLM.

To provide examples of unit-scale ecosystem services supplied by dryland DoD lands, I selected examples from across five states in the western US and stratified across ecosystem service category and ecosystem types (Table 2.2). Using specific examples of natural resources present on individual DoD installations, I provide example benefit relevant indicators to connect ecosystems services with their contributions to people and subsequent mechanism for economic value (Olander et al. 2018). Valuation of ecosystem services is much less complex for commodity services (like grazing) but is much more difficult for nonmarket goods (Richter et al. 2021), and I highlight both direct and indirect valuation pathways for ecosystem services from DoD units. I highlight these specific examples to connect the landscape-scale indicators of ecosystem services explored in this manuscript with the economic endpoints across diverse systems.

Table 2.2. Examples of unit-specific and DoD-wide supply of ecosystem services. Each unit contains ecosystem types that produce ecosystem services through management actions (such as permitting livestock grazing) and regional context (such as being in the same watershed or airshed). Benefit relevant indicators provide unambiguous connections between ecosystem processes and human wellbeing and are assigned economic value through direct and indirect valuation methods. Some services, such as carbon sequestration and storage, can occur across all DoD lands and the benefits are not bound to specific people or geographies.

Military Installation	**Primary Ecosystem Types**	**Example Ecosystem Services**	**Benefit relevant indicator**	**Economic Value**

Camp Guernsey	Northern Mixedgrass Prairie/Pine Woodlands	Forage production (livestock grazing)	Animal Unit Months used	Market value of grazing leases
		Recreation (hunting; fishing)	Animals harvested	Willingness to pay for hunting and fishing
Beale Air Force Base	Annual grasslands/Oak woodlands	Wetland protection (freshwater marshes)	Hectares of protected wetlands relative to habitat extent regionally	Avoided water treatment costs downstream
		Forage production (livestock grazing)	Animal Unit Months used	Market value of grazing leases
		Recreation (hunting- military personnel only)	Animals harvested	Willingness to pay for hunting in an area off-limits to the public
Holloman Air Force Base	Chihuahuan Desert Shrublands/Grasslands/Woodlands	Existence of rare vegetation communities (Duneland Cottonwood communities)	Hectares of habitat	Willingness to pay for habitat preservation
		Threatened species habitat management (desert pupfish)	Population estimates relative to population across entire species range	Willingness to pay for threatened species preservation

Hill Air Force Base and ranges	Great Basin Desert Shrublands	Air quality protection (Salt Lake valley)	Number of vulnerable people in Salt Lake City airshed with air quality improved by management action	Willingness to pay for improved air quality
Nellis Air Force Base and ranges	Mojave and Great Basin Desert Shrublands	Large spatial extent of habitat (>1 million hectares of desert lands in mostly natural condition)	Hectares of ungrazed desert lands times the number of people holding existence value for ungrazed desert lands	Willingness to pay for desert lands managed with no surface disturbances
All Installations	Varied	Carbon storage	Pg C stored in soils and vegetation	Social cost of carbon

I used multiple spatial datasets to inform my analyses and quantify a subset of the supply of ecosystem services from DoD drylands, and I compared the DoD land base in drylands to lands managed by the National Park System and the Bureau of Land Management in the same region. To accurately categorize the degree of water deficit from climate across DoD installations, I used the spatially gridded climate data from Terra Climate to quantify aridity across DoD drylands (Abatzoglou, 2013). The aridity values I present here were calculated as the ratio between mean annual precipitation to potential evapotranspiration over the 35-yr period from 1986 to 2019. Because soil water availability is the most limiting control to biological activity in drylands, quantifying this climate parameter across these landscapes is critical for ecological evaluation. The aridity index I use captures both incoming precipitation and the evaporative demand for water once it arrives in an ecosystem. I used an aridity index of 0.5 to capture the breadth of water-limited DoD lands in the Western United States. I conducted a simple sensitivity analysis of varying aridity index levels and decided to use 0.5 as an inclusive measure of water-limited areas, though I acknowledge that 0.65 is a common threshold for considering dryland areas as defined by an aridity index. Because it is an integrated metric of climate, the aridity index allowed for an understanding of where DoD landholdings are in drylands and focus my analysis there.

To quantify net primary productivity (NPP), I used a Landsat-based net primary productivity data set (Robinson et al., 2018) based on the MODIS NPP algorithm (Running et al., 2004; Smith et al., 2016). Because military training areas can be subjected to repeated disturbances that cumulatively affect plant productivity (Milchunas et al., 2000), I used these data to calculate mean annual net primary productivity over the 35-yr period from 1986 to 2019. By considering the mean net primary productivity over a three-and-a-half-decade period, I was able to consider this ecosystem metric across a range of climatic states, as dryland productivity can be quite variable from year to year. Because net primary productivity is usually considered a supporting service (Millennium Ecosystem Assessment, 2005), and supporting services are not consumed by stakeholders in the same manner as regulating, cultural, and provisioning services (Wu, 2013; Zhao et al., 2020), I used net primary productivity as a proxy for land degradation and many critical ecosystem services in drylands that are tightly linked to the abundance and distribution of ecosystem productivity in drylands. Importantly, net primary productivity has been used as a proxy for multiple ecosystem services in the United Nations Land Degradation Neutrality framework (Orr et al., 2017). Specifically, NPP values show ecosystem services in drylands in light of land degradation, can be used to directly calculate carbon stocks, and provides a useful proxy for other ecosystem services like fugitive dust control, infiltration and aquafer recharge, and forage production.

To quantify the variety and extent of ecosystems that the DoD manages in drylands, I used landcover maps that were hierarchically classified using the U.S. Geological Survey's GAP analysis project (Homer et al. 2015). These landcover data captured plant-community scale occurrence data at a 30 x 30 m resolution and were classified into broad land use classes for analyses. Derived from the Landsat thematic mapper platform, classifying individual pixels occurred by parsing reflectance values through a decision tree modeling process driven by expert classification and soils and climate data. Vegetation classification in this data product occurred through the cumulative efforts of many individuals involved in ecological vegetation classification, taking structural, floristic, and cultural patterns of vegetation into account (Faber-Langendoen et al. 2016). This seven-layered hierarchical classification system allowed us to evaluate large-scale ownership patterns of the DoD dryland estate and identify the diversity of ecological communities contained within.

To quantify higher-order biodiversity across DoD drylands, I used total species richness maps for key terrestrial vertebrate functional groups mammals, birds, and reptiles (Jenkins et al., 2015). I derived an estimate of normalized total species richness by normalizing these individual maps and then taking the mean species richness across the functional groups. I include this metric of biodiversity to capture the conservation value and landscape context of DoD drylands. By considering multiple groups of vertebrates simultaneously, I was able to consider two groups of vulnerable species simultaneously: those with small geographic ranges and large-bodied organisms sparsely distributed across large ranges (Pimm et al., 2014). Ecosystem services indicators often positively correlate with species richness (Wehn et al., 2018). Further, vertebrates occupying dryland habitats can be sensitive to human activities, so their presence provides an integrated metric of ecosystem function on these landscapes (García-Vega and Newbold, 2020; Milchunas et al., 1998).

To evaluate the extent of demand of ecosystem services from DoD lands, I assessed demands from different stakeholders by reviewing local, state, and national regulations. In addition, I evaluated stakeholder demand highlighted in existing literature and consider informal demands from the general public. I also drew upon existing models of demand of ecosystem services from drylands to establish large-scale demands from multiple stakeholders by reviewing the literature and synthesizing their findings.

To assess how DoD management plans account for demand for ecosystem services, I evaluated the environmental management plans at DoD installations. Conservation practices and priorities are laid out within environmental management plans and reflect the values and ideals with which a land base is managed (Botts et al., 2019; Carter et al., 2015; Lin et al., 2019). Because of the breadth and abundance of DoD Integrated Natural Resources Management Plans (INRMPs, mean length = 200 pages), I used content analysis to determine the relative frequency that key concepts arise regarding the management of ecosystem services. Integrated Natural Resources Management Plans are required by law for each DoD landholding and follow a uniform guidance for content and structure (www.dodbiodiversity.org). Because these conservation plans have a standardized structure but are written specifically for individual landholdings, in aggregate they provide an excellent opportunity to determine the strategic priorities within a set of management documents. A list of all INRMPs I included in my content analysis can be found in Table S2.1.

Content analysis is a common method for extracting strategic priorities from management and policy documents (Neuendorf, 2017), and is now an established method of determining the relative presence of ecosystem services concepts in environmental planning documents (Cortinovis and Geneletti, 2018; Maczka et al., 2016). Content analysis allows for quantitatively oriented research questions, but the quality of results depends on the sample size, quality of writing, pre- and post-processing steps, and interpretation (Banks et al., 2018). My content analysis focused on a set of natural resource management plans of DoD dryland areas. The use of ecosystem services concepts were examined in the content (Neuendorf, 2017) to how closely the language of these management plans embodied the ecosystem services concept. In analyzing the data, definitions of ecosystem services, the UN Land Degradation Neutrality framework, and other relevant documentation for dryland stewardship were carefully reviewed (Delgado and Marín, 2020; Orr et al., 2017; Zhao et al., 2020).

Content analysis allows for clear accounting of how frequently certain concepts are addressed across documents, which requires less interpretation than thematic analysis but provides finer control of analyses than natural language processing (Banks et al., 2018). I identified those terms that are unambiguously identified with information regarding dryland ecosystem services. I reviewed the documents for the term ‘(ecosystem) services’, whether particular services were mentioned, and if trade-offs were explicitly accounted for when ecosystem services were mentioned. For analytical and illustration purposes, however, I assigned specific ecosystem services mentioned in the INRMPs into the three categories being provisioning, regulating, and cultural ecosystem services.

Results

Supply of ecosystem services from DoD-managed drylands

DoD-managed drylands in the western US are located in many different ecosystem types, which has some influence on what ecosystem services they provide. Remote sensing analyses revealed that DoD drylands have net primary productivity values comparable to lands managed by other landholding groups, with a mean of 65.5 g C m^{-2} $year^{-1}$ of primary production across all lands (Figure 2.3, Table 2.1). Across aridity classes, NPP values of DoD drylands were on average greater than National Park Service arid lands, and greater than semiarid Tribal and Bureau of Land Management lands (Figure 2.3, Table 2.1).

Across the same spatial extent, DoD drylands had high values of vertebrate richness, with a mean value per pixel greater than any other national land holding group across all lands and within aridity classes (Figure 2.3, Table 2.1).

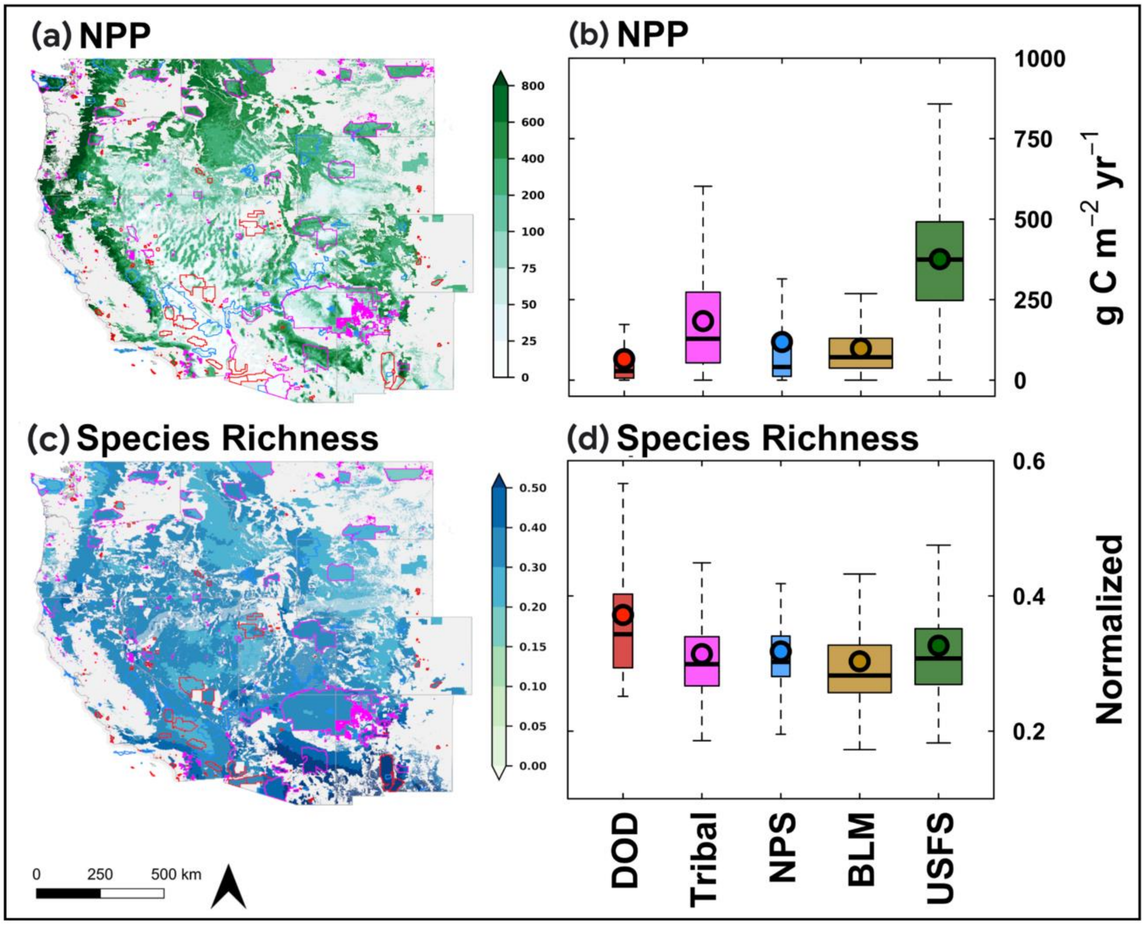

Figure 2.3. Net primary productivity (g of carbon/m^2/y, a) across the DoD land base (red polygons) in the western United States. Boxplot (b) displays distribution of net primary productivity across major land holding organizations in the western US. Biodiversity across the DoD land base (red, c) in the western United States, alongside Tribal lands (pink), National Park Service (blue), Bureau of Land Management (brown), and US Forest Service (green). Values represent an interpolated count of mammal, reptile, and bird species per pixel. Boxplot (d) displays distribution of these interpolated biodiversity values per pixel across major land holding organizations in the western United States. In the boxplot, solid lines indicate median values.

Beyond the broad ecosystem service indicators I analyzed across all DoD and other land management types, I highlight unit-scale ecosystem services from across Western North America (Table 2.2). Some ecosystem services from DoD units can be assigned economic value directly, such as forage production utilized through livestock grazing. Other ecosystem services are only provided economic value through indirect economic valuation approaches, such as willingness to pay. Further, I connect the broad-scale indicators of ecosystem services (NPP and vertebrate richness) with specific benefit relevant indicators and economic valuation methods across all DoD lands (Table 2.2).

The diversity and abundance of ecosystem types are shown in Table S2.2 and Table S2.1. DoD drylands encompass thousands of hectares of desert shrublands, water-limited woodlands, and grasslands, and the distribution of ecosystem macrogroups (Faber-Langendoen 2016) of over 10,000 hectares is provided in Figure 2.4. Mojave Desert shrublands was by far the most common ecosystem macrogroup- at over 1,000,000 hectares, they are over three times more abundant than the next most common type across DoD drylands (Figure 2.4). The diversity of ecosystem types is striking, with over 100 alliance-level ecosystem types of at least 100 hectares contained within DoD drylands (Faber-Langendoen 2016, Table S2.2).

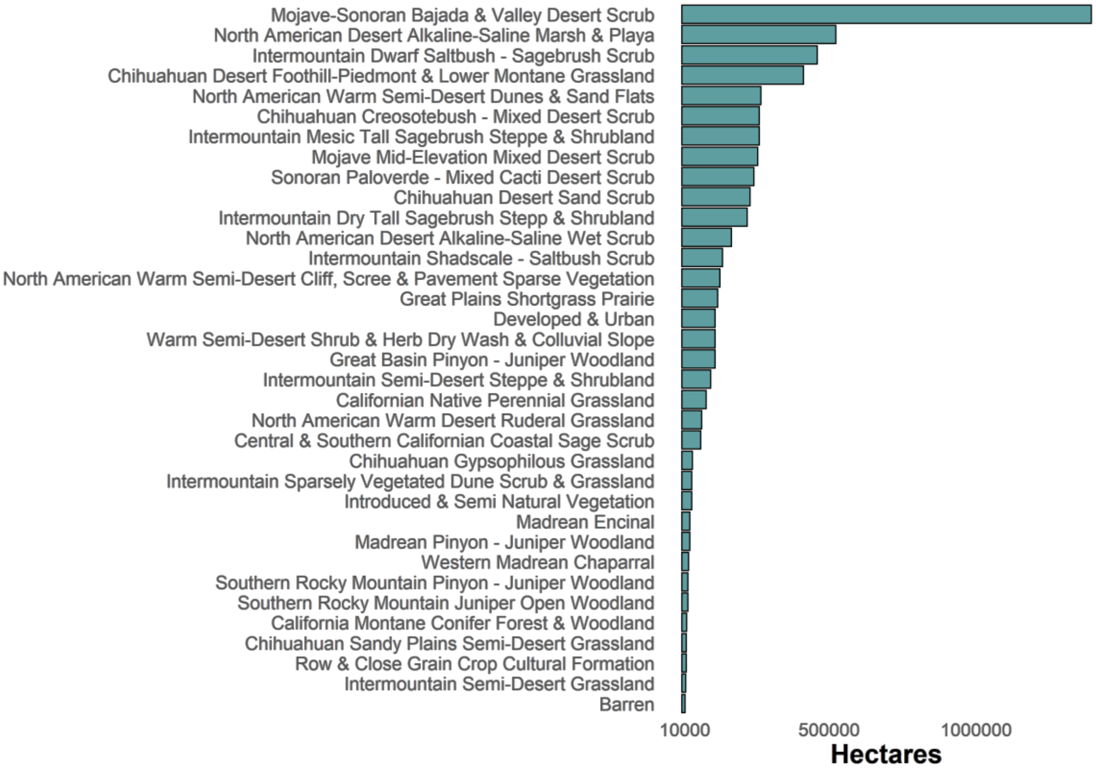

Figure 2.4. Distribution of ecosystem types by area of the DoD land base in drylands of the western US. Only ecosystem types over 1000 hectares are displayed.

Demand of ecosystem services from DoD-managed drylands

I evaluated how key legislation affects demand for ecosystem services from DoD drylands (Table 2.3). The Sikes Act and the Endangered Species Act deserve special attention, as they have shaped the environmental management of military lands more strongly than any other legislation. While the Endangered Species Act is applicable beyond DoD environmental management, the Sikes Act essentially mandated environmental planning and stewardship across the DoD land estate. Other legislation, such as the Migratory Bird Act or NEPA, also have an ongoing regulatory impact on the supply of ecosystem services from military lands.

Table 2.3. Relevant legislation that governs the demand of ecosystem services from DoD lands. We provide examples of the effects of these laws on the demand of ecosystem services.

Legislation and its scale/origin	Demand effects
ESA (federal) 1973	• Causes training disruptions • Changes long-term behavior • Increases public awareness and research interest
Sikes Act (federal) 1960	• Creates demand for ecosystem services through legislation • Identifies actions that all military lands must follow
Migratory Bird Treaty Act 1918	• Creates legal incentive to protect migratory birds
National Environmental Policy Act 1970	• Creates accountability and accounting systems for environmental impacts of human actions
Clean Air Act, Resource Conservation and Recovery Act, Comprehensive Environmental Response, Compensation, and Recovery Act	• Multiple
Land use planning laws (state level)	• Can shape long-term management outcomes
Notification of military planning laws (state level	• Requires extensive communication and explicit review of training activities (influencing demand)
Land conservation laws (state level)	• Depends on state
County or town ordinances	• Can create or restrict access opportunities
Site-level management plans	• Can restrict access

Broadly, the demands of ecosystem services from dryland areas has been changing over recent decades away from provisioning services to a different suite of other services (Havstad et al., 2007; Yahdjian et al., 2015). Legislation can affect the flow of ecosystem services over time (Liu et al., 2023), and updating the language of environmental management across the military land base to include ecosystem services could greatly improve the capacity of these lands meet demands for ecosystem services (Zentelis and Lindenmayer, 2015).

Outside of regulatory demands placed on DoD drylands, there may be informal demands of services from the military land estate. These may manifest in the form of ecosystem services that are not directly captured in regulatory policy or resource management plans. For example, the military may curtail training activities to avoid disturbing communities nearby. In some circumstances, there are non-military organizations working to secure appropriate land use surrounding military bases (see Compatible Lands Foundation). Since 2012, the DoD has used the Readiness and Environmental Protection Integration program to address encroachment effects on DoD bases, combining conservation easements, land purchases, and partnerships to preserve the ability to conduct training activities. This in turn has implications for the supply of ecosystem services from DoD lands themselves.

Managing ecosystem services on DoD lands

Here, I have a review of the environmental management plans on DoD lands to determine the ways in which management of the land can best meet demand with supply of ecosystem services. Within the content and language of the management plans, I was able to isolate which ecosystem services are explicitly managed for, and which ecosystem services originate as emergent properties of other management actions.

With my content analysis, I show that some ecosystem services receive much attention, and others little to none (Figure 2.5). This is common in both management plans and ecosystem services research (Cortinovis and Geneletti, 2018). Endangered species conservation has the most support legally, and thus gets the lion's share of attention within the INRMPs. "Species" is one of the most frequently used terms (n = >17,000 occurrences), whereas "carbon" remains a rarely used term (n = 61 occurrences) across all INRMPs.

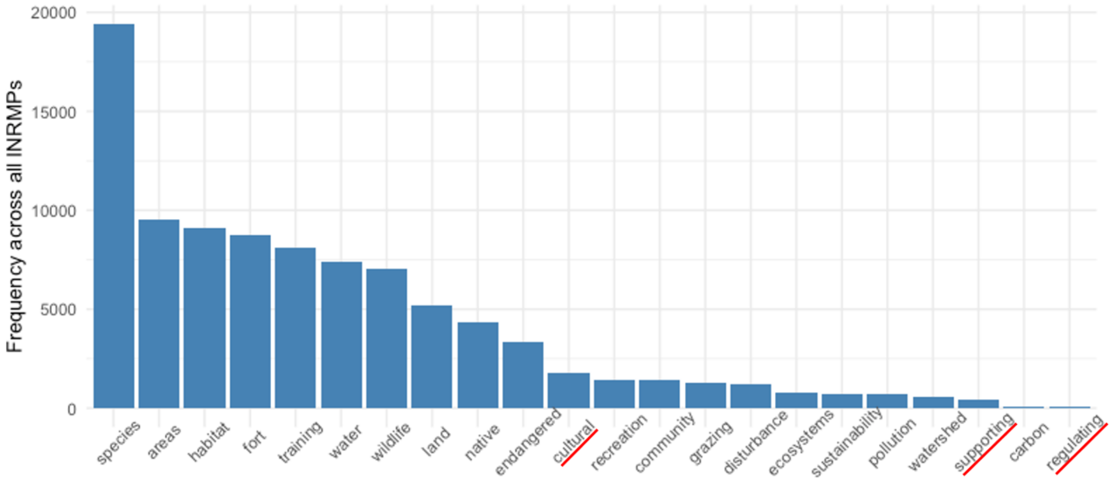

Figure 2.5. Content analysis of the Integrated Natural Resource Management Plans of 35 DoD bases in water-limited landscapes. Major categories of ecosystem services are highlighted in red, and "provisioning" <10 uses across all documents analyzed.

Discussion

Supply and demand of ecosystem services from military lands

Across DoD lands in the western US, there is a large and valuable supply of key ecosystem services to society. My spatial analyses showed that most of the DoD land based in the western US are in drylands, yet these areas have net primary productivity values and are especially species rich when compared to other federal land types. The large total area, the diversity of ecosystems contained within, and the ability to intensively manage are key considerations for how researchers might value the DoD land base in drylands.

Restricted access as well as the combination of increased public scrutiny and funding availability for management interventions into DoD lands modified the supply of ecosystem services relative to other public lands in the United States (Zentelis and Lindenmayer, 2015). A central challenge to quantifying and valuing the supply of ecosystem services is adequate accounting of regulating services, and this is reflected in management plans, policy documents, and scientific research (Villamagna et al., 2013). Thus, the extent to which researchers can attribute regulating services to the DoD land base in drylands likely underestimates the scale of regulating services provided, especially considering the large areas within the DoD land base that are relatively preserved from grazing and overgrazing (de Groot et al., 2010; Warren et al., 2007).

Beyond the specific ecosystem services that I assessed, DoD drylands provide ecosystem services in a similar way to other drylands. Ecosystem services from dryland areas include forage production (Havstad et al., 2007), water supply & watershed protection (Huber-Sannwald et al., 2006), biodiversity (Perrings and Walker, 2004), carbon sequestration (Poulter et al., 2014), and recreational and cultural values (Zhao et al., 2020). DoD lands provide ecosystem services across spatial scales considering the extent of intact or semi-natural areas within the dryland portion of the DoD land base (Figures 2.3, 2.4). Within the Land Degradation Neutrality framework, DoD drylands represent both degraded and functioning ecosystems, representing an opportunity to employ the principles of neutrality across scales and management objectives. Specifically, DoD can simultaneously protect intact ecosystems, restore degraded ecosystems, and prevent further degradation intensively used areas (Balletto et al., 2020; Orr et al., 2017).

DoD drylands also supply ecosystem services in ways different from other drylands. Notably, these areas often have highly disturbed areas juxtaposed with minimally disturbed areas, which can foster high levels of biodiversity. The phenomenon is so pronounced that it has led previous researchers to posit the "heterogeneous disturbance hypothesis" and argue that the disturbance regimes of these DoD drylands has illuminated ecological principles (Warren et al., 2007), and there are examples of specific positive effects of military activities on species across ecosystems (Aycrigg et al., 2015; Dvořáková et al., 2023; Warren and Büttner, 2008; Zentelis and Lindenmayer, 2015). Despite unique management history, the magnitude and type of ecosystem services from the DoD land base is primarily controlled by the biophysical constraints of terrestrial ecosystems: average and extremes in climate, geologic history, biogeographic influences, and other controls (Maestre et al., 2022). Understanding the primacy of these controls helps contextualize the type and magnitude of ecosystem services supplied by a given location given its management history. Importantly, there are inherent climatic and biophysical differences within the lands held by the land-managing agencies analyzed here. For example, lands original transferred to the DoD may have been historically degraded or have inherently low productivity, and further analyses could account for these differences.

Supply of ecosystem services from these lands are similar to both other government-managed lands and private lands in several important ways as well, especially when considering local-scale cultural services. While provisioning services have historically been viewed as the primary value of rangelands (Havstad et al., 2007), views towards rangelands have shifted over time, with cultural and regulating services viewed as more valuable (Martín-López et al., 2012). Communities in proximity to the DoD land base are provided cultural and aesthetic services from the preservation of open space and, in certain instances, increased access to outdoor amenities.

Cultural ecosystem services are derived across spatial scales, with most delivered at local scales (Carpenter et al., 2009). I found that DoD drylands provide cultural services both at local and landscape scales. Many evaluations of ecosystem services do not identify military use as an ecosystem service, instead listing this land use outside of the ecosystem services framework (Ma et al., 2016). Given that the US has explicitly managed millions of hectares of land across ecosystem types expressly for their natural characteristics, I suggest that military use be explicitly identified as a cultural ecosystem service.

Indeed, at the national scale, DoD land estate is larger than all state parks (Li and Male, 2020), controls more ecosystem types than the US Forest Service, US Fish and Wildlife Service, or Bureau of Land Management (Aycrigg et al., 2015), and even though the majority of federal designation of these lands occurred a century ago they have not been converted to other, more ecologically focused ownership (Havlick, 2014, 2011). The militaries of the United States and other nations demand semi-natural conditions for training, large areas of land for operations and security, and sufficient land buffers to safeguard civilian quality of life and prevent litigation. These lands enable the scale and intensity of the world's militaries and supply cultural ecosystem services to societies. Though not commonly assessed as ecosystem services, federal governments and militaries are intrinsically part of societies as they exist now and will continue to be so until societies no longer value military capabilities and manage military training areas for other uses (Havlick, 2011). By adopting the language of ecosystem services in their management plans, policies could more effectively consider military use and management in Land Degradation Neutrality framework and quantify their value across spatial scales (Cowie et al., 2018; Orr et al., 2017).

Much of the scientific literature focused on ecosystem services and the military have focused on single geographic locations or single species. There is a lack of synthetic literature for US installations. The integration of natural resources and training plans have been well explored in European and Australian training areas (Zentelis et al., 2017) as well as single base studies in the US (Anderson et al., 2005; Ma et al., 2016), but no studies have synthesized across US training areas. My analyses indicate that the uniqueness and scale of ecosystem services from DoD-managed drylands warrant specific attention. For example, it would be useful to perform landscape scale comparisons with private, tribal, and other federally owned lands (sensu Robinson et al., 2019). Considering the land sparing-land sharing framework, while maintaining land degradation neutrality, could be a powerful mechanism to maximize the supply of ecosystem services directly from DoD drylands while preserving their ecological integrity (Cowie et al., 2018; Grass et al., 2019).

Individual units in the DoD land system could benefit by clearly identifying ecosystem service monetary social values, as the suite of costs and benefits society derives from these areas are not always accounted for. This exercise has been done in rare cases for individual units (see Ma et al. 2016), but it could be standardized across units through the process of developing and administering their environmental management plans. There is evidence to suggest that comprehensive, unit-scale accounting and valuation of ecosystem services is the most robust approach for capturing what services an area produces. For example, the total value of ecosystem services can vary by ecosystem type in drylands (Schild et al. 2018), and benefit-relevant indicators are best developed with stakeholders in a manner that makes them relevant and recognizable (Olander et al. 2018). There are excellent examples of unit-scale evaluations of ecosystem services beyond academic journals (Conte et al. 2015, Kagan et al. 2019) that provide robust frameworks for unit-scale accounting.

Management of ecosystem services from DoD lands

By analyzing the content of many environmental management plans, I was able to capture the relative emphasis that natural resource management in the DoD land has embodied the concept of ecosystem services. The degree to which these ecosystem service concepts were captured in management plans is driven by the legislation that created them, the Sikes Act. I found that the language and content of the management plans reflect the culture within the US federal government at the time and language of this legislation. The ways that environmental management manifested after the Sikes act was strongly affected by norms within the federal government and US military at the time (Scarlett and Boyd, 2015). While management plans and their governing legislation have been updated over time (Hollingsworth, 1999), the absence of key ecosystem service concepts in modern plans reflects the institutional legacy from the passing of the Sikes Act decades ago.

There is a large degree of implicit adoption of ecosystem services concepts, for instance many management plans explicitly state the goal of “ecosystem management”. Vague mentions or implicit assumptions about managing for ecosystem services has been highlighted as a concerning shortcoming in policy and management documents that can result in undervaluing or improper stewardship of certain services (Maczka et al., 2016), and the phrases used in the INRMPs may not appropriately capture these concepts. However, classifying and clearly defining ecosystem services concepts for management has been done poorly over time because it is an inherently difficult task (Fisher et al., 2009). DoD drylands may be implicitly managed for the supply of ecosystem services, but these services are not identified in the language of the ecosystem services concept (Millennium Ecosystem Assessment, 2005). While it is important that lands be managed for the supply of ecosystem services, the exclusion of the ecosystem services concept from these management plans could cause difficulty with national- or international-level accounting for services in the land degradation neutrality or land sparing, land sharing framework (Grass et al., 2019; Maczka et al., 2016; Orr et al., 2017).

I highlight specific examples where supply has been allowed to meet demand as well as examples where management actions prevent the flow of ecosystem services. Some military installations are able to meet some demand for provisioning services: in Fort Hood, TX, some ranchers are allowed to graze cattle on military land (Guretzky et al., 2006), and state-owned land within the Gurnsey National Guard training center is also grazed. Some DoD lands are managed explicitly for biodiversity conservation, especially when species listed under the ESA are negatively impacted by training activities. Notable examples of this include managing for the Mojave Desert tortoise in Fort Irwin, CA and famously the Palo Verde Blue butterfly at the Naval Defense Fuel Support Point in San Pedro, CA.

The future of ecosystem services from military lands

I forecast that DoD-managed drylands will face large changes in supply and demand of ecosystem services. Supply, as discussed, will be strongly affected by changes in temperature, precipitation, and climate variability (Zhang et al., 2021). Across the dryland portion of the DoD land estate, climate change will have prolonged and substantial impacts on the supply and demand of ecosystem services. Over the next century, many DoD installations in drylands will experience less annual precipitation and more drought stress (Cook et al., 2015; Seager et al., 2007), or changes in the seasonality and form of precipitation (Palmquist et al., 2016; Zhang et al., 2021). DoD installations are expected to increase in temperature over the coming decades (Watson et al., 2000). There is a growing literature that these changes in climate will interact with other drivers to spur large changes in dryland ecosystem structure and function (Burton et al., 2020; Jordan et al., 2020). A large source of uncertainty is the interaction of multiple global-change drivers. Across landscape types, there are many overlapping drivers that can interact in synergistic ways. For example, above average temperatures can quickly drive down soil moisture levels, creating what is known as a "flash drought" (Basara et al., 2019; Dannenberg et al., 2022). For ecosystem services from DoD-managed drylands, there is a strong potential for the interaction of ecological disturbances created by military training activities and altered precipitation regimes. Across all of the drylands of North America, climate change models predict some degree of precipitation change (Anderegg and Diffenbaugh, 2015; Diffenbaugh et al., 2008). For many systems, such as the Sonoran, Mojave, and Colorado Plateau deserts, these forecasted changes are towards drier conditions (Gutzler and Robbins, 2011; Seager et al., 2007). When these forecasts are combined with the effects of high temperatures, the potential for severe and prolonged drought conditions is substantial.

Demand for ecosystem services from DoD lands will change through time (Yahdjian et al., 2015). Key influences on demand will be encroaching towns and associated population growth, the change in ecosystem services demanded from urban populations, and uncertain new regulations for these areas. In addition to population growth at the global and national scale, the southwest US or "sun belt" has seen unprecedented population growth in recent decades, ushering in demographic changes and land-use change (Wu et al., 2011; York et al., 2011) These demographic and land use changes synergistically increase demand for ecosystem services from the DoD land base: as populations grow, the demand ecosystem services like recreation (cultural) and air quality (provisioning) increase in step, and demand also grows through the loss of formerly natural areas to new housing and urban areas to support these populations (Martín-López et al., 2012). Finally, as small towns grow into urban centers, there can be a shift in regulatory attitude toward environmental stewardship, as wealthy, urban populations typically have different demands than a rural population with access to fewer resources (Brunson, 2020).

Interactions of changing supply and demand will pose new challenges for managing DoD lands. Many of these systems have been shown to be sensitive to military training activities, even under historical precipitation regimes (Belnap and Warren, 2002; Kade and Warren, 2002). Thus, the effects of military training on ecosystem structure and function under novel climate conditions is highly uncertain, and will only exaggerate the complexity of trade-offs for multiple ecosystem services management (Aryal et al., 2022;

Rodríguez et al., 2006; Zentelis et al., 2020). A perennial challenge of managing these lands will be selecting the best indicators of ecosystem services as climate and society continue to change (Hummel et al. 2019).

My analyses show that the legislative legacy of the DoD land base has had large-scale consequences for the production of ecosystem services across spatial scales. Likely, any large-scale changes in land management for ecosystem services will be most successful with a top-down approach on behalf of the federal government, changing the language used to manage across the many environments with DoD land. In short, DoD management plans are result of people doing their jobs. Adopting new legislation with clear directives across organizational scales is what changes their job responsibilities. If managing for ecosystem services is something society values, then expressly quantifying them in the language of ecosystem services within management plans would allow for comprehensive management at the national scale. This quantification is critical across the Land Degradation Neutrality framework, and would more clearly identify for opportunities to increase the supply of ecosystem services from DoD lands (King et al., 2015; Maczka et al., 2016; Orr et al., 2017).

There have been several critical periods in development of management practices on DoD lands, and the post-9/11/2001 US may represent another pivot in how ecosystem services of the western US are affected by DoD land management with the expansion of defense infrastructure and budgets. As climate change is increasingly considered a national security threat, we may be entering another era of environmental management action. The DoD recently introduced ambitious, but not required, climate adaptation guidelines to be considered in their management plans (Stein et al., 2019). These plans highlight the depth of expertise necessary to successfully plan for changes in climate and the uncertainty around managing natural capital at the landscape scale. If implemented, they provide an opportunity for the DoD land base to enter a new era of more adaptable environmental management (Morecroft et al., 2019).

By considering the most robust signals in climate forecasts and considering one ecosystem service type at time, researchers can identify the potential for future management challenges. Additional research could illuminate idiosyncratic climate projections for individual DoD installations and interactions between ecosystem services and multiple stakeholders. Studies that experimentally manipulate multiple global change drivers and different management actions could be especially useful.

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Supplementary Material to Chapter 2

Table S2.1. List of military installations included in the content analysis of their Integrated Natural Resources Management Plans.

Holloman Air Force Base
Biak Training Center
Fort Riley
Barstow Marine Core Logistics Base
Barry M. Goldwater Range
Fort Huachuca
Camp Navajo
Yuma Proving Ground
Edwards Air Force Base
San Clemente Island
Fort Hunter Liggett
Vandenberg Air Force Base
Beale Air Force Base
Camp Pendleton
Chocolate Mountain Aerial Gunnery Range
Marine Corps Air Ground Combat Center
Naval Weapons Training Facility Boardman
March Air Reserve Base
Naval Support Activity Monterey
Naval Base Port Hueneme
San Joaquin Defense Distribution Depot
Naval Weapons Station Seal Beach
Susanville Indian Rancheria
Naval Base Ventura County
Fort Carson
Pinon Canyon Maneuver Site
Hawthorne Army Depot
Nellis Air Force Base
Naval Air Station Fallon
Fort Hood
Fort Bliss
Camp Guernsey
Fort Irwin
Hill Air Force Base
Offutt Air Force Base

Table S2.2. Ecosystem types by area across the US DoD land base in drylands of the western United States. Ecosystem classifications follow Faber-Langendoen et al. (2016). Only ecosystem types over 100 hectares are included.

Hectares	Ecosystem
1390961.4	Sonora-Mojave Creosotebush-White Bursage Desert Scrub
522879.6	Inter-Mountain Basins Playa
459619.4	Inter-Mountain Basins Mat Saltbush Shrubland
413230.9	Apacherian-Chihuahuan Semi-Desert Grassland and Steppe
268976.9	North American Warm Desert Active and Stabilized Dune
263624.6	Chihuahuan Creosotebush, Mixed Desert and Thorn Scrub
257322.2	Mojave Mid-Elevation Mixed Desert Scrub
245342.9	Sonoran Paloverde-Mixed Cacti Desert Scrub
235535.6	Inter-Mountain Basins Big Sagebrush Shrubland
231807.9	Chihuahuan Stabilized Coppice Dune and Sand Flat Scrub
127364	Inter-Mountain Basins Big Sagebrush Steppe
121944.9	Western Great Plains Shortgrass Prairie
118669.5	Sonora-Mojave Mixed Salt Desert Scrub
113358.4	North American Warm Desert Wash
112789.9	Great Basin Pinyon-Juniper Woodland
98087.3	Inter-Mountain Basins Semi-Desert Shrub Steppe
94477.9	Great Basin Xeric Mixed Sagebrush Shrubland
90087.7	North American Warm Desert Playa
82692.8	California Central Valley and Southern Coastal Grassland
78426	Inter-Mountain Basins Greasewood Flat
67788.5	Apacherian-Chihuahuan Mesquite Upland Scrub
66701.9	North American Warm Desert Volcanic Rockland
63940.1	Southern California Coastal Scrub
48868.4	Developed, Open Space
43700.4	Developed, Low Intensity
36391.5	Chihuahuan Gypsophilous Grassland and Steppe
35863.7	North American Warm Desert Bedrock Cliff and Outcrop
34118.6	Inter-Mountain Basins Active and Stabilized Dune
33531.4	Introduced Upland Vegetation - Annual Grassland
27404.7	Columbia Plateau Steppe and Grassland
27315.1	North American Warm Desert Pavement
23161.3	Mogollon Chaparral
20916.1	Developed, Medium Intensity
20701.7	Southern Rocky Mountain Pinyon-Juniper Woodland
20623.1	Southern Rocky Mountain Juniper Woodland and Savanna
19260.8	Inter-Mountain Basins Mixed Salt Desert Scrub

16385.6	Mediterranean California Mesic Serpentine Woodland and Chaparral
15206.6	Chihuahuan Sandy Plains Semi-Desert Grassland
14953.9	Cultivated Cropland
13546.6	Inter-Mountain Basins Semi-Desert Grassland
10932.2	Undifferentiated Barren Land
10242.7	Introduced Upland Vegetation - Shrub
10115.1	Inter-Mountain Basins Juniper Savanna
9487.9	Southern California Dry-Mesic Chaparral
9228.7	Developed, High Intensity
8614.7	Western Great Plains Foothill and Piedmont Grassland
8492.2	Northwestern Great Plains Mixedgrass Prairie
7661.7	Inter-Mountain Basins Montane Sagebrush Steppe
7255.2	Rocky Mountain Gambel Oak-Mixed Montane Shrubland
7253	Pasture/Hay
7077.6	Southern Rocky Mountain Ponderosa Pine Woodland
5782.2	Columbia Plateau Scabland Shrubland
5756.6	Chihuahuan Mixed Salt Desert Scrub
5128.8	Inter-Mountain Basins Cliff and Canyon
4829.1	Inter-Mountain Basins Shale Badland
4803.1	Willamette Valley Upland Prairie and Savanna
4309.3	Mediterranean California Foothill and Lower Montane Riparian Woodland
3368.2	Chihuahuan Loamy Plains Desert Grassland
3347.7	North American Warm Desert Riparian Woodland and Shrubland
3270.4	Columbia Basin Foothill and Canyon Dry Grassland
2971.1	Temperate Pacific Freshwater Emergent Marsh
1984.1	North American Arid West Emergent Marsh
1925.7	California Mesic Chaparral
1670	Temperate Pacific Tidal Salt and Brackish Marsh
1650.9	Recently burned shrubland
1566.7	Northern Rocky Mountain Lower Montane, Foothill and Valley Grassland
1425	Western Great Plains Sandhill Steppe
1422	Southern California Coast Ranges Cliff and Canyon
1409.7	Introduced Upland Vegetation - Perennial Grassland and Forbland
1210.1	Madrean Juniper Savanna
1103.8	Mediterranean California Northern Coastal Dune
975.6	Disturbed/Successional - Shrub Regeneration
939.1	Harvested Forest - Northwestern Conifer Regeneration
900.6	Harvested Forest-Shrub Regeneration
871.3	Harvested Forest - Grass/Forb Regeneration

849.4	Chihuahuan Mixed Desert and Thorn Scrub
847.2	Disturbed/Successional - Grass/Forb Regeneration
771.6	Rocky Mountain Lower Montane Riparian Woodland and Shrubland
565.4	Great Basin Foothill and Low Montane Riparian Woodland and Shrubland
548.6	Chihuahuan Succulent Desert Scrub
487.5	California Maritime Chaparral
480.3	Mediterranean California Southern Coastal Dune
426.8	Colorado Plateau Pinyon-Juniper Woodland
421.2	Western Great Plains Mesquite Woodland and Shrubland
387.1	N. Am. Warm Desert Lower Montane Riparian Woodland and Shrubland
359	Sierra Nevada Cliff and Canyon
332	North American Warm Desert Riparian Mesquite Bosque
287.1	California Central Valley Riparian Woodland and Shrubland
276.1	Rocky Mountain Lower Montane-Foothill Shrubland
243.9	North Pacific Maritime Coastal Sand Dune and Strand
232.5	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland
216.5	California Northern Coastal Grassland
215.4	Recently burned forest
214.5	Western Great Plains Sand Prairie
172.1	Rocky Mountain Cliff, Canyon and Massive Bedrock
165.2	Southwestern Great Plains Canyon
159.2	Introduced Riparian and Wetland Vegetation
134.6	Western Great Plains Cliff and Outcrop
132.4	North Pacific Herbaceous Bald and Bluff
130.7	Recently burned grassland

References for supplemental material

Faber-Langendoen, D., T. Keeler-Wolf, D. Meidinger, C. Josse, A. Weakley, D. Tart, G. Navarro, B. Hoagland, S. Ponomarenko, G. Fults, and E. Helmer. 2016. Classification and description of world formation types. Page RMRS-GTR-346. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

CHAPTER 3

DISTURBANCE EFFECTS ON DRYLAND PRODUCTIVITY MODULATED BY SHORT AND LONG TERM PRECIPITATION

Abstract

Human demands on arid and semiarid ecosystems, which comprise one-third of Earth's terrestrial environment, create an urgent need to understand how precipitation and disturbance affect their productivity. Precipitation is an important driver of productivity in these dryland ecosystems, but anthropogenic disturbances can interact with precipitation amount to disrupt or redistribute productivity within dryland plant functional groups. Using a manipulative field experiment in three dryland ecosystems, I explored how dryland ecosystem structure and function responded to changes in precipitation and simulated anthropogenic physical disturbance. As expected, I found that precipitation amount positively affected productivity, but the strength of this relationship was greatly influenced by site. Disturbance negatively affected total aboveground productivity, but the effect of disturbance had both positive and negative relationships within plant functional types. I found a significant interaction between disturbance and precipitation amount within and across dryland ecosystem type. These results suggest that reduced precipitation following a disturbance can create synergistic reductions in aboveground net primary productivity. Because physical disturbances are so widespread in North American drylands from energy extraction, development, and recreational uses, these findings have relevance for addressing modern management challenges of dryland ecosystem structure and functioning in a changing climate.

Introduction

Understanding the responses of water-limited ecosystems to human actions and climate change is one of the most pressing challenges in ecology, with implications to human livelihoods, the global carbon cycle, and regional- and site-scale land management. Drylands are home to 1 in every 3 humans on the planet and are rapidly changing, owing to overlapping ecosystem stressors (Reynolds et al. 2007). Understanding how these ecosystems respond to global change is essential to preserve ecosystem services and protect human livelihoods (Kareiva et al. 2007, Turner 2010, Maestre et al. 2021). Aboveground plant productivity (ANPP) is a key integrative response variable that captures ecosystem processes in these water-limited ecosystems (Noy-Meir 1973, Lauenroth 1979). Any predicted changes in climate that may affect ecosystem water balance are expected to have significant impacts on ANPP and ecosystem processes in drylands, and these climate-driven impacts on ecosystems have the potential to be amplified by interactions with other global change drivers (Lian et al. 2021).

Changes in precipitation can occur over short- and long-timescales and cause changes in dryland ecosystems by different mechanisms across each timescale (Huxman et al. 2004b). Here I define short-time scales as the interannual and interdecadal patterns of precipitation observed within sites, and long-time scales as those occurring across multiple centuries or longer. In practical terms, short-time scales are most easily understood and observed as variability within sites and long-time scales are most easily understood and observed as variability across sites and climate gradients.

On short-time scales, water stress in ecosystems reduces carbon uptake via stomatal limitation, reduces germination and recruitment of new plants, and decreases the rate of major nutrient cycles (Noy-Meir 1973, Lauenroth 1979, Lian et al. 2021). At long-timescales, there is a very strong spatial relationship between mean annual precipitation and ANPP because precipitation tends to vary across space (Sala et al. 1988, Sala et al. 2012). This spatial precipitation pattern (hereafter long-term) means that differences in mean annual precipitation create large differences in ecosystem productivity across sites as ecosystem structure and function respond to the precipitation regime at that site. Biogeochemical responses include maximum potential carbon gain, water fluxes, and the spatial heterogeneity of soil water and nutrients (Huxman et al. 2004, Schlesinger et al. 1990, Reynolds et al. 1999). Given that dryland ecosystems are sensitive to changes in ecosystem water balance, any change in precipitation has the potential to influence ecosystem processes. Specifically, changes in both short- and long-term precipitation can force changes in ecosystem structure and function.

Ecological disturbances influence key ecosystem processes, and human actions are increasing the extent and intensity of disturbances across biomes (White and Jentsch 2001, Kareiva et al. 2007). The long-accepted definition of a disturbance remains useful for understanding these dynamic processes: a discrete event that disrupts ecosystem structure, changes resources, substrate, or physical environment (Pickett and White 1985, White and Jentsch 2001). Variation in disturbance events and outcomes creates a challenge for developing robust ecological theory of disturbances (White and Jentsch 2001, Jentsch and White 2019). Additionally, climate-driven increases in water deficits create additional challenges to existing disturbance frameworks: ongoing climate change consequences include decreases in plant establishment and increases in plant mortality as conditions get drier, dynamics perhaps not fully accounted for in our existing understanding of disturbances (Schwalm et al. 2017).

Disturbances affect ecosystems through mechanisms that influence resource dynamics and competitive interactions. Disturbances affect ecosystem structure in drylands, primarily driven by long-term precipitation through ecosystem structure prior to a disturbance and short-term precipitation through resource dynamics following a disturbance (Jentsch and White 2019). Disturbance effects are further driven by disturbance type and intensity, and environmental conditions leading into and following a disturbance (Turner 2010, Burton et al. 2020). Theory predicts that the degree to which a disturbance affects resource dynamics is tightly linked to the magnitude of resource flow, meaning that in drylands, disturbance effects on resource dynamics can be modulated by both long- and short-term precipitation (Jentsch and White 2019). Empirical data suggest that the ecosystem-level outcomes of disturbance are indeed driven by both long- and short-term precipitation, with long term precipitation modulating ecosystem resistance, or an ecosystem's ability to withstand drivers, and short-term precipitation modulating ecosystem resilience, or an ecosystem's ability to return to a starting point after disruptions (Milchunas et al. 2000, Hannusch et al. 2020, Geppert et al. 2021).

The objectives of this study were to investigate a) the interactions of disturbance and precipitation along a long-term aridity gradient and b) evaluate the mechanisms behind the interactive effects of short- and long-term precipitation and disturbance. Three hypotheses guided this work **H1)** There is a positive relationship between short-term precipitation and ANPP. The slope of this relationship decreases with increasing long-term precipitation. **H2)** Physical disturbance reduces ANPP and its effect decreases as within-site precipitation increases. Similarly, disturbance effects decrease as long-term precipitation increases among sites. **H3)** The disturbance effect on ANPP is greater at low mean annual precipitation (MAP) sites than high MAP sites because disturbance reduces soil water availability at low MAP sites and increases soil water availability at high MAP sites.

To answer these questions and test these hypotheses, I deployed rainout shelters, experimental disturbance, and rainout shelters + experimental disturbance in three dryland ecosystems in North America. The ecological breadth of the three sites confers generality to the results of these experiments. I assessed ANPP as a main response variable and measured soil water at different soil depths to unravel mechanisms.

Theory and empirical data support each of these three hypotheses. The spatial and temporal relationships of ANPP to precipitation in drylands are well established (Huxman et al. 2004b, Sala et al. 2012). Short-term reductions in precipitation almost always cause reductions in ANPP through reductions in available resources within sites. Long-term differences in precipitation have over time strongly influenced community structure and ecosystem processes in a manner that will modulate responses to experimental treatments across sites. Disturbance effects on ANPP in drylands have mostly been explored for fire (Glenn and Collins 1992, Johnson and Matchett 2001, DeFalco et al. 2010) or grazing (Milchunas et al. 1990, Bestelmeyer et al. 2013), and the effects of other disturbances have been less thoroughly investigated (but see Davidson and Fox 1974, Belnap and Warren 2002, Inouye 2006). However, there is support that disturbance effects will be greatest at drier sites and will attenuate as long-term precipitation increases (Jentsch and White 2019). Finally, the interaction of disturbance and soil water dynamics and subsequent effects on ANPP in drylands has only had limited investigation.

Methods

I selected sites in three unique dryland ecosystems for this study: the Mojave Desert, the Chihuahuan Desert, and the Great Basin Desert (Table 3.1, Figure S3.1.3). Each ecosystem is an arid (Mojave and Chihuahuan) or semi-arid shrubland (Great Basin), with different seasonality of precipitation at each site (Figures S3.1.2-3.1.6). Each site experiences seasonal dry periods when the evaporative demand of the atmosphere exceeds precipitation (Figures S3.1.2-3.1.6). I selected sites and applied experimental treatments in the summer of 2019 and maintained the experiment for three additional growing seasons, concluding the experiment in 2022. For the duration of the experiment, sites were protected from livestock grazing while native herbivores were not excluded.

In each of the three sites, I delimited 40 2.5 x 5 m plots and randomly assigned the four experimental treatments (disturbed and undisturbed in ambient and reduced rainfall). I replicated treatments 10 times each across these 2.5 x 5 m plots to yield 40 plots in total. I selected the plot size to capture the ecological dynamics of the dominant shrub species in this study as well as the interspace immediately surrounding the shrubs.

I used a passive rainfall-manipulation technique to reduce ambient precipitation in this study. Specifically, rainout shelters were constructed around plots and slats were placed to intercept incoming precipitation and move it off the plot (Figure S3.1.1). All infrastructure was at least 30 cm above the plant canopies. The slats were V-shaped acrylic and allowed the transmission of photosynthetically active radiation while intercepting precipitation. There were 14 slats on each of plot half for Mojave, 10 for Great Basin, and 16 for Chihuahuan sites. I evenly spaced the acrylic slats across the 2.5 m width of the plot for each of these precipitation reduction levels. The plots were not trenched due to the high level of disturbance and data interpretation complications trenching can cause (Ngao et al. 2007, Beier et al. 2012). The rainout shelters were constructed at each site in 2019 on relatively flat areas with vegetation representative of the site. Since dryland vegetation is heterogeneous in space, I centered the plots on individual shrubs so that vegetation was similar across all plots prior to treatment. I selected shrubs that were typical of each site in size, number of stems, and canopy vigor. These shelters were maintained until the end of the growing season in 2022, thus allowing for the manipulations to occur for three growing seasons.

I determined the degree of rainfall exclusion and simulated first-percentile precipitation based on long-term historical precipitation extremes unique to each site. This first-percentile approach considers the variability of annual precipitation over time within a site to determine the lowest annual rainfall amount received at a site over the previous 100 years (Lemoine et al. 2016). After identifying the driest of the last 100 years, I calculated the percentage difference between the driest of the last 100 years and mean annual precipitation within a site. This percentage difference provided the percentage rainfall reduction amount that I would design to be intercepted with the passive rainfall exclusion shelters. I scaled precipitation reductions to achieve a 1-in-100 year low rainfall year when precipitation was average for a site. Thus, the precipitation reduction treatments relative to the control resulted in a 40% reduction in ambient precipitation at the Great Basin site, 60% at the Mojave site, and 70% at the Chihuahuan site (Table 3.1). Climate history prior to the experiment, seasonality of precipitation, and summary climate diagrams are provided in the supplemental material (Figures S.3.1.2-S3.1.5).

To understand how the experimental treatments affected available soil moisture across sites and sampling years, I used soil moisture data from my sensor array within each site across the duration of my field experiment. Specifically, I compared mean volumetric water content (VWC) in disturbed and undisturbed conditions within each site and within ambient and experimentally reduced precipitation regimes. I calculated the mean percent change in VWC resulting from disturbance in each of my six unique site-precipitation regime combinations and compared them within sites and across mean annual precipitation.

Table 3.1. Site characteristics for the Nevada National Security Site, NV, Orchard Combat Training Center, ID, and Jornada Basin LTER, NM. Precipitation seasonality represents the amount of precipitation that occurs during warm vs cold seasons and is calculated by taking the correlation coefficient of monthly temperature and precipitation. The aridity index is a metric of dryness and is calculated as the ratio of mean annual precipitation to evapotranspiration. Rainfall reduction is the amount of ambient precipitation reduced by rainfall exclusion shelters at each site.

	Mojave Desert	**Chihuahuan Desert**	**Great Basin Desert**
Climate type	Arid	Arid	Semiarid
Latitude	36°49'N	32°33′ N	43°15'N
Longitude	116°01'W	106°49′ W	116°13'W
Mean annual precipitation (mm/year)	147	245	271
Precipitation seasonality (correlation coefficient of monthly temperature and precipitation)	-0.12	0.64	-0.87
Mean annual temperature (degrees C)	6.4	14.7	6.6

Aridity Index (mean annual precipitation/potential evapotranspiration)	0.08	0.16	0.18
Rainfall reduction (relative to ambient)	-60%	-70%	-40%
Soil texture class	Sandy loam	Fine sandy loam	Silt loam
USDA soil type	Ultisol	Aridisol	Aridisol
Soil Unit	Corbilt gravelly fine sandy loam, warm	Simona-Harrisburg association	Chilcott-Catchell-Chardoton complex

I created a physical disturbance to plant communities and the soil surface. I used a novel technique to apply a one-time physical disturbance to the experimental plots. Using a 4-wheel drive all-terrain vehicle, I pulled a JRCO model MSAT 48” (122 cm) tow-behind spiked drum aerator (Figure S3.1.6). This steel implement had 102 spikes (7 cm long x 5 cm wide at the base) welded to the outside of the drum and weighed 165kg when filled with water. I estimate the all-terrain vehicle and operator to weigh 340kg. Each plot receiving this treatment underwent exactly four overlapping passes from this implement in alternating directions. I also subjected a 1-meter buffer around the plot to this same treatment to minimize edge effects within the plots.

I observed that the disturbance method I used caused crushing and compaction of aboveground plant material and the soil surface. Unlike a grazing disturbance, the disturbance did not remove any aboveground biomass and left all plant material in place following the event. The repeated passes of the machinery and the weight and destructive capability of the spiked drum aerator caused the key mechanisms of disturbance relevant to the research questions in a manner that should apply beyond the specific experimental context. While this disturbance method was novel in these ecosystems and not a perfect mimic of a real-world disturbance, the destructive outcome is likely similar to other actions that cause disturbance to intact native vegetation and surface soil layers, such as operating tracked vehicles off of established roads.

I evaluated treatment effects each year for four years- once to collect pre-treatment data in 2019 when I deployed the experiment, and then each year at the peak of each site's growing season in 2020, 2021, and 2022. To avoid harvesting biomass out of plots in the multiyear experiment, I estimated aboveground net primary production (ANPP) using a non-destructive method, converting plant-species cover and shrub volume to estimates of ANPP (Flombaum and Sala 2007). To estimate plant cover, I measured three 5 m permanent cover lines per plot, recording all living plant parts (basal or canopy) at 1 cm increments along each of the three permanent cover lines in every plot. I did not record plant cover data for the first 20 cm and the final 20 cm of each cover line to avoid capturing edge effects. I recorded all species cover at this 1 cm resolution, even when living plant parts of multiple species overlapped. I only recorded nonliving cover class elements (bare ground, litter, dead plants) when there was no living plant biomass at that position along the transect. In other words, I did not record nonliving cover class elements underneath living plant biomass. To measure shrub volumes, I measured two perpendicular diameters and height. I then estimated ANPP using allometric equations for each plant functional type developed on site for two of the three sites. Overall, the allometric equations for functional types in Mojave and Great Basin sites had poor predictive capacity (Figures S3.3.4-S3.3.10), and I provide plant-cover data by functional type to support these analyses focused on aboveground productivity as the primary response variable (Figure S3.2.3). I used previously published allometric equations for the Chihuahuan site (Gherardi and Sala 2015), where allometric equations had already been developed for the species that occurred in those plots.

I deployed soil moisture and temperature sensors at 0.5, 0-30, and 50 cm depths. To measure soil moisture at 0.5 cm depth, I deployed custom-manufactured soil moisture and temperature sensors. For the 0-30 and 50 cm-depths, Campbell Scientific CS650 probes recorded volumetric soil moisture content and soil temperature every 30 minutes in four replicates of each treatment and the data were logged onto CR300 or CR1000 data loggers. The 0-30 cm CS650 probes were installed vertically at the soil surface, pointing down into the soil profile. The majority of probes that I installed had 30 cm prongs that integrate soil moisture measurement along the entire 30 cm length. A portion of probes that I installed only had 15 cm prongs, but I display the data from both 30 cm length probes and 15 cm length probes as representing 0-30 cm of the soil profile for simplicity. The 50 cm CS650 probes were installed with great care to capture soil water dynamics at that depth in the soil profile while minimally disturbing the surface soil structure or vegetation within plots. I accomplished this by carefully boring a 10 cm diameter shaft into the soil profile at a 45 degree angle until reaching a 50 cm depth. I then installed the CS650 probe at a 50 cm depth in the soil profile, using the soil I excavated in the installation process to bury the probe.

Importantly, the construction of the CS650 probe is such that soil moisture is measured along the entire length of the prongs on the sensor, while temperature is measured with a thermocouple embedded in the body of the sensor. Thus, I did not measure soil temperature at any positions in the soil profile other than 0 cm and 50 cm, as the sensors installed to measure 0-30 cm in depth still had the body of the sensor (and thus the thermocouple) above the surface of the soil profile.

Analysis

I conducted all analyses in R v.4.3.2 (R Core Development Team 2017). To test for the effects of precipitation and disturbance on aboveground net primary productivity I modelled ANPP responses to precipitation within and across sites. Disturbance was considered a binary variable in all models. To test for the interaction of precipitation and disturbance in the response variables across all years of experimental data (Hypothesis 2), I tested the slope of the productivity–precipitation relationships in both disturbed and undisturbed conditions within and across sites. I fit a linear mixed-effects model using the “lmer” function in the nlme package in R and included site as a random effect in the global model, with disturbance and precipitation included as fixed effects (Zuur et al. 2009, Bates et al. 2015). To test for differences between individual shrub volume, height, and horizontal extent, I used t-tests within each site to compare mean shrub canopy measurements across disturbed and undisturbed plots. For simplicity, I did not account for repeat measures on the same individual shrubs, as that information is contained within the mixed models of ANPP. Rather, I used pooled t-tests to make a general conclusion about the effects of disturbance on shrub architecture over time.

I used three additional statistical methods to look for interactions between the two drivers in this experiment beyond the slopes of the ANPP–precipitation relationships. Specifically, I used Johnson-Neyman tests, estimated marginal means, and Hedge’s G as each one of these approaches offered a different perspective to understand interactions. There are additional statistical approaches that can be used to test for interactions beyond these three, and I decided to use these particular approaches to test for interactions because they best fit my data and research questions.

I used Johnson-Neyman tests to identify the range in short-term precipitation over which effects of disturbance on ANPP are not significantly different from controls (Huitema 2011). These analyses allow a deeper look at the ANPP–precipitation relationships I observed, revealing the short-term precipiation amounts at which there is a significant interaction between precipitation amount and disturbance effects on productivity. Johnson-Neyman plots are useful of when a grouping variable (disturbance) and continuous variable (precipitation) interact in a linear regression model. This approach creates a Johnson-Neyman interval, which can identify the range of values of the moderator in which the slope of the predictor is significant vs. nonsignificant at a specified alpha level. In essesence, using this approach for this dataset was useful to understand if disturbance had a significant effect on ANPP at all short-term precipitation values or if it was only significant for a portion, in this case when short-term precipitation was experimentally reduced by the treatments.

To further explore the interaction between short-term precipitation amount and disturbance effects on productivity, I used Tukey's comparison of estimated marginal means across all precipitation levels and sample years (Kenward and Roger 1997). Estimated marginal means is an approach that statistically models means, rather than describing them from the data, meaning that the means are extracted from the models themselves. Estimated marginal means are means for groups that are adjusted for means of other factors in the model. In essence, marginal effects use model prediction as a tool for model interpretation. I used estimated marginal means to understand if interactions were present in the modeled relationships between ANPP and precipitation when disturbance had occurred and in undisturbed conditions.

To explore the magnitude of interaction and understand if synergism or antagonism occurred in the responses, I calculated effect sizes using Hedge’s G. Comparing the effect size on the response variables in analysis (here ANPP) allows insight into the effects of both individual drivers and when they co-occurred. The effect sizes of experimental treatments within sites allows for explicit testing of synergism between disturbance and short term precipitation manipulations. By examining the size and direction of effects from individual drivers, I could assess whether the combined effect of both drivers is simply the sum or product of individual drivers, or alternatively, if the effect size is made larger by synergism between the two drivers. This calculation of effect sizes creates a useful definition of ecological synergism that is scaled to site-level data: a synergism occurs when the effect of co-occurring drivers is larger than the than the sum or product of effects created by individual drivers (Folt et al. 1999).

To determine the degree of antagonism or synergism between short-term precipitation amount and disturbance across the sites, I used Hedge’s G to determine effect size and constructed the dominance, additive, and multiplicative null hypotheses to test with each site’s data (Folt et al. 1999). Hedges’ G is an estimate of the standardized mean difference of treatment from control and is not biased by small sample size and can be considered a treatment effect in the context of this study. A p-value reports the likelihood that a sample would have produced an observed effect or one more extreme if the null hypothesis was true. Effect size is a way researchers can communicate the magnitude of the effect in a straightforward way and set aside the probability. For this study, the mean difference represented by Hedge’s D is a useful index because the measure (ANPP) is meaningful through its widespread use in ecological research.

To understand how disturbance might affect how efficient ecosystems are at converting precipitation into biomass, I calculated precipitation use efficiency (PUE) for disturbed and undisturbed conditions within each site. PUE is simply the ratio between ANPP and precipitation over a set time period, here calculated as ANPP/short-term (annual) precipitation. PUE is a useful way to estimate ecosystem performance in the presence of disturbance. If an ecosystem is performing at an efficient rate, represented by high PUE, that indicates that the plant community is maximally converting precipitation into aboveground biomass. If an ecosystem is performing less optimally, it would have a lower PUE, meaning that for the same level of precipitation, the lower-performing ecosystem would produce less ANPP than a higher-performing ecosystem. To calculate PUE, I divided total aboveground net primary productivity by the amount of precipitation received in a given sample year, accounting for the reductions in precipitation caused by the rainout shelters in the precipitation reduction treatments.

Results

Ambient precipitation patterns and precipitation reduction treatments

I carried out this experiment during a two-year severe regional drought at the Mojave site, during above-average precipitation years at the Great Basin site, and during average precipitation years in the Chihuahuan site (Figure 3.1).

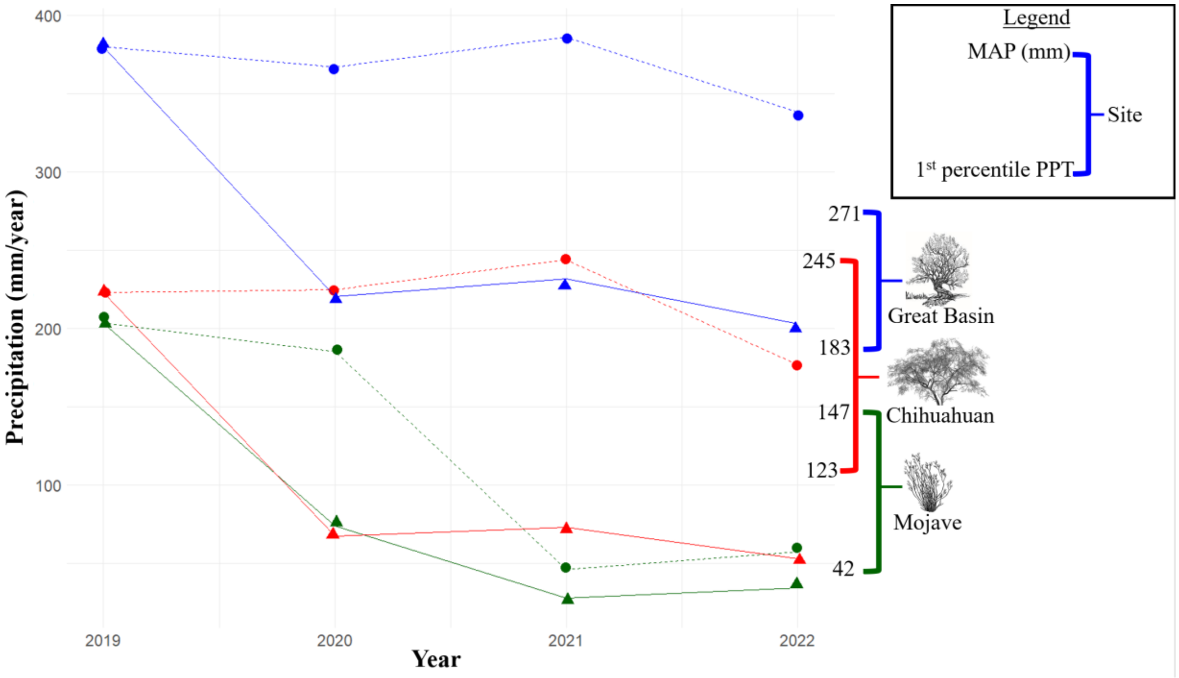

Figure 3.1. Ambient and reduced precipitation during field experiment for the three sites: Mojave (green points and lines), Great Basin (blue points and lines), and Chihuahuan (red points and lines). Circles display ambient precipitation at each site over the experiment, while triangles display reduced precipitation in experimental treatments with rainfall exclusion shelters. On the right margin of the figure, brackets indicate the mean annual precipitation at each site and the 1st percentile in precipitation over a 100-year period for each site. The upper bracket and value for each site displays mean annual precipitation in millimeters, while the lower bracket and value displays the 1st percentile precipitation amount in millimeters.

Soil moisture was dynamically affected by disturbance across the precipitation values within each site (Figure 3.2). Within and across sites, soil moisture was less available in disturbed conditions at lower precipitation values and more available in disturbed conditions as precipitation increased.

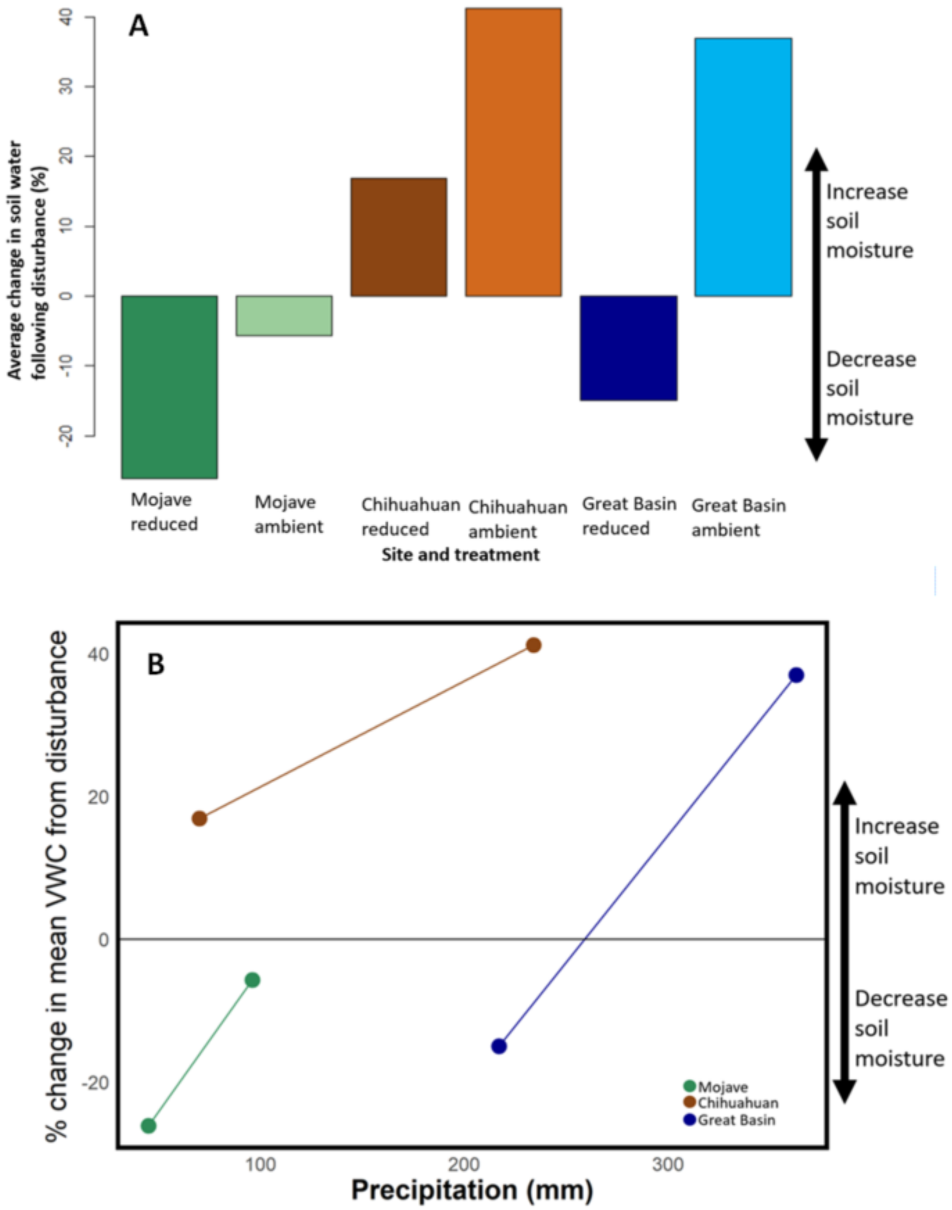

Figure 3.2. Percent change in mean volumetric water content (VWC) resulting from disturbance across mean ambient and mean experimentally reduced precipitation values across treatment years within sites by treatment within sites (A) and across an annual precipitation gradient (B). Each value represents the comparison between disturbed and undisturbed conditions within a site at each precipitation value (((VWC_undisturbed-WVC_disturbed)/(WVC_undisturbed))*100), averaging across three years of post-treatment data to generate one ambient precipitation change value and one experimentally reduced precipitation change value per site. Mojave (green bars, points, and lines), Great Basin (blue bars, points, and lines), and Chihuahuan (brown bars, points, and lines). Data are from soil moisture sensors in the upper soil layers (0-30 cm) and were measured year-round.

Individual effects of precipitation and disturbance

Productivity increased with increasing precipitation in the Mojave and Chihuahuan sites but had no relationship with precipitation at the Great Basin site (within-site variation in precipitation was the result of both interannual variability and precipitation manipulation treatments; Figure 3.1). There were both positive and negative relationships between productivity and precipitation within plant functional types in undisturbed plots. Grass and forb productivity were positively related to precipitation at the Mojave and Chihuahuan sites but had no relationship to precipitation at the Great Basin site. The correlation of undisturbed shrub productivity with precipitation was positive at the Mojave site, negative at the Chihuahuan site, and non-significant at the Great Basin site (Figure 3.3, tables S3.2.2-S3.2.12).

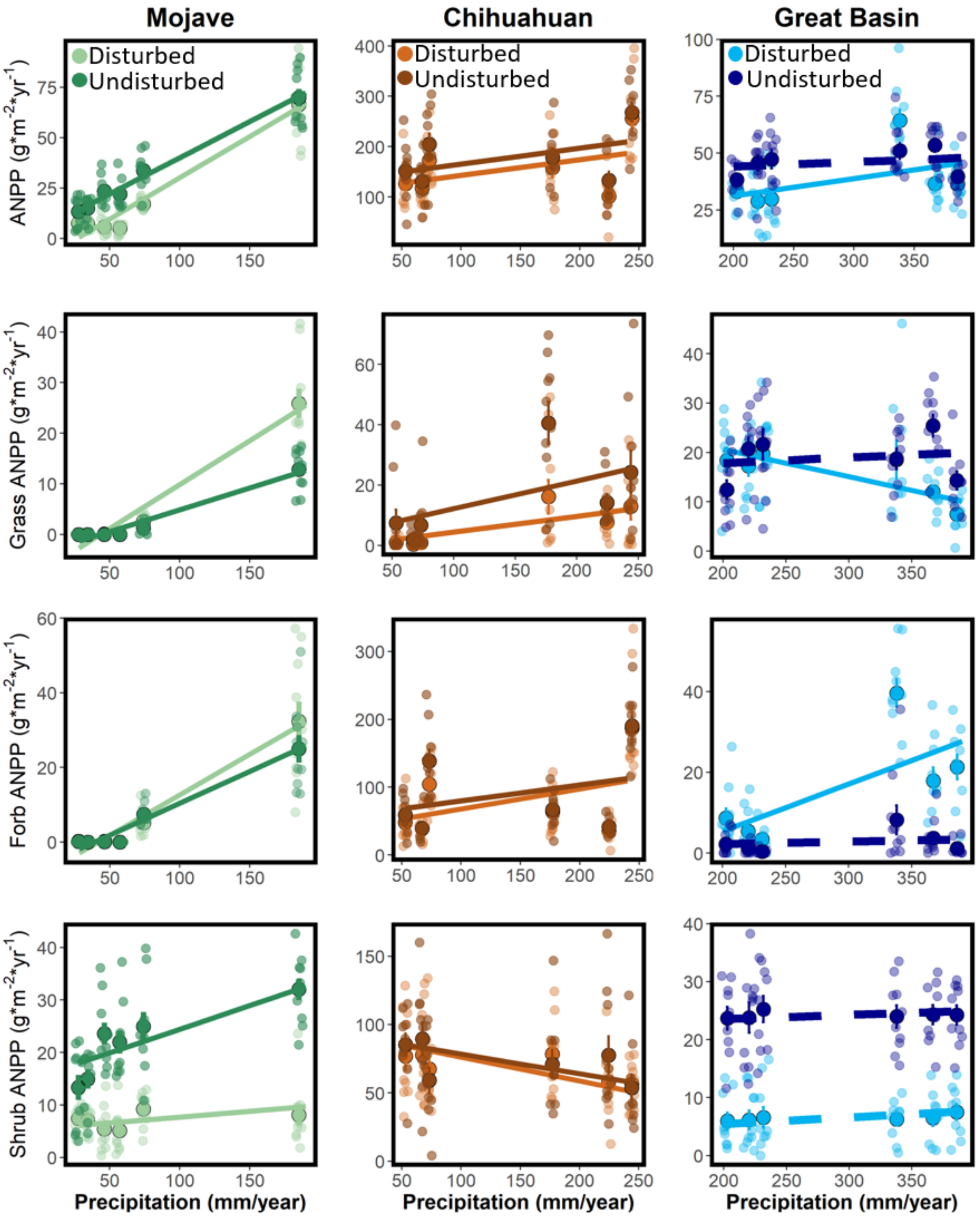

Figure 3.3. Productivity responses to annual precipitation in disturbed and undisturbed conditions across three dryland ecosystems. Dark colors represent control conditions, and light colors represent disturbed conditions. Aboveground net primary productivity (ANPP- top panel) includes the sum productivity of the entire plant community, grass, shrub, and forb productivity include the sum of all species within those functional types. Within-year means are plotted as large circles along with error bars displaying +/- one standard error and plot-level data points are plotted as smaller circles.

Interpreting the slope of the ANPP–precipitation models as site-level sensitivity of ANPP to precipitation, I explored how this sensitivity varied across long term precipitation values in both disturbed and undisturbed conditions. Within sites, I found that total and functional type ANPP was broadly most sensitive to precipitation at low MAP values (Figure 3.3, Figure S3.2.1). There were only two exceptions to this pattern-forb ANPP was most sensitive at the Chihuahuan site and shrub ANPP at that site was the least sensitive to precipitation (Figure S3.2.1). Given that the sample size of long-term precipitation values was only three sites, I was constrained in my ability to quantitatively test for differences across the MAP gradient that I sampled.

Disturbance alone decreased total ANPP across sites and years, while disturbance effects on functional type productivity were both positive and negative within sites. The largest disturbance-cased reduction within a functional type was in shrub productivity in the Mojave and Great Basin sites (Figure 3.3). Disturbance reduced shrub volume, height, and horizontal extent of canopy coverage in the Mojave and Great Basin sites, but shrubs in the Chihuahuan site were unaffected (Figure 3.4). Disturbance increased productivity within grass and forb functional groups at the Mojave site and in the forb functional group at the Great Basin site. Notably, the largest increases in productivity from disturbance were primarily driven by non-native annual grass and forb species (Figure S3.2.2)

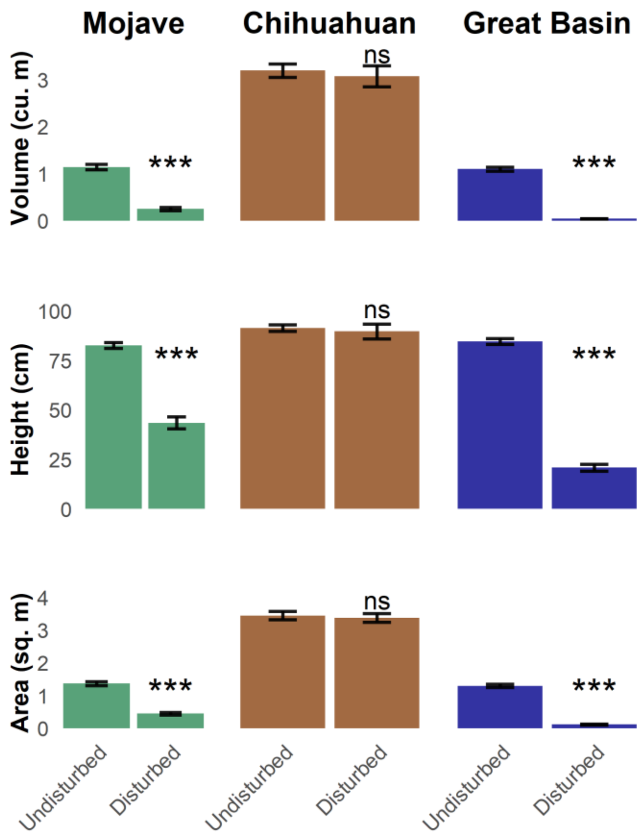

Figure 3.4. Shrub canopy responses to physical disturbance in three dryland ecosystems. Significant differences are indicated by asterisks. Shrub volumes were measured with one height measurement and two perpendicular canopy breadth measurements; shrub area is the product of the canopy breadth measurements. Data include all repeated measurements of shrub canopies during experimental treatment years (2020-2022).

Combined effects of precipitation and disturbance

Through complimentary analytical methods, I found evidence for synergistic reductions in ANPP from the interaction of reduced precipitation and physical disturbance at each site. Across sites, disturbance changed the relationship between total productivity and short term precipitation (Figure 3.3). Johnson-Neyman diagrams reveal that disturbance interacts with precipitation at low precipitation values at two of the three sites (Figure 3.5). Specifically, these diagrams show that total ANPP was reduced by disturbance across all sites, and this effect decreased with increasing short term precipitation within two of the three sites (Figure S3.2.1).

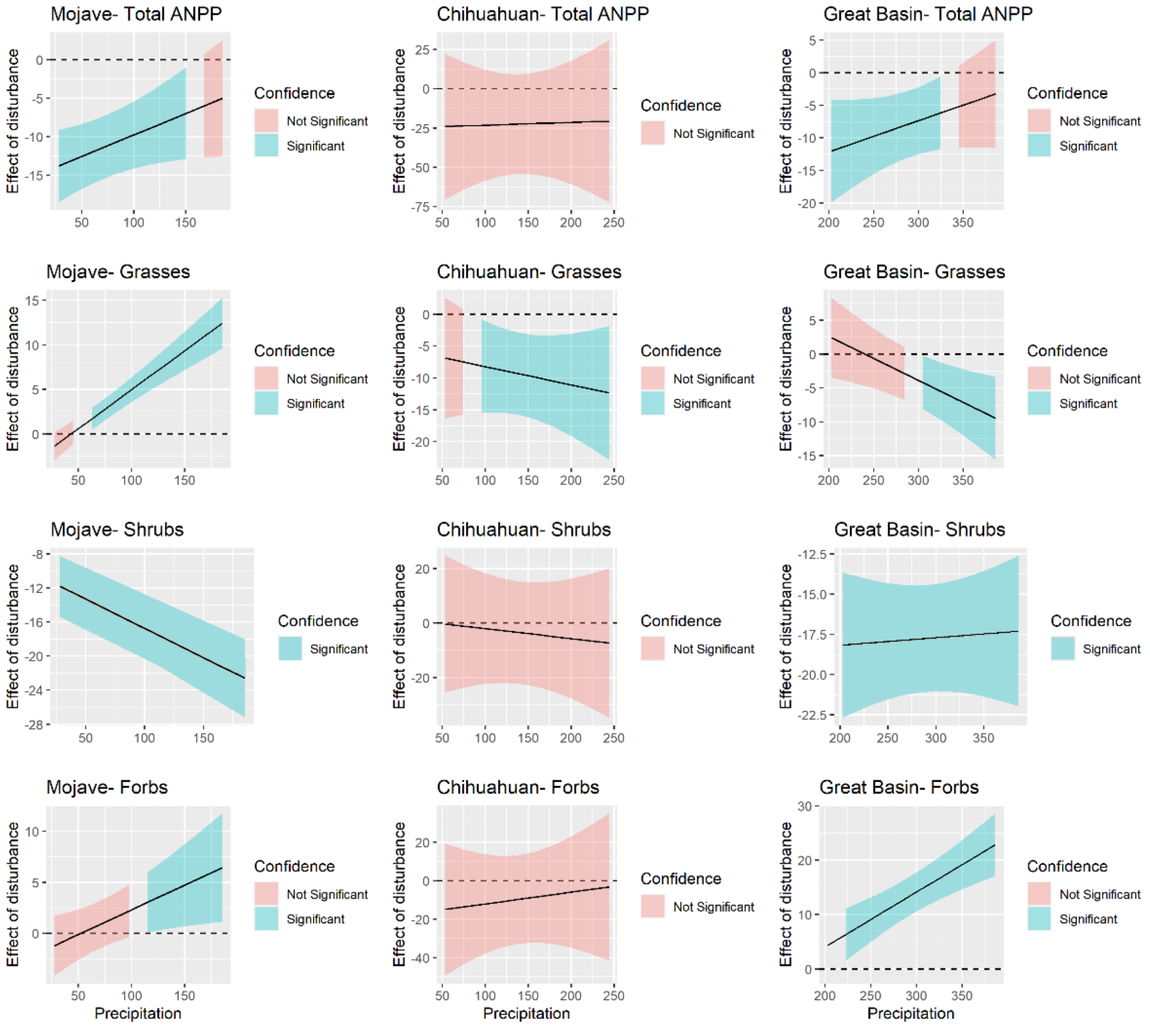

Figure 3.5. Johnson-Neyman plots showing the effect of disturbance (predictor, y-axis) on total and functional type ANPP at different annual precipitation amounts (moderator, x-axis). Values are derived from a linear mixed effect model of within-site ANPP predicted by the interaction of disturbance and annual precipitation as fixed effects along with random effects of plot. The horizontal line represents a slope of 0 (i.e., non-significant, red); values below and above the horizontal line represent negative and positive slopes, respectively; in turquoise are statistically significant slopes ($p < 0.01$).

Two sites showed that the effect of disturbance on aboveground productivity varied across annual precipitation amounts, with a clear trend of greater disturbance effects at lower annual precipitation values. One site, Chihuahuan, had no sigificant effects of disturbance across the entire range of preciption values that I observed. Across each site, I observed interactive effects of precipitation and disturbance on ANPP within at least one plant functional type, grasses. Specifically, grasses were the only functional type that consistently had some portion of the range of precipitation values that significantly interacted with disturbance. Shrubs and forbs had significant interactions between precipitation amount and disturbance at the Mojave and Great Basin sites only (Figure 3.3). The two sites where native perennial grasses were dominant, Great Basin and Chihuahuan, disturbance reduced grass ANPP more, relative to undisturbed conditions, at higher annual precipitation values over lower precipitation values (Figure 3.3). At the Mojave site, disturbance had a positive effect on grass productivity as precipitation increased (Figure 3.3). Shrubs were negatively affected (two sites) or not affected (one site) by disturbance across the sites, with no change in significance across precipitation values among all of the sites. Forbs were the only functional type where all sites had a trend in the same direction- positively increasing with precipitation (Figure 3.3); however, disturbance had variable interactions with precipitation to affect forb productivity across sites, with disturbance increasing forb production at the Mojave and Great Basin sites but decreasing forb production at the Chihuahuan site.

Estimated marginal means provide a way to test for interactions between disturbance and precipitation across short- and long-term precipitation patterns from models. Models indicated that disturbance at the Mojave site always interacted with precipitation to reduce ANPP, and disturbance at the Great Basin site only interacted with precipitation in the experimentally reduced short term precipitation (Figure 3.6). At the

Chihuahuan site, with its extremely disturbance-resistant dominant shrubs, disturbance never interacted with precipitation to affect ANPP. These results suggest that the largest synergism between short term precipitation amount and disturbance occurred at the Great Basin site, which I then tested in explicitly using Hedge's G Effect Sizes.

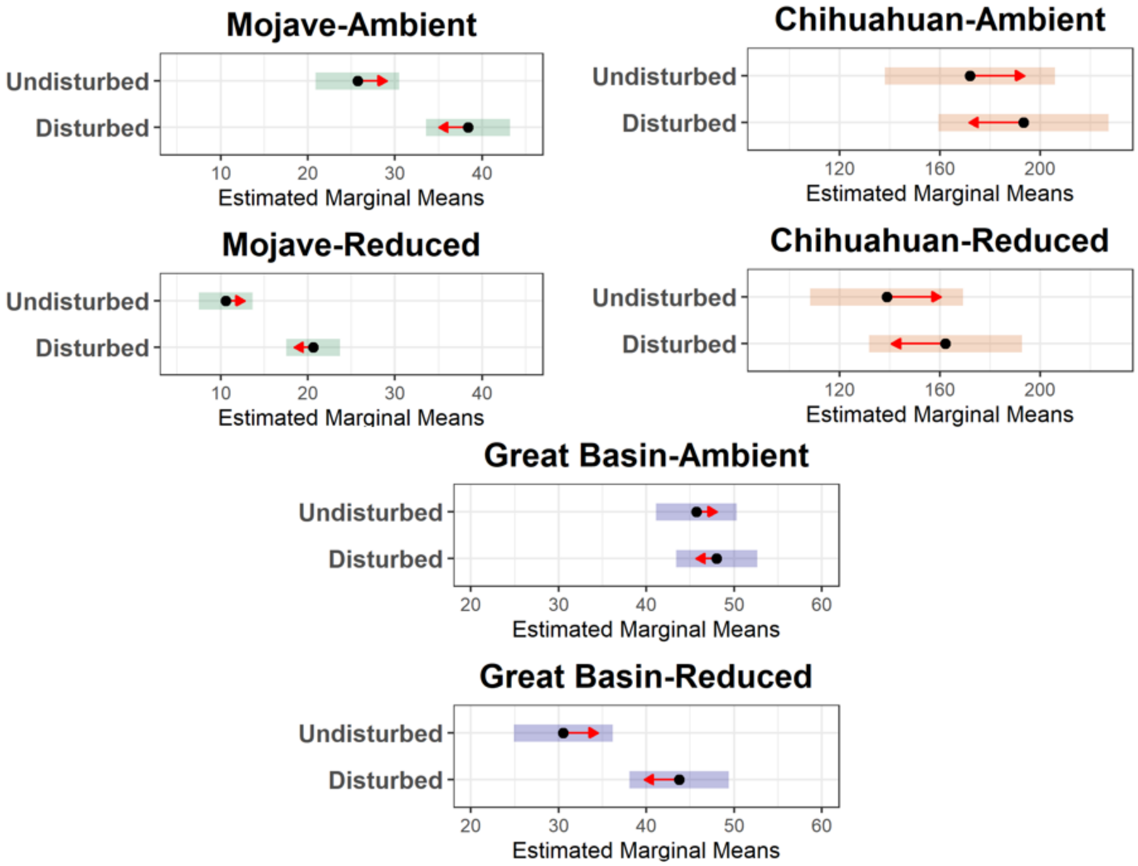

Figure 3.6. Tukey pair-wise comparisons of estimated marginal means (means extracted from linear mixed effects models of ANPP) of disturbed and undisturbed conditions across precipitation levels. Black dot = mean value; Blue bar = confidence intervals; Red arrows = comparison arrows. The degree to which red comparison arrows overlap reflects the significance ($p = 0.05$) of the comparison of the two estimates. Overlap of the red comparison arrows indicates no significant difference between precipitation and disturbance under either ambient or experimentally reduced precipitation regimes, while lack of overlap indicates there is a significant difference.

I found that in all three ecosystems included in this experiment, co-occurring reductions in precipitation and a physical disturbance interacted in a synergistic manner to reduce total ANPP (Figures 3.7-3.9). Specifically, the effect sizes of the individual drivers I tested were smaller than the effect size of co-occurring drivers. Not only was the effect size of co-occurring drivers larger than either disturbance or precipitation reductions alone (which I identify as dominance null), the effect size of co-occurring drivers was larger than individual drivers added together (additive null) or multiplied together (multiplicative null) at each site (Figures 3.7-3.9). As suggested by the estimated marginal means analysis, the largest synergism I observed was at the Great Basin site, where disturbance did not interact with precipitation amount under the ambient precipitation regime but did interact with disturbance under the experimentally reduced precipitation regime (Figures 3.6 & 3.9). I found no evidence for antagonistic interactions between disturbance and precipitation reductions affecting ANPP at any site (Figures 3.7-3.9), specifically instances where the effect size of the two experimental drivers on ANPP was greater than the two drivers combined.

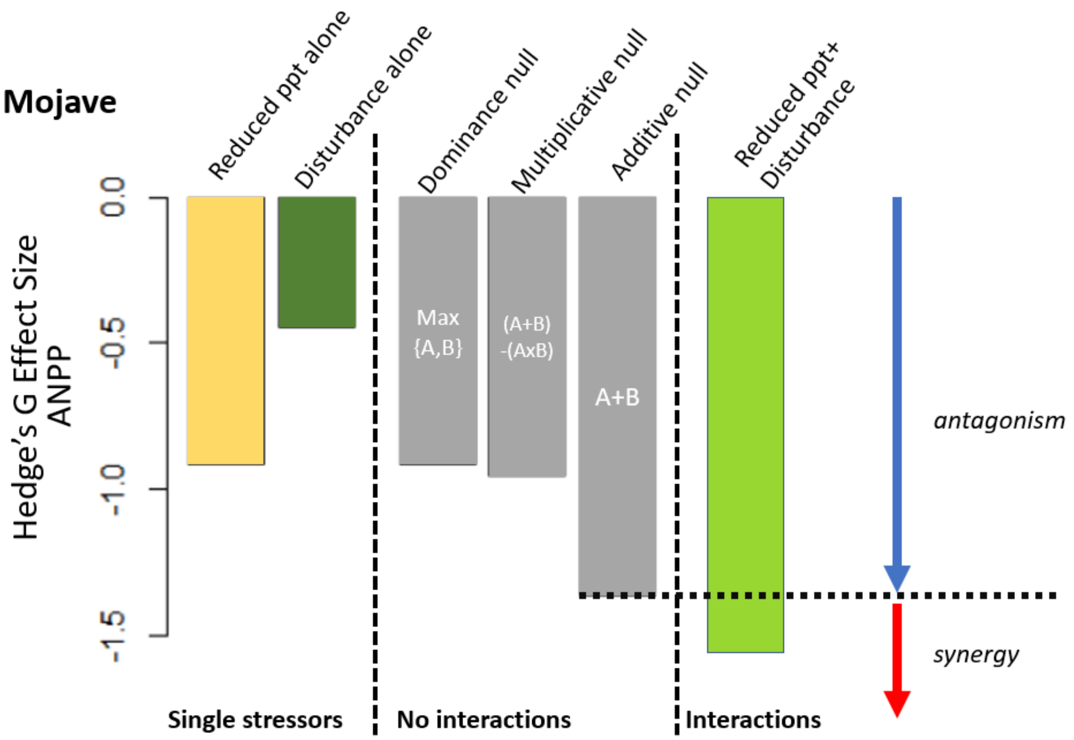

Figure 3.7. Model defining ecological synergies between multiple stressors on ANPP: precipitation reduction and disturbance–Mojave. Hedge's g reflects effect sizes relative to control conditions across all experimental years at the Mojave site. **Single stressors:** two stressors (A and B) impact a biological response in the same direction when acting separately. **No interactions:** their combined effect could simply be equal to the effect of one of the two stressor, i.e. a dominance effect, or be additive, i.e. the sum of the two stressor effects with or without a multiplicative-risk correction. **Interaction:** by combining both stressors, I observed that there was a synergistic interaction as defined by Folt et al. (1999).

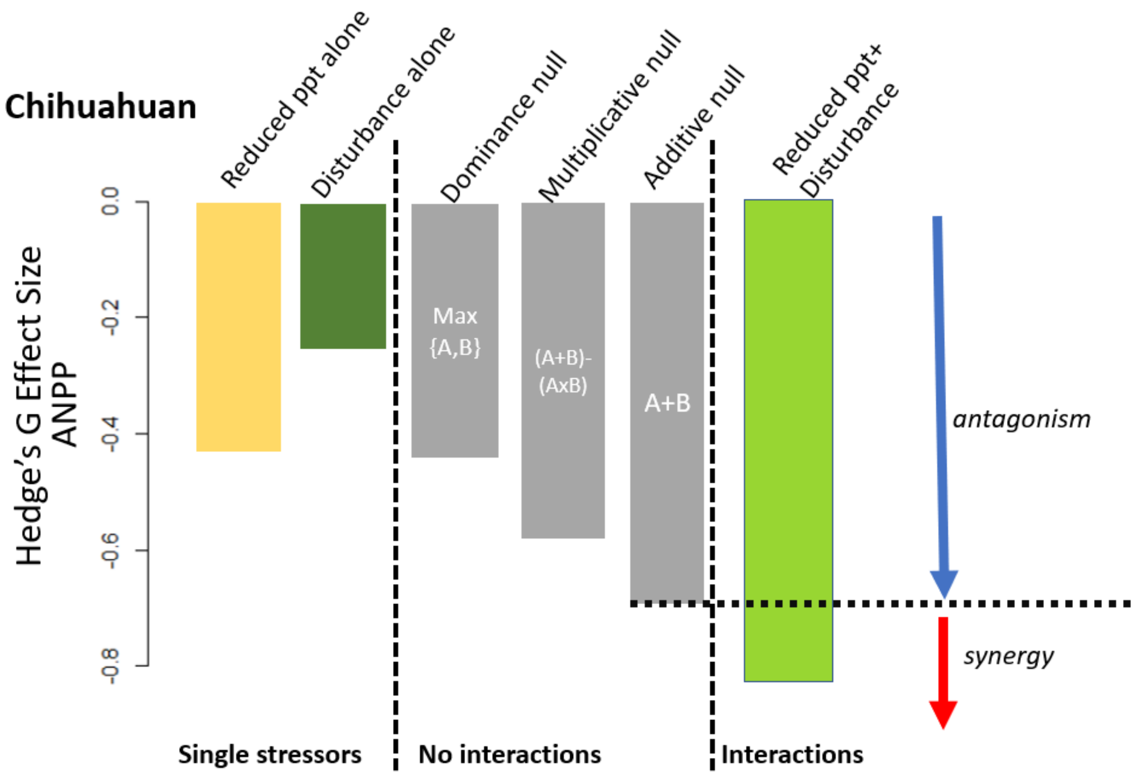

Figure 3.8. Model defining ecological synergies between multiple stressors on ANPP: precipitation reduction and disturbance–Chihuahuan. Hedge's g reflects effect sizes relative to control conditions across all experimental years at the Mojave site. **Single stressors:** two stressors (A and B) impact a biological response in the same direction when acting separately. **No interactions:** their combined effect could simply be equal to the effect of one of the two stressor, i.e. a dominance effect, or be additive, i.e. the sum of the two stressor effects with or without a multiplicative-risk correction. **Interaction:** by combining both stressors, I observed that there was a synergistic interaction as defined by Folt et al. (1999).

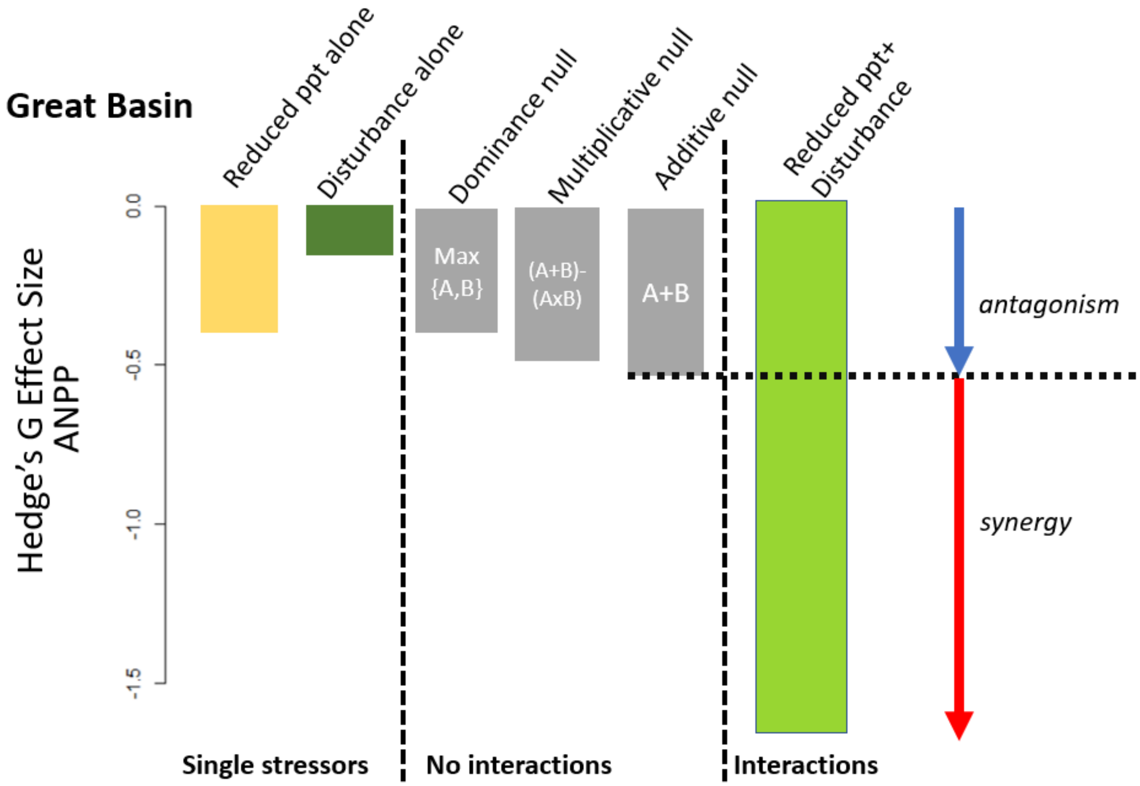

Figure 3.9. Model defining ecological synergies between multiple stressors on ANPP: precipitation reduction and disturbance–Great Basin. Hedge's g reflects effect sizes relative to control conditions across all experimental years at the Mojave site. **Single stressors:** two stressors (A and B) impact a biological response in the same direction when acting separately. **No interactions:** their combined effect could simply be equal to the effect of one of the two stressor, i.e. a dominance effect, or be additive, i.e. the sum of the two stressor effects with or without a multiplicative-risk correction. **Interaction:** by combining both stressors, I observed that there was a synergistic interaction as defined by Folt et al. (1999).

Disturbance and precipitation reductions interacted to affect resource use efficiency across precipitation amounts (Figure S3.2.4). Across all sites, resource use efficiency differed between disturbed and undisturbed conditions at low precipitation amounts, but PUE converged between disturbed and undisturbed conditions at high precipitation amounts. At the Mojave site, disturbance creates an unexpected positive relationship between PUE and precipitation, possibly because of the severe regional drought during two of the three sample years. The Chihuahuan site's PUE was increased by reduced precipitation but was less affected by disturbance than the other two sites (Figure S3.2.4).

Discussion

This study provides a unique perspective of the effects of short- and long-term precipitation and disturbance as controls of ANPP across a range of dryland ecosystems. I experimentally reduced short-term precipitation within distinct ecosystems and observed how physical disturbance interacts with precipitation reductions to modulate ANPP and soil water availability across a long-term precipitation gradient, following predicted changes in climate and land use across dryland ecosystems (Anderson and Inouye 2001, Maestre et al. 2016, Jentsch and White 2019). Here I found evidence for interactions between short- and long-term precipitation and disturbance effects on aboveground productivity and worked to unravel the potential mechanisms explaining these interactions.

Individual effects of precipitation and disturbance on productivity

These results support the first hypothesis that productivity was positively related to short-term precipitation across sites, and this relationship was strongest at the site with the least long-term precipitation (i.e., MAP), the Mojave. These findings parallel existing understanding of how precipitation patterns shape ecosystems, with less variance explained in short-term, within-site patterns and more variance explained in long-term, across-site patterns (Huxman et al. 2004b, Sala et al. 2012). Specifically, precipitation amount is a reasonable predictor of productivity in drylands, but within-sites precipitation-productivity relationship is often non-significant with productivity. For example, Huxman et al. (2004b) found compelling results across sites, but most of the within-site relationships they reported not significant. In a similar manner, I did not find a significant relationship between precipitation and ANPP at the Great Basin site in undisturbed plots. Unravelling patterns of primary productivity remains a key challenge for dryland ecologists, and these results indicate that existing conceptual models of precipitation–ANPP relationships could readily integrate with disturbance dynamics to more fully capture variability in production over space and time.

The single effects of disturbance, in the absence of any climate manipulations, offer important perspective for evaluating the interactive effects of precipitation and disturbance. Disturbance alone reduced total ANPP across all long term precipitation values I sampled. Disturbance has been shown to reduce total ANPP across other dryland ecosystems, often for years or decades after the disturbance occurred (Knapp 1992, Steiger and Webb 2000, Rottler et al. 2017). Disturbance can increase productivity in mesic ecosystems (Jones and Schmitz 2009), but these results add to a growing body of literature that disturbance reduces total productivity in drylands (Rottler et al. 2017, Jentsch and White 2019, Burton et al. 2020).

In each of the study systems, previous research has documented instances where disturbance events cause large impacts on plant productivity. Disturbance reduced the cover of dominant shrubs and had lasting negative effects on herbaceous productivity in Mojave systems (Steiger and Webb 2000), suggesting that I would continue to observe reductions in productivity for more growing seasons at the Mojave experiment location. Similarly in Great Basin ecosystems, productivity declines have been shown to persist for decades following disturbances (Avirmed et al. 2015, Ripplinger et al. 2015), mostly attributable to the low recruitment rate and relative slow growth of the dominant shrubs in that system (Anderson and Inouye 2001). In previous disturbance experiments in the Chihuahuan Desert, disturbance was shown to alter, but not reduce, plant productivity and did not modify transpiration rates compared to undisturbed conditions (Hochstrasser et al. 2005).

Contrary to the total ANPP patterns I observed, disturbance increased ANPP above undisturbed conditions within functional types when non-native species were present (Figure S3.2.2). I found that the amount of short term precipitation following disturbance is a major control over non-native species abundance. In ecosystems where non-native species are present, high resource availability following disturbance can lead to large increases in the abundance of non-native species, with propagule presence a key modulating factor (Prevéy et al. 2010). One of the sites, the Chihuahuan, had no non-native species present before the disturbance treatment, and no non-native species appeared in communities even after the disturbance treatment. In contrast, the other two sites saw large increases in non-native species abundance following disturbance because these sites had non-native propagules present before the disturbance occurred. These data point to the role of propagule abundance and pre-disturbance plant community in helping to determine physical disturbance effects.

The two sites where non-native propagules were present, Mojave and Great Basin, also saw the largest reduction in shrub productivity from disturbance (Figures 3.3 & 3.4). The large increase in non-native species productivity likely represents compensation for the loss of these dominant shrubs. Compensation often occurs among functional groups different from the species that were removed from disturbance (Bret-Harte et al. 2008). The annual non-native species present at these sites can utilize resources made available by dominant species reductions more quickly than other functional groups (Buonopane et al. 2005). The mass-ratio effects lost when these dominant shrubs were reduced by the treatment likely played a role in determining ecosystem responses to disturbance (Winfree et al. 2015, Smith et al. 2020).

Combined effects of precipitation and disturbance on productivity

Understanding how human-caused disturbances will interact with climate change is a major research priority for ecologists, and these results identify patterns that emerge when disturbance occurs across short and long term precipitation gradients. Understanding the interplay of disturbance and ANPP sensitivity to precipitation has important implications for major land use patterns in drylands, such as grazing or restoration after energy extraction, as well as larger-scale phenomena like predicting the carbon flux between the land and atmosphere (Maestre et al. 2016).

I found partial support of the second hypothesis, that disturbance decreased ANPP within sites and that this effect attenuated as short-term precipitation increased. This pattern is most obvious at the Mojave and Great Basin sites, where disturbance at low precipitation values created the greatest reduction in ANPP (Figure 3.3). The Chihuahuan site, with the disturbance-resistant shrubs that dominate there, showed more consistent negative effects of disturbance throughout the range of short-term precipitation values that I sampled (Figures 3.2 & 3.3).

I reject the second portion of the second hypothesis: I did not find consistent patterns of disturbance effects across long-term precipitation values of each of the three sites. Despite a lack of a consistent pattern, there are compelling cross-site results nonetheless. The most consistently negative effects of disturbance occurred at the Mojave site- this was the only site where disturbance interacted with precipitation at both ambient and reduced precipitation regimes (Figure 3.4). This may indicate that the driest systems are vulnerable to disturbance at any annual precipitation level. Further, I found the largest synergism between short term precipitation amount and disturbance at the wettest site- the Great Basin. At the Great Basin site, disturbance interacted with precipitation amount only in the reduced precipitation regime and produced a large degree of synergism in the magnitude of effects (Figures 3.4 & 3.7). This result suggests that this system may exist near a tipping point of resiliency, and that reductions in precipitation may greatly increase its vulnerability to disturbance.

I found that resistance at all sites to the reductions in short term precipitation I imposed in the absence of disturbance, and this resistance increased as long-term precipitation increased. However, a key result of this study is that disturbance can disrupt ecosystem resistance to short-term water deficits. Across the long-term precipitation gradient I sampled, I found that disturbance can increase the sensitivity of ANPP to short-term precipitation while reducing absolute ANPP values relative to undisturbed conditions. The mechanisms behind this pattern and the landscape-level consequences of the interaction of precipitation and disturbance are explored in the following section.

Mechanisms driving sensitivity to precipitation and disturbance

I found partial support for the third hypothesis, that ANPP is more greatly reduced at low MAP values than high MAP values, and found contrasting patterns of disturbance effects on the distribution of soil water along a MAP gradient. At the Mojave site (the driest site of the three), disturbance reduced available soil moisture, while at the other two sites, disturbance mostly increased soil moisture. I attempt to link these observed patterns in soil moisture dynamics to biotic and abiotic processes within and across the sites.

Disturbance reduced resource use efficiency across all sites with the greatest reductions occurring at low annual precipitation values, providing partial support for H3. Much of this reduction occurred because of the changes in functional type abundances discussed above (i.e., loss of dominant shrubs) but was also driven by soil water. Disturbance destroyed existing shrub architecture, likely increasing bare soil evaporation by reducing shrub canopy shading and ultimately reducing available soil water at low precipitation values. At high precipitation values, disturbance caused an increase in available soil water by reducing evapotranspiration. The reduction of resource use efficiency and available soil water are likely mechanisms behind the differences in synergism I observed across the three sites.

Why did I observe contrasting patterns of soil water changes across short- and long-term precipitation gradients? There could have been a switching of dominant mechanisms driving soil water dynamics across MAP values. At higher MAP, disturbance leads to reduced water use through transpiration, increasing available soil water. At low MAP, disturbance decreases the shading of the soil surface and the highly adapted shrub canopy architecture that increases stem flow and infiltration, ultimately reducing soil water through reduced infiltration and increased bare soil evaporation. In other words, both abiotic and biotic factors likely drove the soil moisture mechanisms behind the ANPP responses I observed. Biotic mechanisms were likely changes in root-shoot and hydraulic lift, canopy interception, and stemflow, while possible abiotic mechanisms were changes in infiltration, bare soil evaporation, pore space, boundary layer effects, and feedback loops affecting atmosphere-soil surface interactions.

Biotic influences on water movement through dryland ecosystems and soil water balance is both fascinating and only partially understood. The presence or absence of any perennial vegetation and the structure of perennial vegetation are first-order effects on soil water dynamics, both of which the disturbance and climate manipulations affected. Soil water availability in drylands has been positively correlated with the abundance of perennial vegetation (Roundy and Chambers 2021), and intact vegetation patches capture run-on and promote greater rates of infiltration and soil moisture (Pueyo et al. 2013). Further, transpiration is considered to be the major driver of vegetation effects on ecohydrology in drylands, and when intact aboveground biomass is present, transpiration dominates actual evapotranspiration and is greater under shrubs than other functional types (Huxman et al. 2004a, Wilson et al. 2018). Additionally, hydraulic redistribution of soil water by root systems has been empirically proven each of the dominant shrub species at the sites (Yoder and Nowak 1999, Hultine et al. 2004, Cardon et al. 2013), and this redistribution of soil water by shrubs was almost certainly disrupted by the disturbance treatment. Finally, dryland shrub architecture can be finely tuned to channel precipitation intercepted by plant canopies to stems and ultimately into the soil profile through stemflow, especially true for the dominant shrub at the Mojave site, *Larrea tridentata* (Whitford and Duval 2020).

While biotic influence of water movement through dryland ecosystems is complex and dynamic, all biotic mechanisms are in response to the overwhelming abiotic influence of water movement through dryland ecosystems, namely the insatiable atmospheric demand for water. Evidence supports that, beyond climate, abiotic forces could also drive soil water responses to disturbance and precipitation in drylands. These abiotic influences occur across spatial scales, from plot to landscape. While the experiment was only performed at the plot scale, my results offer insight across scales and provide insight for how dryland vegetation structure affects the soil to atmosphere continuum.

Previous study of disturbance and soil water interactions in drylands found that disturbance by a military tank increased soil moisture more when soil conditions were wet more than when they were dry, supporting my results (Althoff and Thien 2005). Further, disturbance by off-road vehicles (Davidson and Fox 1974) and military training activities (Prose et al. 1987) decreased bulk density and compacted soil, reducing infiltration and available soil water. The disturbance treatment likely interacted with soil variables at the time of the disturbance, and the legacy of disturbance on the physical properties of soil within this study interacted with precipitation during the experiment. Though I did not measure these variables directly, it is likely that changes in pore space and rates of infiltration and bare soil evaporation occurred as a result of the disturbance treatments.

Why didn’t the changes in soil moisture from disturbance occur in a linear fashion from negative to positive effects across the long term precipitation gradient that I sampled? Experimental manipulations suggest system-specific soil water responses to shrub removals across long term aridity gradients. Plant removal experiments in sagebrush have shown that removal of perennial plants increases soil moisture (Sturges

1993, Prevéy et al. 2010, Roundy and Chambers 2021) while plant removal experiments in the Mojave show that removing perennial shrubs decreases soil moisture due to a loss of shading effects by shrub canopies (Walker et al. 2001). The Chihuahuan site had the greatest deviation from the pattern I might have expected. The patterns of disturbance sensitivity at this site were likely driven by the two most abundant plants present: *Prosopis glandulosa* and *Bouteloua eriopoda*. The dominant shrub in the Chihuahuan was the least affected by the disturbance across the three sites, while the dominant grass there was quite sensitive to disturbance. The combination of disturbance-resistant shrubs and disturbance-sensitive grasses played a critical role the unique site-level patterns that I saw. Specifically, the extreme resistance of this shrub to disturbance prevented the reductions in soil water from biotic mechanisms from occurring. The shrubs in the Chihuahuan site had larger volume canopies than shrubs at the other two sites before I applied the disturbance treatment, which may have contributed to their disturbance resistance (Lortie et al. 2018).

Only one of the sites, Great Basin, had contrasting soil moisture responses, where reduced short term precipitation and disturbance caused a decrease in soil moisture compared to undisturbed conditions, but ambient short term precipitation and disturbance caused an increase in soil moisture. As discussed, removal of shrubs under ambient precipitation in this ecosystem tends to increase soil moisture (Sturges 1993, Prevéy et al. 2010). The high synergism I found between disturbance and short term precipitation at this site may indicate nonlinear or threshold dynamics when disturbance and short term precipitation reductions co-occur.

Disturbance and climate interactions in dryland ecosystems

An improved understanding of where ecological synergisms occur, how to manage for them, and what it means for ecological theory could benefit science and decision making alike (Folt et al. 1999, Brook et al. 2008, Buma 2015). I provide insight into where and how synergism can occur between short and long term precipitation and disturbance across dryland ecosystems.

Theory predicts that the magnitude of change from a disturbance is constrained by the total energy flux through an ecosystem (Jentsch and White 2019). Across our study systems, total energy flux is tightly linked to available soil water (Noy-Meir 1973). Prior to disturbance, productivity and standing biomass in the study systems were strongly influenced by the mass-ratio effects of the dominant shrub species (Grime 1998, Dee et al. 2019). The disturbance treatment clearly interrupted these dynamics within the Mojave and Great Basin sites and altered the flow of resources and patterns of production within these communities. Models suggest biomass has greater effects on soil moisture than either functional group or climate change, underscoring the need to recognize vegetation structural changes that emerge from human disturbances (Wilson et al. 2018). For example, I observed that the increase in non-native species from disturbance was greater with increasing short term precipitation (Figure S3.2.2), indicating that the loss of dominant shrub biomass from disturbance created an opportunity for non-native species to increase through changes in available soil water when resources were more abundant.

Theory suggests that in drylands, facilitation most frequently occurs under levels of intermediate stress and competition occurs under very high or very low stress, and that increases or decreases in available soil water will increase competition (McCluney et al. 2012). Specifically, dominant species can facilitate growth of subdominant species by decreasing heat stress and altering soil moisture and nutrient levels (Bertness and Callaway 1994, Lortie and Callaway 2006). The synergisms I observed between precipitation and disturbance are likely attributable to changes in both facilitation and competition through physical plant and soil structure effects. At the plot scale, the disturbance treatment likely increased stress through reductions in shading and hydraulic redistribution in water, tipping the scales towards competitive interactions and lower overall productivity. This finding has implications for human-caused disturbances across dryland ecosystems: preventing degradation of dryland ecosystems and maintaining perennial vegetation are land management objectives at the global scale (Reynolds et al. 2007, Maestre et al. 2016).

Climate change is projected to increase the extent of drylands globally, creating long term precipitation change over much of the planet's terrestrial surface (Huang et al. 2015, Bradford et al. 2020). Anticipating ecosystem changes from these precipitation shifts and forecasting interactions with disturbance will be essential, and these findings build on a small body of literature that experimentally capture the interaction of disturbance and precipitation change. Of studies that examine the interaction of disturbance and precipitation in drylands, results indicate that when a disturbance is lower-intensity (e.g. moderate grazing, low intensity fires, dispersed human use), precipitation tends to have primacy over ecosystem structure and function following the disturbance (Wan et al. 2015, Rito et al. 2017, Hannusch et al. 2020, Ye et al. 2022). When disturbances are more severe (e.g. heavy military training, prolonged human presence, high intensity fire, overgrazing), the recovery of perennial vegetation following disturbance can take half a century or longer (Knapp 1992, Milchunas et al. 2000, Belnap and Warren 2002, Guo 2004, Avirmed et al. 2015).

Dryland ecosystems are dynamic and spatially heterogeneous, and this heterogeneity is important to consider alongside these results. There are nested scales of heterogeneity in time and space across dryland systems. Spatially, biogeochemical properties vary from the plant scale (Schlesinger et al. 1996) to landforms (Burke 1989) and can drive ecosystem responses to precipitation and disturbance. Because drylands have heterogeneous distribution of vegetation in space, the decision to center the plots on individual shrubs could have influenced these results. Temporally, dryland systems are subject to great variability in precipitation inputs (Noy-Meir 1973) with consequences for current and future productivity (Huxman et al. 2004b, Sala et al. 2012). Though I did not measure spatial organization of vegetation explicitly, anecdotally I observed that the spatial organization of dryland vegetation can be disrupted by physical disturbance, potentially contributing to the soil water effects I observed. Because vegetation patches facilitate the capture and infiltration of water, disruption of vegetation patches could be a mechanism driving the effects I observed in these ecosystems (Mayor et al. 2013, Okin et al. 2015).

The scale of the experimental disturbance could have missed emergent properties of the same disturbance over a larger spatial scale especially boundary layer interactions driven by shrub canopy height and density, or changes in albedo and local weather patterns (Turner 2010). Specifically, landscape-scale disturbances can create negative hydrological-aeolian feedback loops that disrupt vegetation recovery and lead to further ecological degradation (Ravi et al. 2010). Larger-scale disturbance could interact in other ways that influence ecosystem structure and function, including loss of pollinators, seed bank richness, and soil loss and deposition (White and Jentsch 2001). Finally, precipitation variability during the experiment could also have influenced these results. The Mojave, Chihuahuan, and Great Basin sites experienced below average, near average, and above average precipitation amounts, respectively, during the treatment years.

Management Implications

Historically, controlling shrub abundance in drylands as a management practice was regularly attempted to increase forage production. Environmental management objectives have mostly shifted away from shrub control in the Mojave and Great Basin ecosystems because of, among other reasons, recognition of the ecological benefits that shrubs provide in these systems. However, shrub control in the Chihuahuan desert is an area of active research and preventing shrub encroachment a common management goal. These results provide additional evidence of the mechanisms by which shrubs are replacing perennial grasses in this system. The dominant grass species at the Chihuahuan site, *Bouteloua eriopoda*, is known to alter soil resources and increase colonization of other species in interspaces (Schlesinger et al. 1999, Stewart et al. 2014). *B. eriopoda* is stoloniferous and creates a large amount of standing litter when senesced. These life history traits combined likely contribute to seed trapping and altering soil resources in interspaces, promoting greater productivity (Stewart et al. 2014, Peters et al. 2020). Both of the experimentally simulated global change drivers reduced productivity of this species, and the disturbance treatment effectively destroyed the potentially beneficial standing dead biomass it creates. Previous work suggests that the loss of perennial grasses often lead to shrub encroachment (Peters et al. 2006), and in the case of the Chihuahuan site where shrubs were already established, the loss of perennial grasses only contributes to maintaining shrub dominance (Li et al. 2008, Turnbull et al. 2010, Sankey et al. 2012).

I chose a method of physical disturbance that would emulate a pervasive disturbance type in drylands. Explicit study of disturbances by recreational off-road vehicles has received the most attention in the Mojave Desert (Iverson et al. 1981, Hansen and Ostler 2005, Ouren et al. 2009), but has received some attention in the other two study systems (Hochstrasser et al. 2005, Munger et al. 2023). Broadly, these results agree with previous work: disturbances caused reductions in ANPP, tilling of the surface soil layers and increased erosion, and reductions in mean vegetation height. I simulated a tracked vehicle disturbance directly over dominant shrubs, and the presence or absence of vegetation patches in drylands might influence how vehicles are operated in reality (Belnap and Warren 2002). Military training disturbances have also received some attention in the literature, and these results support a growing body of literature's conclusion that tracked vehicle disturbance causes severe reductions in ANPP, shrub heights and area, and changes soil properties (Belnap and Warren 2002, Webb 2002, Jones et al. 2005, Zentelis et al. 2017).

Finally, many legal frameworks that guide land management, such as the National Environmental Policy Act, require the use of science in land management decision-making. It is especially challenging for land mangers implement climate adaption actions since there are such limited experimental data for climate change effects, making it difficult for managers to cite and defend the use of climate science in decision making

(Carter et al. 2023). Climate change modelling would be powerfully supported by field experimentation in a comprehensive way for widespread adoption of land management actions that accurately reflect climate influences. This experiment joins a growing number of datasets derived *in situ* explorations of climate change effects on ecosystem processes, and collectively, these efforts can provide useful and direct data for land management decision-making in a changing climate.

Conclusions

Physical disturbances have rarely been studied in multiple dryland ecosystems simultaneously with climate interactions, despite the widespread occurrence of disturbances across the world's drylands. These results provide valuable field-derived data to capture how ecosystem processes are influenced by individual and overlapping global change drivers. The most consistent reductions in productivity occurred at the Mojave site (the driest site), but the largest synergism between precipitation amount and disturbance effects occurred at the Great Basin site (the wettest site). The Chihuahuan site, with intermediate precipitation, showed small interactions between precipitation amount and disturbance, with compensatory production of the dominant shrub species when the dominant perennial grass species was reduced. Collectively, these results emphasize that the ongoing ecological dynamics of disturbance and climate change will continue to shape dryland landscapes, and if left unmitigated, will have negative consequences for biodiversity and society.

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Supplementary Material to Chapter 3

Supplemental 3.1: Information about sites, climate patterns, and experimental methods

Figure S3.1.1. Photographs of rainfall exclusion shelters at the Mojave, Chihuahuan, and Great Basin sites in this experiment (left, center, and right respectively). Plots were centered over individuals of the dominant shrub species at each site.

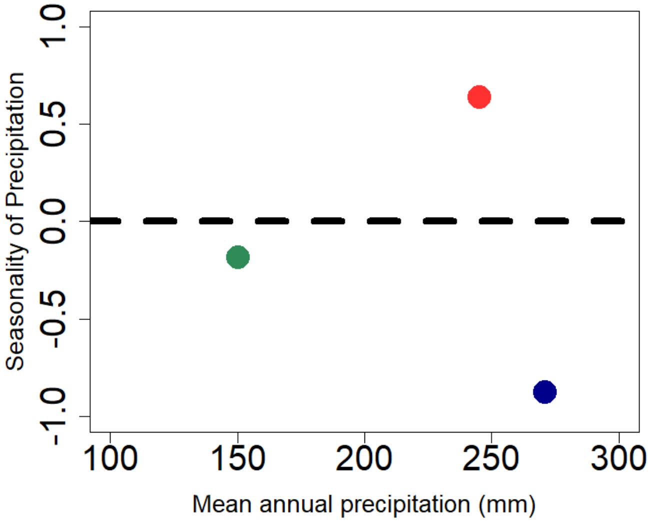

Figure S3.1.2. Seasonality of precipitation across mean annual precipitation values at each site. Mojave is plotted in green, Chihuahuan is plotted in red, and Great Basin is plotted in blue. Seasonality here is the correlation coefficient between mean monthly precipitation and mean monthly temperature.

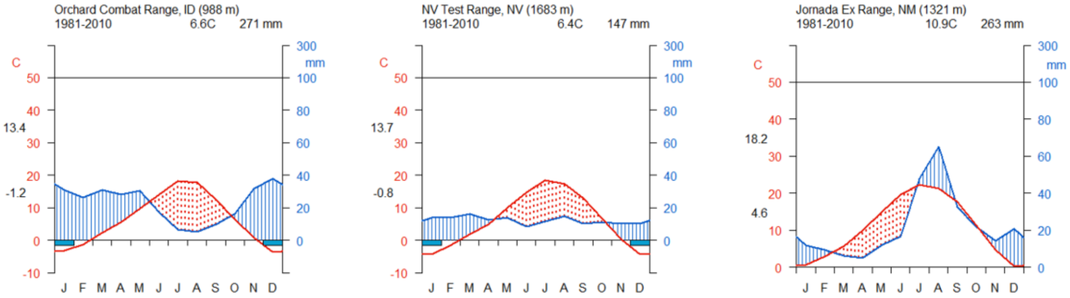

Figure S3.1.3. Walter-Leith climate diagrams for sites in three dryland ecosystems.

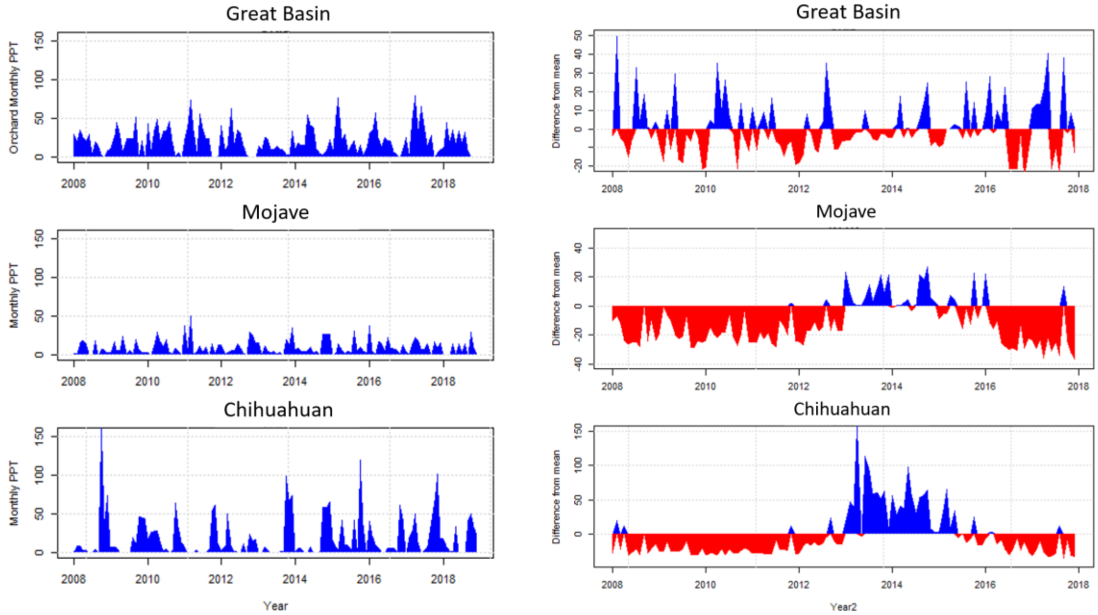

Figure S3.1.4. Monthly precipitation (left) and Reynold's decomposition of precipitation (right) over the ten-year period preceeded installation of the experiment in three dryland ecosystems.

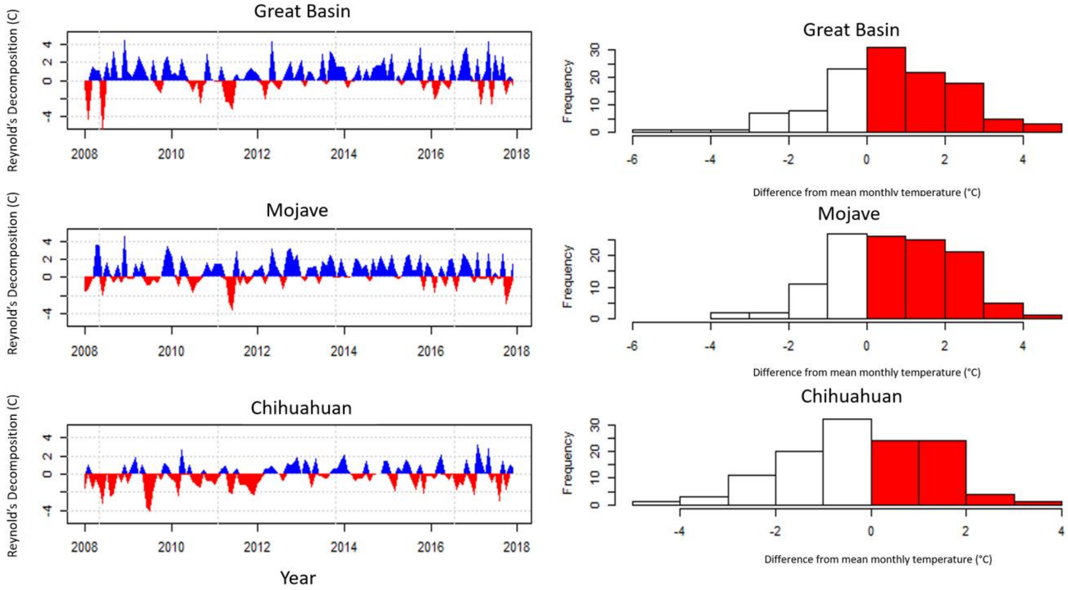

Figure S3.1.5. Reynold's decomposition of temperature (C) over time (left) and frequency distribution of temperature anomoly (right) for sites in three dryland ecosystems. Reynold's decomposition here is calculated as the difference in recorded mean monthly air temperature and 30-year normal air temperature for each site. Frequency distributions are monthly differences in recorded air temperatures and 30-year normals for the ten year period preceeding installation the field experiment.

Figure S3.1.6. The spiked drum aerator used to disturb plots in the experiment.

Supplemental 3.2: Information supporting analyses

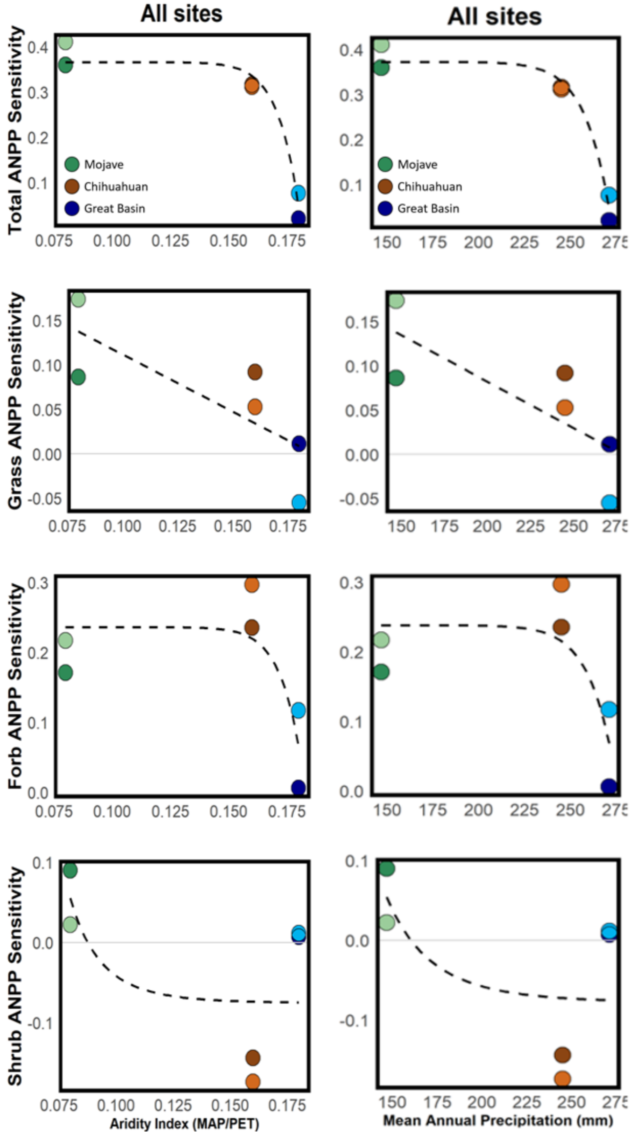

Figure S3.2.1. Sensitivity of the ANPP–precipitation relationship across all three sites and sensitivity of functional type ANPP–precipitation relationships across all three sites in disturbed (light colors) and undisturbed (dark colors) conditions (Mojave = green, Chihuahuan = brown, Great Basin = blue). I calculated sensitivity as the slope of the ANPP–precipitation relationships (Figure 1). Dotted lines represent non-significant relationships and are meant to suggest that ANPP relationships may be linear or non-linear across precipitation and aridity gradients.

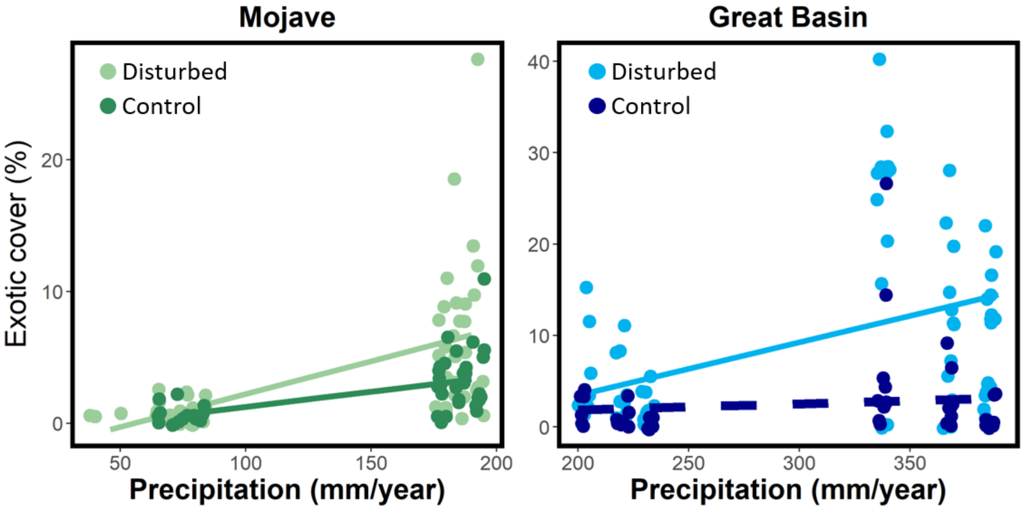

Figure S3.2.2. Non-native species abundance in response to annual precipitation and physical disturbance in two dryland ecosystems. Dark colors represent control conditions, and light colors represent disturbed conditions. The Chihuahuan desert site was not included because it had no non-native species.

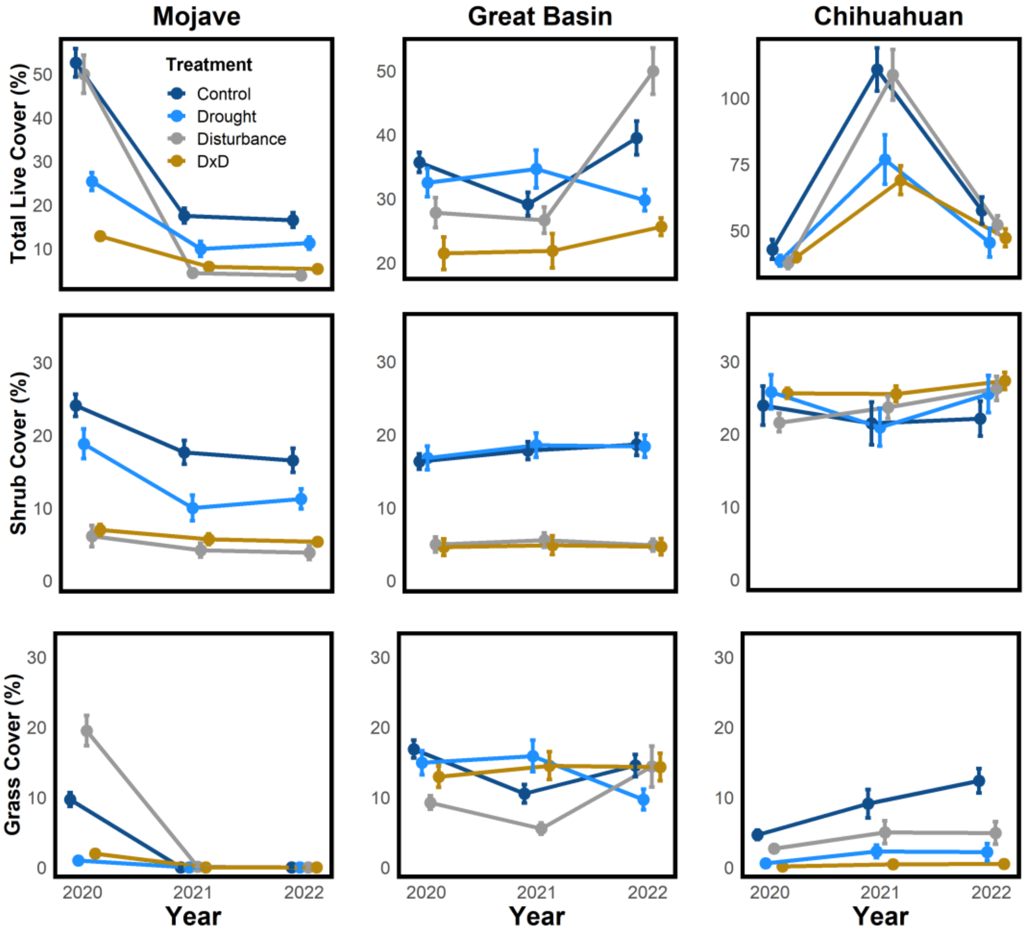

Figure S3.2.3. Changes in total, grass, and shrub live cover in response to three years of experimentally decreased precipitation and physical disturbance in three dryland ecosystems. Letters indicate significant differences between groups include my pretreatment year (2019) and all three treatment years. Colors indicate experimental treatments (dark blue-control, light blue-drought, grey-disturbance, brown-drought and disturbance, and error bars indicate +/- one standard error.

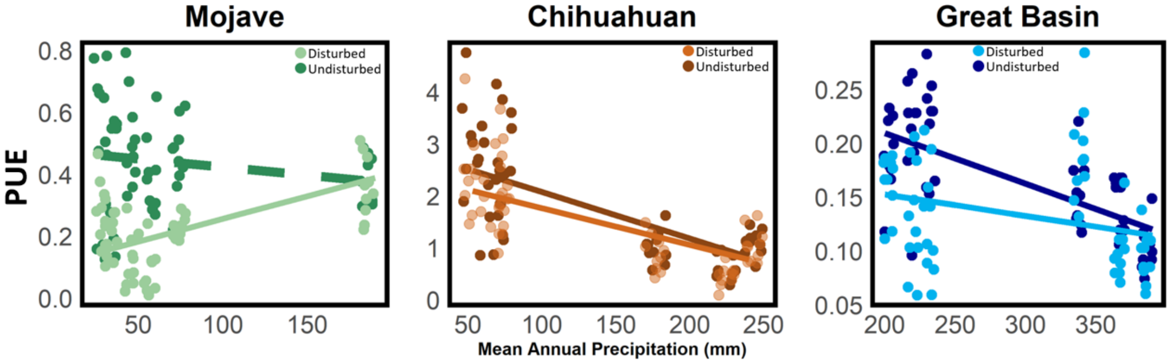

Figure S3.2.4. Precipitation use efficiency (PUE; ANPP (g/m^2/yr^{-1}) divided by precipitation (mm)) across a precipitation gradient in three dryland ecosystems. Colors indicate experimental treatments (dark colors- undisturbed, light colors- disturbed).

Table S3.2.1. Mixed model results of the total aboveground net primary productivity-precipitation relationship at my Mojave site.

	UNDISTURBED ANPP			**DISTURBED ANPP**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	4.06	0.17 – 7.96	**0.041**	-10.91	-14.97 – -6.86	**<0.001**
ppt	0.36	0.32 – 0.40	**<0.001**	0.41	0.37 – 0.45	**<0.001**
Random Effects						
σ^2	47.51			71.80		
τ_{00}	27.12_{plot}			12.43_{plot}		
ICC	0.36			0.15		
N	20_{plot}			20_{plot}		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.833 / 0.894			0.852 / 0.874		

Table S3.2.2. Mixed model results of the total aboveground net primary productivity-precipitation relationship at the Great Basin site.

	UNDISTURBED ANPP			DISTURBED ANPP		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	39.99	26.23 – 53.74	**<0.001**	15.95	0.37 – 31.54	**0.045**
ppt	0.02	-0.03 – 0.07	0.378	0.08	0.02 – 0.13	**0.005**
Random Effects						
σ^2	88.62			223.60		
τ_{00}	31.26 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
ICC	0.26					
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.019 / 0.275			0.128 / NA		

Table S3.2.3. Mixed model results of the total aboveground net primary productivity-precipitation relationship at the Chihuahuan site.

	UNDISTURBED ANPP			DISTURBED ANPP		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	133.54	88.53 – 178.56	**<0.001**	111.71	68.65 – 154.77	**<0.001**
ppt	0.32	0.04 – 0.59	**0.027**	0.31	0.04 – 0.58	**0.023**
Random Effects						
σ^2	3558.52			4089.01		
τ_{00}	1362.34 $_{\text{plot}}$			913.39 $_{\text{plot}}$		
ICC	0.28			0.18		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.112 / 0.358			0.108 / 0.271		

Table S3.2.4. Mixed model results of the shrub productivity-precipitation relationship at the Mojave site.

	UNDISTURBED ANPP_shrub			**DISTURBED ANPP_shrub**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	15.43	12.01 – 18.86	**<0.001**	5.49	3.63 – 7.35	**<0.001**
ppt	0.09	0.06 – 0.12	**<0.001**	0.02	0.01 – 0.03	**<0.001**
Random Effects						
σ^2	24.85			2.81		
τ_{00}	32.38 $_{\text{plot}}$			14.21 $_{\text{plot}}$		
ICC	0.57			0.83		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.290 / 0.692			0.077 / 0.847		

Table S3.2.5. Mixed model results of shrub productivity-precipitation relationship at the Great Basin site.

	UNDISTURBED ANPP_shrub			**DISTURBED ANPP_shrub**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	22.10	13.50 – 30.71	**<0.001**	3.09	-3.04 – 9.22	0.317
ppt	0.01	-0.02 – 0.04	0.608	0.01	-0.01 – 0.03	0.251
Random Effects						
σ^2	7.53			4.02		
τ_{00}	33.17 $_{\text{plot}}$			16.25 $_{\text{plot}}$		
ICC	0.81			0.80		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		

Marginal R^2 / Conditional R^2	0.007 / 0.816	0.036 / 0.809

Table S3.2.6. Mixed model results of shrub productivity-precipitation relationship at the Chihuahuan site.

	UNDISTURBED ANPP_shrub			**DISTURBED ANPP_shrub**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	92.87	67.89 – 117.86	**<0.001**	93.54	72.92 – 114.17	**<0.001**
ppt	-0.14	-0.29 – 0.00	0.053	-0.17	-0.30 – -0.05	**0.006**
Random Effects						
σ^2	334.07			247.82		
τ_{00}	917.05 $_{\text{plot}}$			596.28 $_{\text{plot}}$		
ICC	0.73			0.71		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.094 / 0.758			0.182 / 0.760		

Table S3.2.7. Mixed model results of grass productivity-precipitation relationship at the Mojave site.

	UNDISTURBED ANPP_grass			**DISTURBED ANPP_grass**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-3.76	-4.60 – -2.92	**<0.001**	-7.55	-9.36 – -5.75	**<0.001**
ppt	0.09	0.08 – 0.10	**<0.001**	0.17	0.15 – 0.19	**<0.001**
Random Effects						
σ^2	3.82			17.59		

τ_{00}	0.00_{plot}	0.00_{plot}
N	20_{plot}	20_{plot}
Observations	60	60
Marginal R^2 / Conditional R^2	0.849 / NA	0.833 / NA

Table S3.2.8. Mixed model results of grass productivity-precipitation relationship at the Great Basin site.

	UNDISTURBED ANPP_grass			**DISTURBED ANPP_grass**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	15.58	5.10 – 26.06	**0.004**	31.62	20.99 – 42.25	**<0.001**
ppt	0.01	-0.02 – 0.05	0.517	-0.06	-0.09 – -0.02	**0.003**
Random Effects						
σ^2	48.68			37.84		
τ_{00}	19.29_{plot}			25.16_{plot}		
ICC	0.28			0.40		
N	20_{plot}			20_{plot}		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.011 / 0.291			0.214 / 0.528		

Table S3.2.9. Mixed model results of grass productivity-precipitation relationship at the Chihuahuan site.

	UNDISTURBED ANPP_grass			**DISTURBED ANPP_grass**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	2.96	-7.87 – 13.80	0.586	-0.90	-7.45 – 5.64	0.784
ppt	0.09	0.02 – 0.16	**0.008**	0.05	0.01 – 0.09	**0.011**
Random Effects						
σ^2	261.84			64.65		
τ_{00}	56.83_{plot}			33.35_{plot}		
ICC	0.18			0.34		

N	20 plot	20 plot
Observations	60	60
Marginal R^2 / Conditional R^2	0.141 / 0.295	0.150 / 0.439

Table S3.2.10. Mixed model results of forb productivity-precipitation relationship at the Mojave site.

	UNDISTURBED ANPP_forb			DISTURBED ANPP_forb		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-6.66	-8.87 – -4.46	**<0.001**	-9.02	-12.04 – -5.99	**<0.001**
ppt	0.17	0.15 – 0.19	**<0.001**	0.22	0.18 – 0.25	**<0.001**
Random Effects						
σ^2	23.38			49.44		
τ_{00}	2.02 plot			0.00 plot		
ICC	0.08					
N	20 plot			20 plot		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.769 / 0.787			0.733 / NA		

Table S3.2.11 Mixed model results of forb productivity-precipitation relationship at the Great Basin site.

	UNDISTURBED ANPP_forb			DISTURBED ANPP_forb		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	1.08	-6.17 – 8.32	0.767	-18.00	-30.37 – -5.64	**0.005**
ppt	0.01	-0.02 – 0.03	0.619	0.12	0.08 – 0.16	**<0.001**
Random Effects						
σ^2	21.78			140.81		
τ_{00}	9.84 plot			0.00 plot		

ICC	0.31	
N	20 $_{\text{plot}}$	20 $_{\text{plot}}$
Observations	60	60
Marginal R^2 / Conditional R^2	0.006 / 0.316	0.355 / NA

Table S3.2.12. Mixed model results of forb productivity-precipitation relationship at the Chihuahuan site.

	UNDISTURBED ANPP_forb			**DISTURBED ANPP_forb**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	56.31	23.21 – 89.41	**0.001**	38.16	5.50 – 70.82	**0.023**
ppt	0.24	0.03 – 0.44	**0.026**	0.30	0.09 – 0.50	**0.005**
Random Effects						
σ^2	3897.05			3793.75		
τ_{00}	0.00 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.081 / NA			0.126 / NA		

Supplemental 3: Environmental sensor and allometry data

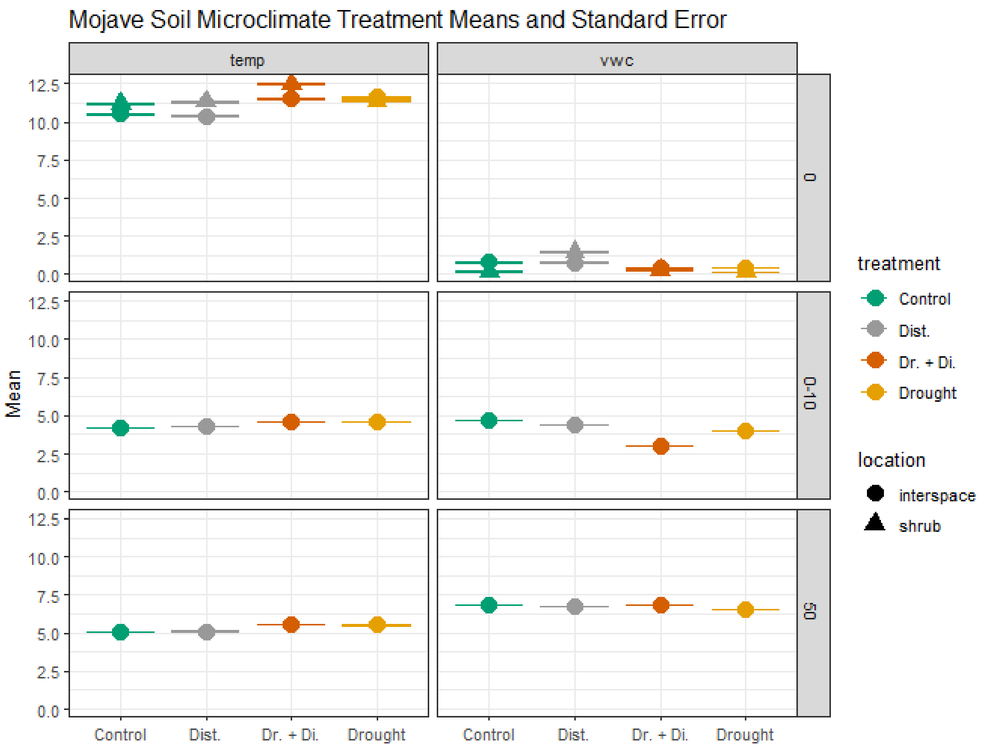

Figure S3.3.1. Soil moisture and temperature dynamics for the Mojave site across years. Depths are represented by panels- top panel = surface, middle panel = 0-10 cm, bottom panel = 50 cm. Temperature data are shown in the left column in degrees Celsius, volumetric water content (VWC) is shown in the right panel as a percentage.

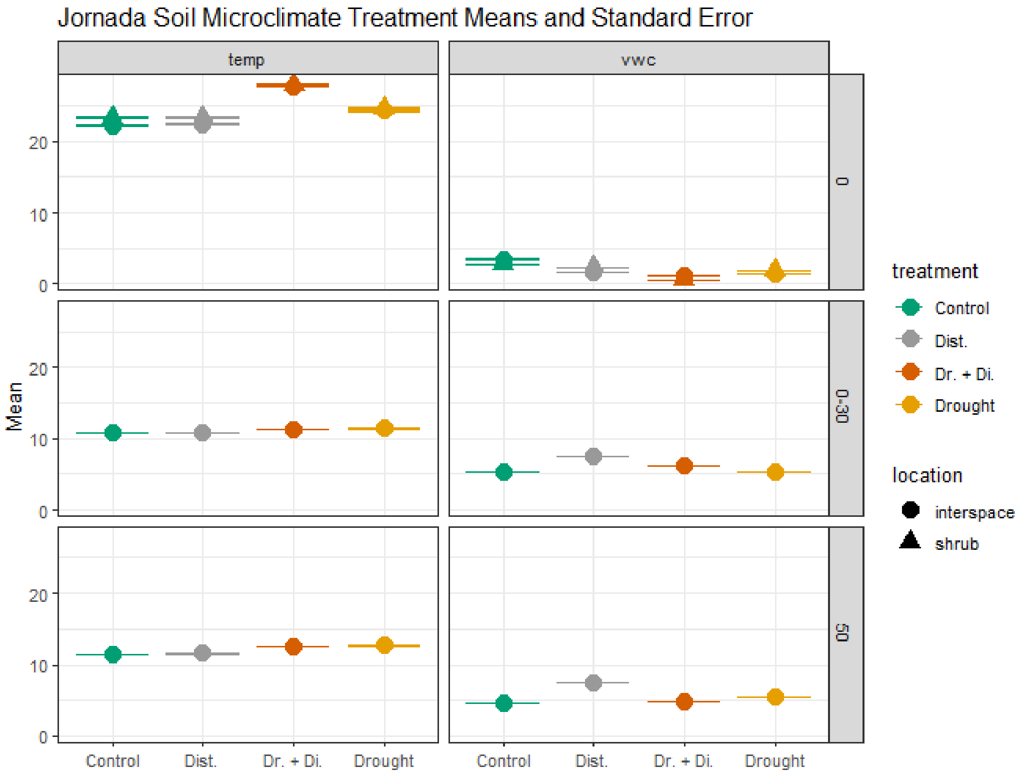

Figure S3.3.2. Soil moisture and temperature dynamics for the Chihuahuan site across years. Depths are represented by panels- top panel = surface, middle panel = 0-10 cm, bottom panel = 50 cm. Temperature data are shown in the left column in degrees Celsius, volumetric water content (VWC) is shown in the right panel as a percentage.

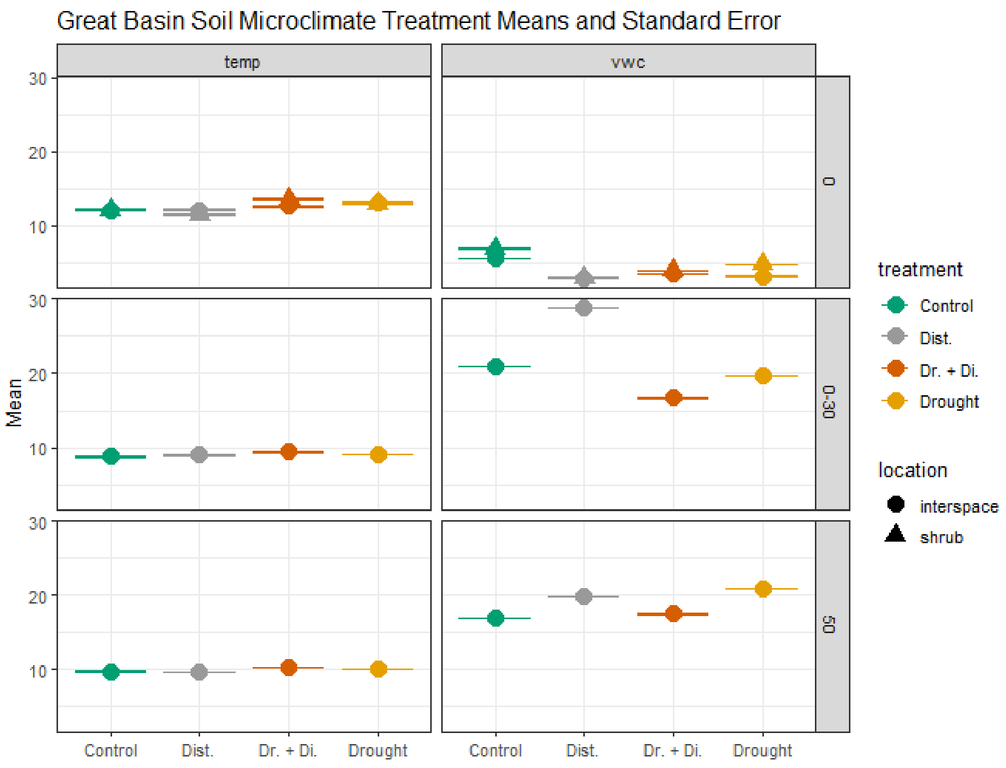

Figure S3.3.3. Soil moisture and temperature dynamics for the Great Basin site across years. Depths are represented by panels- top panel = surface, middle panel = 0-10 cm, bottom panel = 50 cm. Temperature data are shown in the left column in degrees Celsius, volumetric water content (VWC) is shown in the right panel as a percentage.

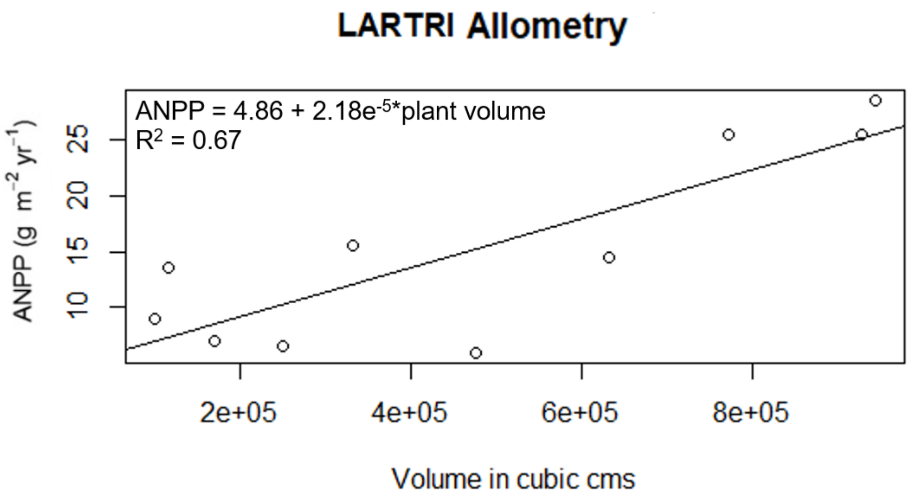

Figure S3.3.4. Allometric relationship between shrub volume and aboveground net primary productivity for dominant shrub in Mojave site, *Larrea tridentata.*

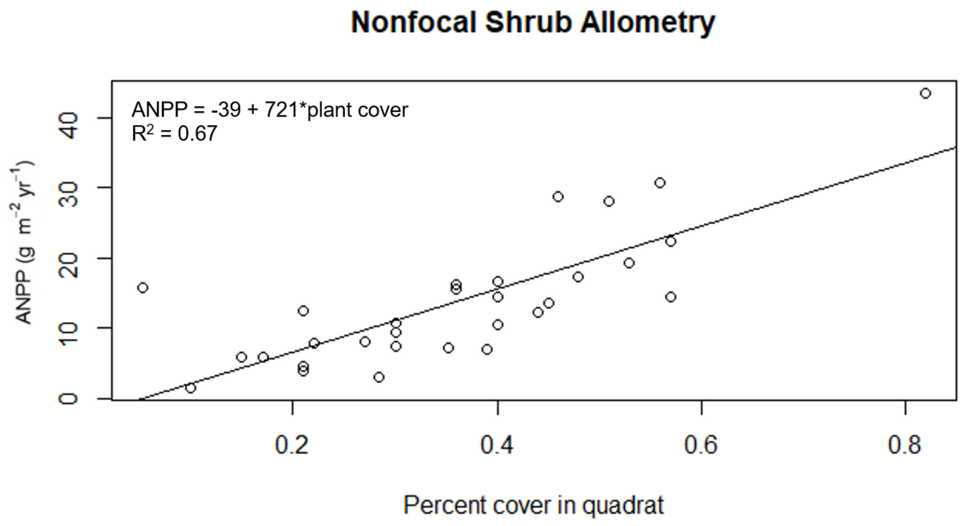

Figure S3.3.5. Allometric relationship between plant cover and aboveground net primary productivity for subdominant shrubs in Mojave site (n = 3 species: *Ephedra nevadaensis, Lycium pallidum,* and *Ambrosia dumosa*).

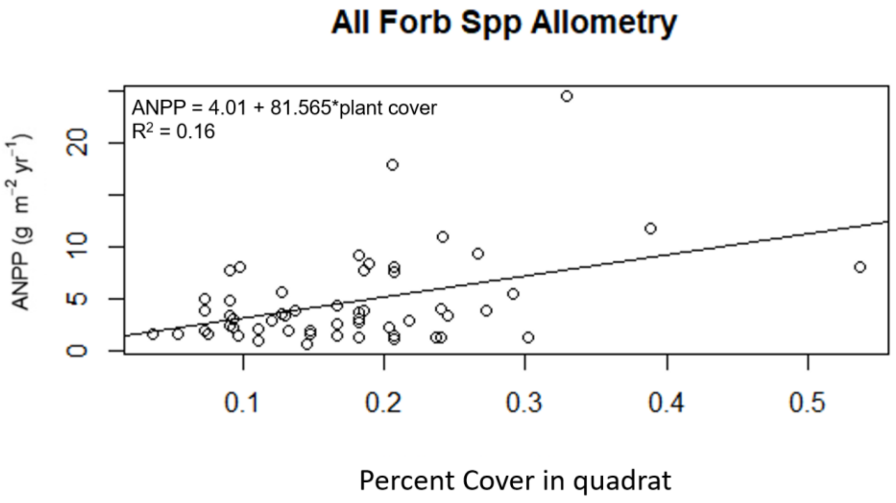

Figure S3.3.6. Allometric relationship between plant cover and aboveground net primary productivity for annual forb species in Mojave site (n=5 species: *Chaenactis fremontii, Cryptantha circumcissa, Nama aretioides*, *Eriophyllum pringlei,* and *Amsinckia tessellata*)

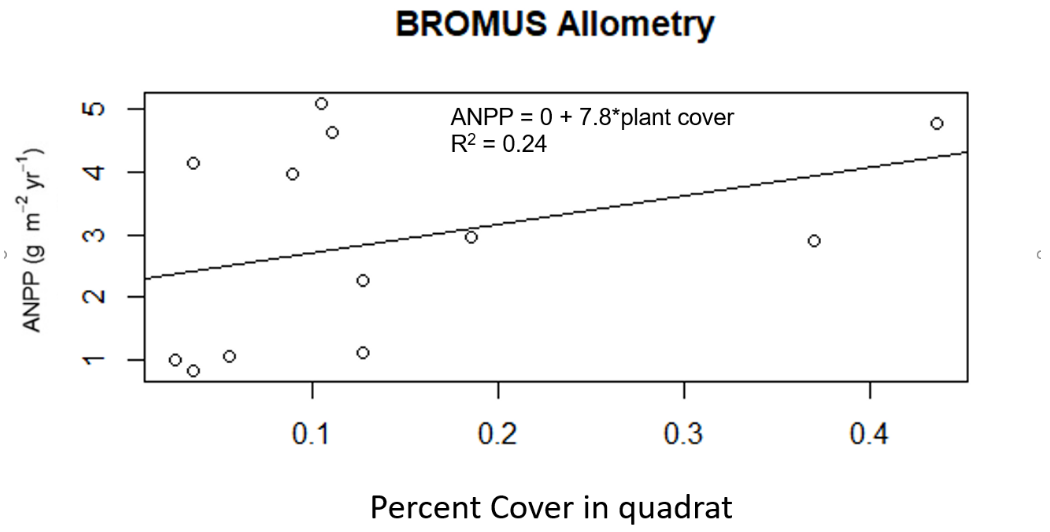

Figure S3.3.7. Allometric relationship between plant cover and aboveground net primary productivity for annual grasses in Mojave site (n = 2 species: *Bromus tectorum* and *Bromus rubens*).

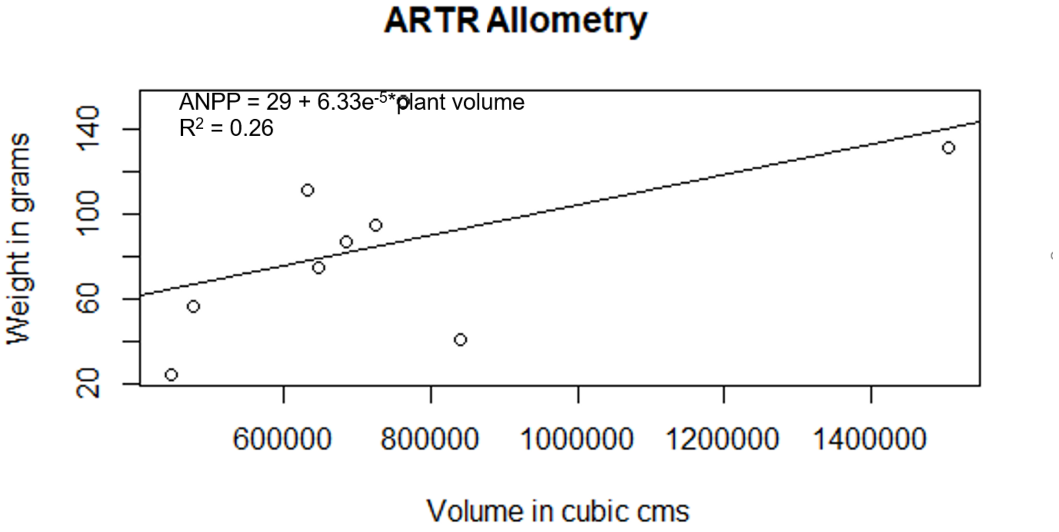

Figure S3.3.8. Allometric relationship between shrub volume and aboveground net primary productivity for dominant shrub in Great Basin site, *Artemisia tridentata.*

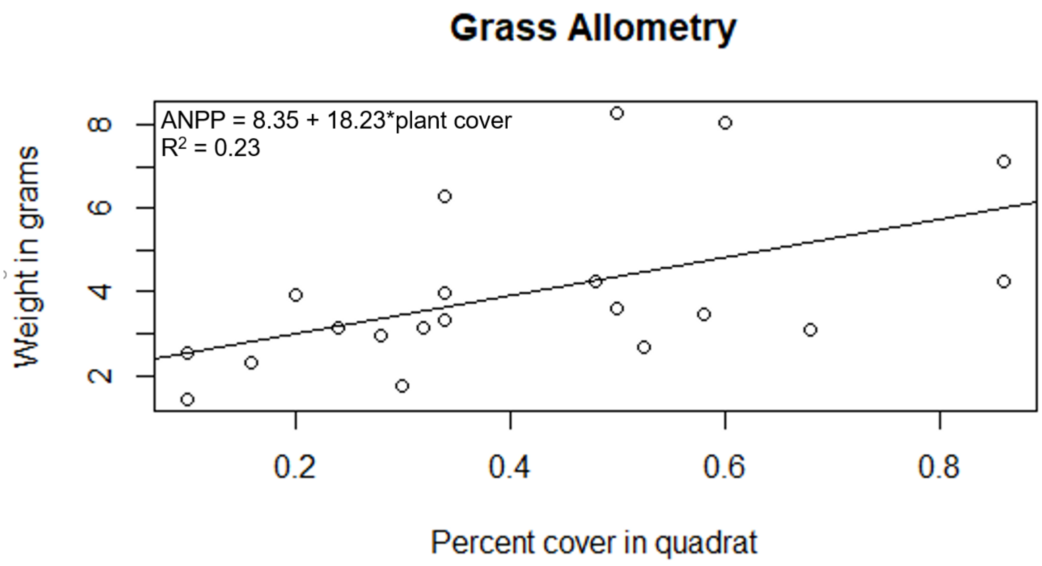

Figure S3.3.9. Allometric relationship between plant cover and aboveground net primary productivity for perennial grasses in Great Basin site (n=2 species, *Poa secunda and Elymus elymoides*).

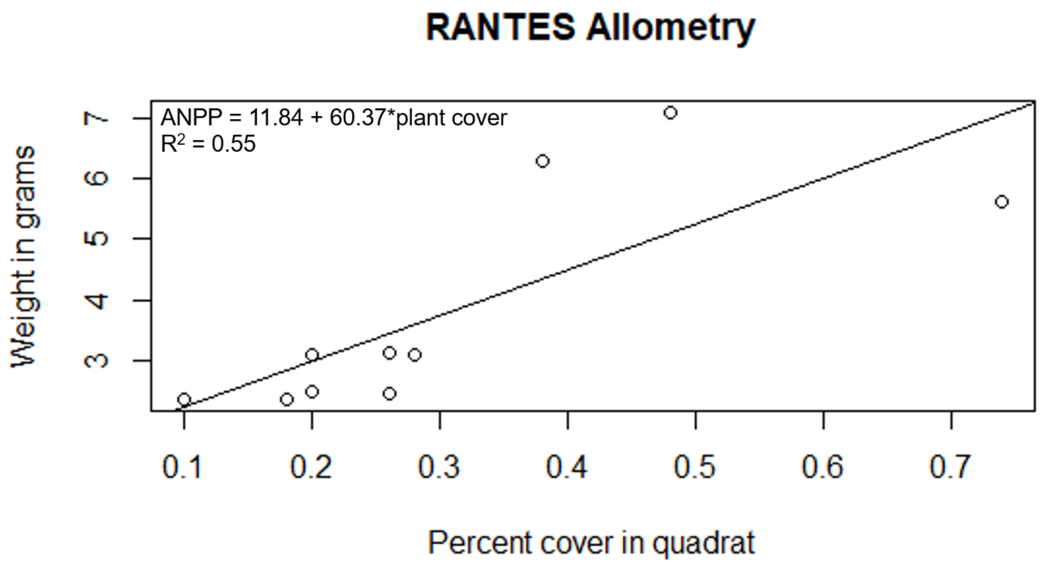

Figure S3.3.10. Allometric relationship between plant cover and aboveground net primary productivity for annual forbs in the Great Basin site (n=1 species, *Ranunculus testiculatus*).

CHAPTER 4

EFFECTS OF DISTURBANCE ON DRYLAND PLANT COMMUNITY COMPOSITION ARE MODULATED BY PRECIPITATION

Abstract

Dryland ecosystems are predicted to be responsive to both changes in precipitation and physical disturbance. Further, the interaction of precipitation and disturbance may exacerbate negative effects on ecosystem structure and function when disturbances occur during periods of low precipitation. I conducted a long-term field experiment where I combined rainfall manipulation and physical disturbance treatments on in situ plant communities in the Mojave, Great Basin, and Chihuahuan Deserts, USA. I evaluated the individual and combined effects of three years of precipitation reduction and severe physical disturbance on plant communities. I assessed the effects of precipitation, disturbance, and their interaction on species richness and evenness, as well as on dominant shrub species and subdominant grasses, forbs, and subshrubs. I found that across sites, precipitation deficits and disturbance had interactive effects, with larger changes in the mean and variability of community composition with combined drivers than precipitation reduction or disturbance alone. This pattern likely occurred through the interaction of abiotic stress and community dynamics, which I explore through changes in soil water availability. Finally, I found that the interaction of precipitation reductions and disturbance can serve as major drivers of undesirable changes in ecosystems: I observed large increases in non-native species at two of the sites and an acceleration of shrub encroachment at the third site resulting from the treatments. These results offer

field-derived biodiversity responses to interacting global change drivers to inform additional research and dryland ecosystem management practices.

Introduction

Understanding the biodiversity responses of water-limited ecosystems to human actions and climate change is one of the most pressing challenges in ecology with implications for human livelihoods through the functioning of ecosystems and the provisioning of ecosystem services. Multiple aspects of dryland ecosystems make them vulnerable to global change drivers such as climate change and disturbances associated with land-use change, including relatively low productivity, severe abiotic conditions, high spatial heterogeneity, and consistently severe water deficits that limit plant growth and maintenance, reproduction, germination, and recruitment (Reynolds et al. 2007, Ferrenberg et al. 2015, Bestelmeyer 2015, Maestre et al. 2016). The global extent of drylands covers around 41%, or 60 million square kilometers, of the Earth's terrestrial surface, an extent that is projected to increase 11%–23% by the end of this century (Huang et al. 2015, Prăvălie 2016, Bradford et al. 2020). In these regions, explosive human population growth has led to widespread land use change via urbanization, energy development, and fragmentation (Knick et al. 2003, Welch 2005, Wu et al. 2011, York et al. 2011). Concomitant with population growth, human-caused disturbances are also increasing, including grazing disturbances, the most widespread land use in drylands. In these ecosystems, empirical studies demonstrate that responses to disturbance are modulated by functional diversity (Chambers et al. 2017, Roundy and Chambers 2021), dominant vegetation condition (Monroe et al. 2022), richness, and composition (Johnson and Matchett 2001). Therefore, understanding plant species composition and functional responses is key for maintaining ecosystem functioning under changing climate and disturbance regimes (Chapin et al. 1997, Tilman et al. 2014).

Changes in precipitation are projected to occur over short- or long-timescales resulting in dryland ecosystem responses that are driven by different mechanisms specific to each timescale (Huxman et al. 2004). Here I define short-time scales as the interannual and interdecadal patterns of precipitation observed within sites and define long-time scales as those occurring across multiple centuries or longer. In practical terms, short-time scales are most easily understood and observed as variability within sites and long-time scales are most easily understood and observed as variability across sites and climate gradients.

On short-time scales, water stress in ecosystems reduces carbon uptake via stomatal limitation, reduces germination and recruitment of new plants, and decreases the number and relative abundance of species present in a community (Noy-Meir 1973, Lauenroth 1979, Lian et al. 2021). Across long-timescales, changes in the long-term mean precipitation patterns resulting in either drier or wetter that historical conditions will result in large changes in species richness and evenness (Sala et al 2012).

The slope of the relationship between long-term mean annual precipitation and richness is much steeper than the relationship between short-term precipitation and richness, meaning that changes in long-term precipitation result in larger differences in biodiversity (Cleland et al. 2013). Specifically, species richness is positively related to precipitation across long-term precipitation gradients, but consistent relationships to short-term precipitation variability within sites are rare, with these relationships only appearing at drier sites (Cleland et al. 2013). Thus, there are major differences in short-versus long-term changes in precipitation with important implications for ecosystem structure, function, and management. Understanding plant community metrics across long-term precipitation gradients can reveal how ecosystems are structured as a result of long-term precipitation (Yang et al. 2011, Cleland et al. 2013, Jordan et al. 2020)

Ecological disturbances influence key ecosystem processes and human actions are increasing the extent and intensity of disturbances across biomes (White and Jentsch 2001, Kareiva et al. 2007). Disturbance as an ecological process has long been studied, and it is here defined as a discrete event that disrupts ecosystem structure, changes resources, substrate, or physical environment (Pickett and White 1985, White and Jentsch 2001). The variability in disturbance events and outcomes has posed a challenge for the development of a consistent ecological theory that remains unresolved (White and Jentsch 2001, Jentsch and White 2019). Indeed, a recent meta-analysis indicated that disturbance may be more important than water availability in driving patterns of diversity in grassland ecosystems, the most productive drylands (Smith et al. 2022).

Existing evidence indicates that disturbance affects ecosystems through mechanisms that influence resource dynamics and competitive interactions (Chesson 2000, Fox 2013, Kraft et al. 2015) that result in changes in ecosystem structure and functioning. Disturbance effects are further modulated through disturbance type and intensity, and environmental conditions leading into and following a disturbance (Turner 2010, Burton et al. 2020). This is especially obvious in dryland plant communities that have a high proportion of annual species in both recently disturbed and undisturbed communities; the relative abundance of annuals across successional ages of communities makes interspecific interactions especially important to dryland resilience and resistance to disturbance (Abella 2010). Resource availability for these communities is primarily modulated by long-term precipitation through ecosystem structure prior to a disturbance and short-term precipitation through resource dynamics following a disturbance (Jentsch and White 2019) highlighting the broad importance of interactions between disturbance characteristics and environmental conditions across temporal scales.

Theory predicts that the degree to which a disturbance affects resource dynamics is tightly linked to the magnitude of resource flow, meaning that in drylands, disturbance effects on resource dynamics can be modulated by both long- and short-term precipitation (Jentsch and White 2019). Community theory indicates that richness and evenness will respond in different ways to global change drivers, sometimes quite slowly, suggesting that species distributions and patterns of dominance, which can respond more rapidly, may be valuable metrics for understanding the effects of global change (Hillebrand et al. 2008). Further, empirical data suggest that the ecosystem level outcomes of disturbance are indeed driven by both long- and short-term precipitation, with long-term precipitation modulating ecosystem resistance and short-term precipitation modulating ecosystem resilience (Milchunas et al. 2000, Hannusch et al. 2020, Geppert et al. 2021).

Previous research provides specific examples precipitation and disturbance as community drivers in dryland communities, however, the scientific community's understanding of how precipitation across short- and long-timescales interacts with disturbance to affect dryland plant communities is less well developed. The importance of precipitation in driving plant community composition in drylands is well established (Báez et al. 2013, Munson et al. 2015, Alon and Sternberg 2019), and changes in short-term precipitation can change the abundance of functional types in dryland plant communities (Munson et al. 2015, Holdrege et al. 2023). Studies across grassland sites have revealed that species richness is positively related to precipitation across sites but species richness is sensitive to temporal variation in annual precipitation only at the driest sites (Cleland et al. 2013). For disturbances, observational work has shown that disturbances can leave long-lasting reductions in dominant species, and that precipitation amount following disturbance can modulate the rate of recovery (Guo 2004, Abella 2010). Because of the interaction of precipitation and disturbances is dynamic, fewer studies have identified clear patterns. Because climate can interact with disturbance to affect both ecosystem resistance are resilience to changes in precipitation (Ruppert et al. 2015), ongoing climate change makes a more developed understanding elusive.

Both changes in precipitation and disturbances can change the identity of the most dominant plants in a dryland community, in some cases from perennial grasses to disturbance-resistant shrubs and in others from long-lived perennial shrubs to non-native annual species. Long-term precipitation strongly shapes the dominant species of dryland plant communities, and changes in long-term precipitation can shift which species are most abundant (Lauenroth 1979). Changes in short-term precipitation can cause major shifts in dominant species, with several cases of mortality of entire landscapes of dominant plants in dryland communities as a result of short-term precipitation patterns (Renne et al. 2019). The interaction of disturbance and precipitation, both long- and short-term, is likely a major driver of shrub encroachment in many dryland ecosystems (Archer 1994). As dominance of the most abundant species increases in a community (in many dryland systems, the most abundant species are shrubs) from global change drivers, the formerly even community experiences changes in species interactions: greater intraspecific interactions for dominant species and greater interspecific interactions for rare species (Hillebrand et al. 2008). As dominance increases and evenness decreases, experimental evidence suggests that extinctions are more likely (Wilsey and Polley 2004), further exaggerating the degree of dominance of the surviving plants. In addition to changing the structure and composition of dryland communities, the strength of these species interactions can affect ecosystem functioning and community-level responses to further climate change or physical disturbances over time.

Precipitation and disturbance can interact to cause changes in non-native species abundance in drylands: dryland ecosystems around the world are experiencing major shifts in structure, composition, and function because of non-native species. In many cases, the increase of non-native species has been attributed to a cycle of disturbance and the direct effects that increasing abundance of non-native species has on the likelihood of additional disturbances (D'Antonio and Vitousek 1992). New evidence suggests that single types of disturbance are not the primary driver, and that connections among precipitation and multiple disturbances must be taken into account (Smith et al. 2023). When changes in precipitation and disturbance occur simultaneously, interactions between these drivers can lead to rapid, nonlinear change (Turner 2010), creating opportunities for severe invasion of non-native species. A mechanism behind these rapid changes is likely the native species mortality that can occur in the face of the extreme abiotic conditions that commonly follow the co-occurrence of physical disturbance and precipitation change. This native plant mortality leaves faster-establishing non-native species to colonize when resources such as soil water become more available (Tilman 1982). Evidence suggests that disturbance interacts with both short- and long-term precipitation to control the abundance of non-native species within dryland ecosystems, but the exact outcomes of ecosystem-species pairings are far from resolved, especially when the complexity of climate change effects on precipitation are considered.

Because human-caused disturbances and changes in precipitation regimes are occurring in drylands globally, unravelling which mechanisms are driving ecological responses and developing a clear understanding of ecosystem-specific responses is an urgent research need (Buma 2015). Manipulative experiments across ecosystems with different dominant species and precipitation regimes creates a valuable opportunity to explore both ecosystem- and regional-scale patterns. Indeed, the strength of interaction between ecosystem stressors can change along environmental gradients (Mack et al. 2022, Kefford et al. 2023), highlighting the need for understanding the dynamics of overlapping global change drivers across long-term resource gradients. Empirical studies demonstrate that ecosystem responses to disturbance are modulated by functional diversity (Chambers et al. 2017, Roundy and Chambers 2021), dominant vegetation condition (Monroe et al. 2022), richness, and composition (Johnson and Matchett 2001), creating a need to test for difference across community types. However, recovery of dryland plant communities is often non-linear and driven by community dynamics beyond abiotic factors like rainfall (Lawley et al. 2013), making multi-year observations across long- and short-term precipitation regimes especially valuable.

To determine how precipitation and disturbance interact to affect dryland vegetation across ecosystems, I conducted a multiyear factorial field experiment combining the effects of drought and disturbance in the Mojave, Great Basin, and Chihuahuan Deserts or North America. I deployed rainfall-interception shelters, experimental physical disturbance, and shelters + disturbance treatments in at each site. I assessed species richness, evenness, and community composition as response variables and measured soil water at different soil depths to unravel mechanisms that could help explain the results observed aboveground. I focused on the following research question: what are the interactive effects of precipitation and disturbance on plant species abundance, diversity, and composition?

Three hypotheses guided this work: **H1)** reduced precipitation can homogenize plant community structure by reducing less abundant functional types. Plant species have evolved to thrive under modal climatic conditions on a given site in interaction with rare species and species abundances are maintained through stabilizing feedback. Strong changes in precipitation, such as intensification of drought events, would result in levels of water availability that are outside the modal range for which plant species are not adapted. **H2)** Severe physical disturbance affects community structure by shifting the relative proportion of woody species to herbaceous species. Disturbances are well-known to reduce the dominance of long-lived woody species and increase the abundance of herbaceous species, especially non-native species when propagules are present. The severity of disturbance effects are modulated by the species identity of the dominant woody plants and their ability to recover from a disturbance, as well as the amount of short-term precipitation that occurs following a disturbance. **H3)** Changes in precipitation interact with physical disturbance to increase the net effects on plant community structure compared with disturbance alone, and these effects are modulated by long-term precipitation patterns over time. Because long-term precipitation patterns create the modal range of resource within ecosystems and result in different plant communities across sites, differences in resources over long-timescales shape an ecosystem's ability to recover from disturbance.

Methods

I selected sites in three unique dryland ecosystems for this study: the Mojave Desert, the Chihuahuan Desert, and the Great Basin Desert (Table 3.1, Appendix Figure S4.1.1). Each ecosystem is an arid (Mojave and Chihuahuan) or semi-arid shrubland (Great Basin) and experience seasonal dry periods when the evaporative demand of the atmosphere exceeds precipitation, with different seasonality of precipitation at each site (Appendix Figures S3.1.2-3.1.6). I selected sites and applied experimental treatments in the summer of 2019 and maintained the experiment for three additional growing seasons, concluding the experiment in 2022. For the duration of the experiment, sites were protected from livestock grazing while native herbivores were not excluded.

In each of the three sites, I delimited 40 2.5 x 5 m plots and randomly assigned the four experimental treatments (disturbed and undisturbed in ambient and reduced rainfall). I replicated treatments 10 times each across these 2.5 x 5 m plots to yield 40 plots in total. I selected the plot size to capture the ecological dynamics of the dominant shrub species in this study as well as the interspace immediately surrounding the shrubs.

I used a passive rainfall manipulation technique to reduce ambient precipitation in this study. Specifically, shelters were constructed around plots and slats were placed to intercept incoming precipitation and move it off the plot. All infrastructure was at least 30 cm above the plant canopies. The slats were V-shaped acrylic and allowed the transmission of photosynthetically active radiation while intercepting precipitation. There were 14 slats on each of plot half for Mojave, 10 for Great Basin, and 16 for Chihuahuan sites. I evenly spaced the acrylic slats across the 2.5 m width of the plot for each of these precipitation reduction levels. The plots were not trenched due to the high level of disturbance and data interpretation complications trenching can cause (Ngao et al. 2007, Beier et al. 2012). The rainout shelters were constructed at each site in 2019 on relatively flat areas with vegetation representative of the site. Since dryland vegetation is heterogeneous in space, I centered the plots on individual shrubs so that vegetation was similar across all plots prior to treatment. I selected shrubs that were typical of each site in size, number of stems, and canopy vigor. These shelters were maintained until the end of the growing season in 2022, thus allowing for the rainfall manipulations to occur for three growing seasons.

I determined the degree of rainfall exclusion and simulated first-percentile precipitation based on long-term historical precipitation extremes unique to each site. This first-percentile approach considers the variability of annual precipitation over time within a site to determine the lowest annual rainfall amount received at a site over the previous 100 years. After identifying the driest of the last 100 years, I calculated the percentage difference in precipitation amount between the driest of the last 100 years and mean annual precipitation within a site. This percentage difference provided the percentage rainfall reduction amount that I would design to be intercepted with the passive rainfall exclusion shelters. In this manner, I scaled precipitation reductions to achieve a 1-in-100 year low rainfall year when precipitation was average for a site. Thus, the precipitation reduction treatments relative to the control resulted in a reduction of

40% reduction in ambient precipitation at the Great Basin site, 60% at the Mojave site, and 70% at the Chihuahuan site (Table 4.1, Figure S4.1.1).

To understand how the experimental treatments affected available soil moisture across sites and sampling years, I used soil moisture data from my sensor array within each site across the duration of my field experiment. Specifically, I compared mean volumetric water content (VWC) in disturbed and undisturbed conditions within each site and within ambient and experimentally reduced precipitation regimes. I calculated mean VWC by taking all values collected by sensors within an experimental treatment and creating a single mean value to represent that site-treatment pairing. I calculated the mean percent change in VWC resulting from disturbance in each of my six unique site-precipitation regime combinations and compared them within sites and across mean annual precipitation.

Table 4.1. Site characteristics for the Nevada National Security Site, NV, Orchard Combat Training Center, ID, and Jornada Basin LTER, NM. Precipitation seasonality represents the amount of precipitation that occurs during warm vs cold seasons and is calculated by taking the correlation coefficient of monthly temperature and precipitation. The aridity index is a metric of dryness and is calculated as the ratio of mean annual precipitation to evapotranspiration. Rainfall reduction is the amount of ambient precipitation reduced by rainfall exclusion shelters at each site.

	Mojave Desert	**Chihuahuan Desert**	**Great Basin Desert**
Climate type	Arid	Arid	Semiarid
Latitude	36°49'N	32°33′ N	43°15'N
Longitude	116°01'W	106°49′ W	116°13'W
Mean annual precipitation (mm/year)	147	245	271
Precipitation seasonality (correlation coefficient of monthly temperature and precipitation)	-0.12	0.64	-0.87

Mean annual temperature (degrees C)	6.4	14.7	6.6
Aridity Index (mean annual precipitation/potential evapotranspiration)	0.08	0.16	0.18
Rainfall reduction (relative to ambient)	-60%	-70%	-40%
Soil texture class	Sandy loam	Fine sandy loam	Silt loam
USDA soil type	Ultisol	Aridisol	Aridisol
Soil Unit	Corbilt gravelly fine sandy loam, warm	Simona-Harrisburg association	Chilcott-Catchell-Chardoton complex

I created a physical disturbance to plant communities and the soil surface. I used a novel technique to apply a one-time physical disturbance to the experimental plots. Using a 4-wheel drive all-terrain vehicle, I pulled a JRCO model MSAT 48" (122 cm) tow-behind spiked drum aerator (Figure S3.1.6). This steel implement had 102 spikes (7 cm long x 5 cm wide at the base) welded to the outside of the drum and weighed 165kg when filled with water. I estimate the all-terrain vehicle and operator to weigh 340kg. Each plot receiving this treatment underwent exactly four overlapping passes from this implement in alternating directions. I also subjected a 1-meter buffer around the plot to this same treatment to minimize edge effects within the plots.

I observed that the disturbance method I used caused crushing and compaction of aboveground plant material and the soil surface. Unlike a grazing disturbance, the disturbance did not remove any aboveground biomass and left all plant material in place following the event. The repeated passes of the machinery and the weight and destructive capability of the spiked drum aerator caused the key mechanisms of disturbance relevant to the research questions in a manner that should apply beyond the specific experimental context. While this disturbance method was novel in these ecosystems and not a perfect mimic of a real-world disturbance, the destructive outcome is likely similar to other actions that cause disturbance to intact native vegetation and surface soil layers, such as operating tracked vehicles off of established roads.

I evaluated treatment effects each year for four years- once to collect pre-treatment data in 2019 when I deployed the experiment, and then each year at the peak of each site's growing season in 2020, 2021, and 2022. To estimate plant cover, I measured three 5 m long permanent cover lines per plot, recording all living plant parts (basal or canopy) at 1 cm increments along each of the three permanent cover lines in every plot. I did not record plant cover data for the first 20 cm and the final 20 cm of each cover line to minimize capturing edge effects in the data. I recorded all species cover at this 1 cm resolution, even when living plant parts of multiple species overlapped. I only recorded nonliving cover class elements (bare ground, litter, dead plants) when there was no living plant biomass at that position along the transect. In other words, I did not record nonliving cover class elements underneath living plant biomass. To measure shrub volumes, I measured two perpendicular diameters and height.

I deployed soil moisture and temperature sensors at 0.5, 0-30, and 50 cm depths. To measure soil moisture at 0.5 cm depth, I deployed custom-manufactured soil moisture and temperature sensors. I measured volumetric soil moisture content and soil temperature in both the top 0-30 cm of the soil profile and at 50 cm depth every 30 minutes in four replicates of each treatment using Campbell Scientific CS650 probes and the data were logged onto CR300 or CR1000 data loggers. The 0-30 cm CS650 probes were installed vertically at the soil surface, pointing down into the soil profile. The majority of probes that I installed had 30 cm prongs that integrate soil moisture measurement along the entire 30 cm length. A portion of probes that I installed only had 15 cm prongs, but I display the data from both 30 cm length probes and 15 cm length probes as representing 0-30 cm of the soil profile for simplicity.

Importantly, the construction of the CS650 probe is such that soil moisture is measured along the entire length of the prongs on the sensor, while temperature is measured with a thermocouple embedded in the body of the sensor. Thus, I did not measure soil temperature at any positions in the soil profile other than 0 cm and 50 cm, as the sensors installed to measure 0-30 cm in depth still had the body of the sensor, and thus the thermocouple, above the surface of the soil profile. The 50 cm CS650 probes were installed with great care to capture soil water dynamics at that depth without disturbing the surface soil structure or vegetation. I accomplished this by carefully boring a 10 cm diameter shaft into the soil profile at a 45 degree angle until reaching a 50 cm depth. I then installed the CS650 probe at a 50 cm depth in the soil profile, using the soil I excavated in the installation process to bury the probe.

Analysis

I conducted all analyses in R v.4.3.2 (R Core Development Team 2024). I standardized nomenclature to USDA PLANTS (USDA, NRCS 2017). I identified plants that did not possess adequate identifiable characteristics at the species level to genus or functional type. I separated species into functional groups to assess changes in ecosystem structure; groups were defined as “shrubs”, “sub-shrubs”, “grasses”, “leaf succulents”, and “forbs”. I also assigned each species a native or non-native classification based on USDA PLANTS. I calculated vascular plant cover by summing the cover of each species measured within individual transects for and averaging across the three transects within each plot. I used relative plant cover from the cover transects to calculate evenness (Jost 2010) and summed the number of unique species encountered in sampling within plots to calculate species richness.

To explore my first and second hypotheses and understand how functional type abundances changed from individual and combined drivers, I tested for differences in cover of each function group between treatments with a Chi-squared test of proportions using the "chisq.test" function of the "stats" package (R Core Team, 2024). Chi-squared tests allowed me to test if the proportion of functional types changed from pretreatment values after I applied experimental treatments.

I further explored my first and second hypotheses with non-metric multidimensional scaling (NMDS) ordinations based on Bray–Curtis dissimilarity matrix. This approach allowed for understand overall differences in plant community composition among treatments and sites. For both ordinations, I visualized the NMDS using the "ggplot2" package (Wickham 2016) and the "stat_ellipse" function with 95% confidence intervals. I tested for homogeneity of variance (PERMDISP) using the "betadisper" and "permutest" functions from the "vegan" package (Oksanen et al. 2015), and used a t-test to explore differences in dispersions between disturbed and undisturbed plots within sites. I tested for significant differences among plant communities between treatments and sites by performing permutational multivariate analysis of variance (PERMANOVA) using the "adonis" function (999 permutations; Oksanen et al., 2015).

To address my third hypotheses and test for driver interactions, I specifically tested for the effects of precipitation and disturbance by modeling evenness and richness responses within and across sites. Disturbance was considered a binary variable in all models. To test for the interaction of precipitation and disturbance in the response variables across all years of experimental data, I tested the slope of the richness–precipitation and evenness–precipitation relationships in both disturbed and undisturbed conditions within and across sites. I fit a linear mixed effects model using the “lmer” function in the nlme package in R and included site as a random effect in the global model, with disturbance and precipitation included as fixed effects (Zuur et al. 2009, Bates et al. 2015).

To address all three of my hypotheses and explore multiple aspects of plant communities simultaneously, I generated rank-abundance curves across all replicates of each treatment year within sites. I generated rank-abundance curves using the “rankabundance” function in the “BiodiversityR” package (Kindt and Coe 2005). Rank-abundance curves express density of individuals of each species as a function of the range of abundance of species (Mueller-Dombois and Ellenberg 1974, Magurran 2004). I fitted linear models (in the form: $y = mx+b$) for rank-abundance curves for ease of comparison across treatments and sites. To fulfill all the assumptions of the linear model (normality and homoscedasticity), the abundance data are logarithmically transformed. I tested differences between slope of experimental treatments of these log-transformed slopes using ANCOVA. The slopes of the straight-line equation are considered indicative of dominance and/or evenness in the treatments (Magurran 2004); curves with steeper slope correspond to dominance by only a few species and flatter curves indicate greater evenness (Gotelli and Colwell 2001). To quantify specific changes in richness, evenness, rank change, species gains, and species losses from individual plots, I used the "RAC_change" function of the "codyn" package (Hallett et al. 2016).

Results

Climate and soil moisture dynamics

Only one site received around average precipitation during the experiment (the Chihuahuan), while the Mojave and Great Basin sites experienced below and above average precipitation, respectively. The Mojave site experienced a severe drought for the second and third year of the experiment (2021-2022; Figure S4.1.2). Ambient precipitation at that site was 46 and 57 mm in 2021 and 2022, respectively. The severity of this drought event can be contextualized by comparing these annual values to the 1-in-100 year minimum precipitation I determined when developing the experimental design: 42 mm. The Great Basin site experienced above average precipitation during each of the four years of the experiment, and the Chihuahuan site experienced near average precipitation.

Soil moisture was dynamically affected by disturbance along the precipitation gradient I sampled (Figure 4.1, Figures S4.1.13 and S4.1.14). Within and across sites, soil moisture was less available in disturbed conditions at lower precipitation values and more available in disturbed conditions as precipitation increased.

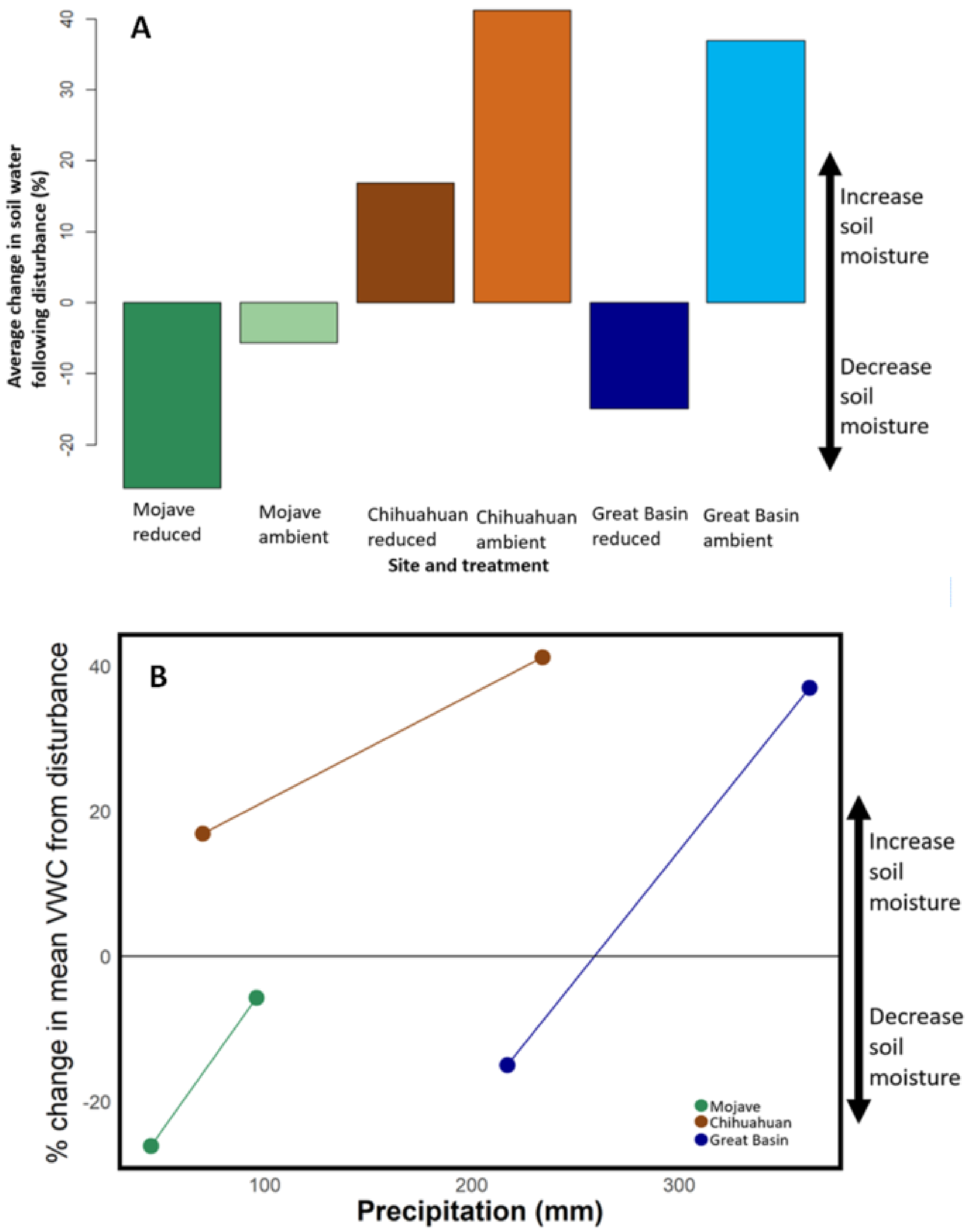

Figure 4.1. Percent change in mean volumetric water content (VWC) resulting from disturbance across mean ambient and mean experimentally reduced precipitation values across treatment years within sites by treatment within sites (A) and across an annual

precipitation gradient (B). Each value represents the comparison between disturbed and undisturbed conditions within a site at each precipitation value (((VWC_undisturbed-WVC_disturbed)/(WVC_undisturbed))*100), averaging across three years of post-treatment data to generate one ambient precipitation change value and one experimentally reduced precipitation change value per site. Mojave (green bars, points, and lines), Great Basin (blue bars, points, and lines), and Chihuahuan (brown bars, points, and lines). Data are from soil moisture sensors in the surface soil layers (0-30 cm) and were measured year-round.

Richness and evenness sensitivity to interannual precipitation and disturbance across sites

Across sites, richness tended to increase with annual (i.e. short term) precipitation in support of the first hypothesis. Disturbance did not substantially change the relationship between richness and short term precipitation at any site. Richness sensitivity to precipitation was greatest at the lowest mean annual precipitation site, the Mojave (Figure 4.2; Figure S4.1.2), though this relationship reflects the intense regional drought that was occurring at that site in 2021-2022.

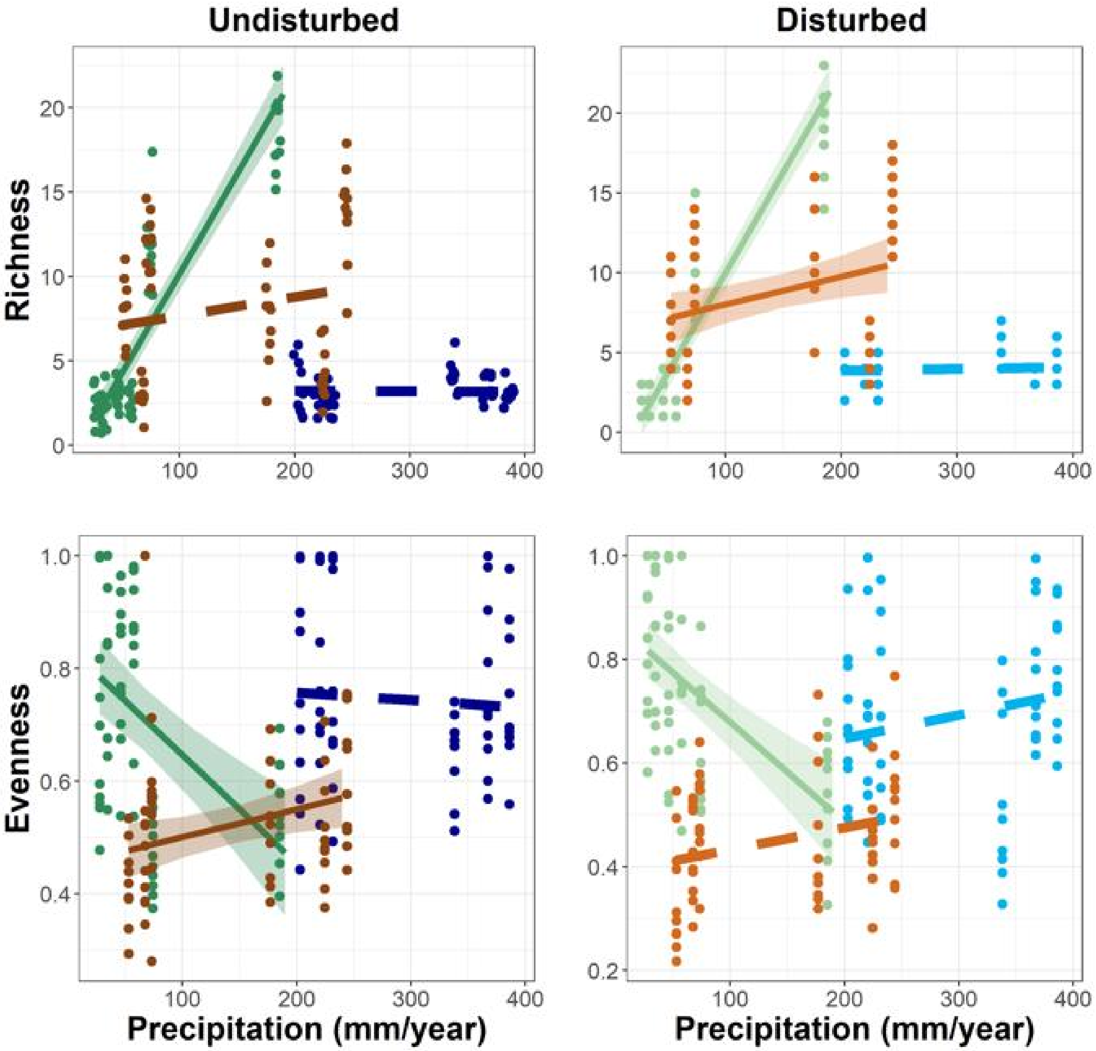

Figure 4.2. Species richness and evenness across a precipitation gradient in disturbed and undisturbed conditions in three dryland ecosystems. Green = Mojave, Brown = Chihuahuan, Blue = Great Basin. The figures in the right column display the sensitivity of richness (upper) and evenness (lower) to gradients of short term precipitation across each site's mean annual precipitation value, with undisturbed conditions plotted in dark colors, and disturbed conditions plotted in light colors. Data are from all three treatment years of the field experiment.

Evenness was affected by short-term precipitation manipulation, with the Mojave site (the driest site in this experiment) strongly positively affected by precipitation and the other sites have a negative or near zero relationship (Figure 4.2). Disturbance did not substantially change the relationship between evenness and precipitation at any site. Evenness sensitivity to precipitation was greatest at the lowest mean annual precipitation site (Figure 4.2). Model results for all richness and evenness relationships with precipitation and disturbance can be found in Supplemental 4.2 (Tables S4.2.1-S4.2.6).

Individual and combined effects of disturbance and precipitation on species rank abundance and functional type abundance

Disturbance and precipitation changed the abundance of functional types across sites, in partial support of the second hypothesis (Figure 4.3, Figures S4.1.6-S4.1.8). I found significant differences in abundance and composition of plant communities and cover elements across the experimental treatments. As expected, no site had significant differences among treatments in the pretreatment year, but the Mojave and Great Basin sites were significantly different across treatments in years 1-3, and the Chihuahuan site had significant differences in years 2 and 3 only (Table S4.2.7). Broadly, I found a shift from woody plants to herbaceous plants resulting from disturbance across precipitation regimes in two of the three sites (Mojave and Great Basin), but found the opposite pattern at the Chihuahuan site (Figure 4.3, Figures S4.1.6-S4.1.8).

Figure 4.3. Percent cover of plant functional types and nonliving cover class elements (bare soil, standing dead plants, and litter) by site, treatment, and year. Note: because I recorded overlapping plant canopies, the methods accommodated recording cover values >100%.

The effects of the treatments and differences in richness and evenness are visible across all sites (Figure 4.1.3, Figures S4.1.6-S4.1.11). Prior to the experimental manipulations, the shapes of rank-abundance curves were identical across treatments, but treatment differences are clear following treatment initiation within each site-year (Figure S4.1.4). The slopes of the log transformed rank-abundance curves differed significantly across treatments during each treatment year at the Mojave and Chihuahuan sites, but only during the third treatment year (Figure 4.4, Tables S4.2.11-S4.2.13). The greatest evenness was in either the control or reduced precipitation treatment across sites-disturbance treatments always had lower evenness than undisturbed treatments across all sites and years (Figure 4.4).

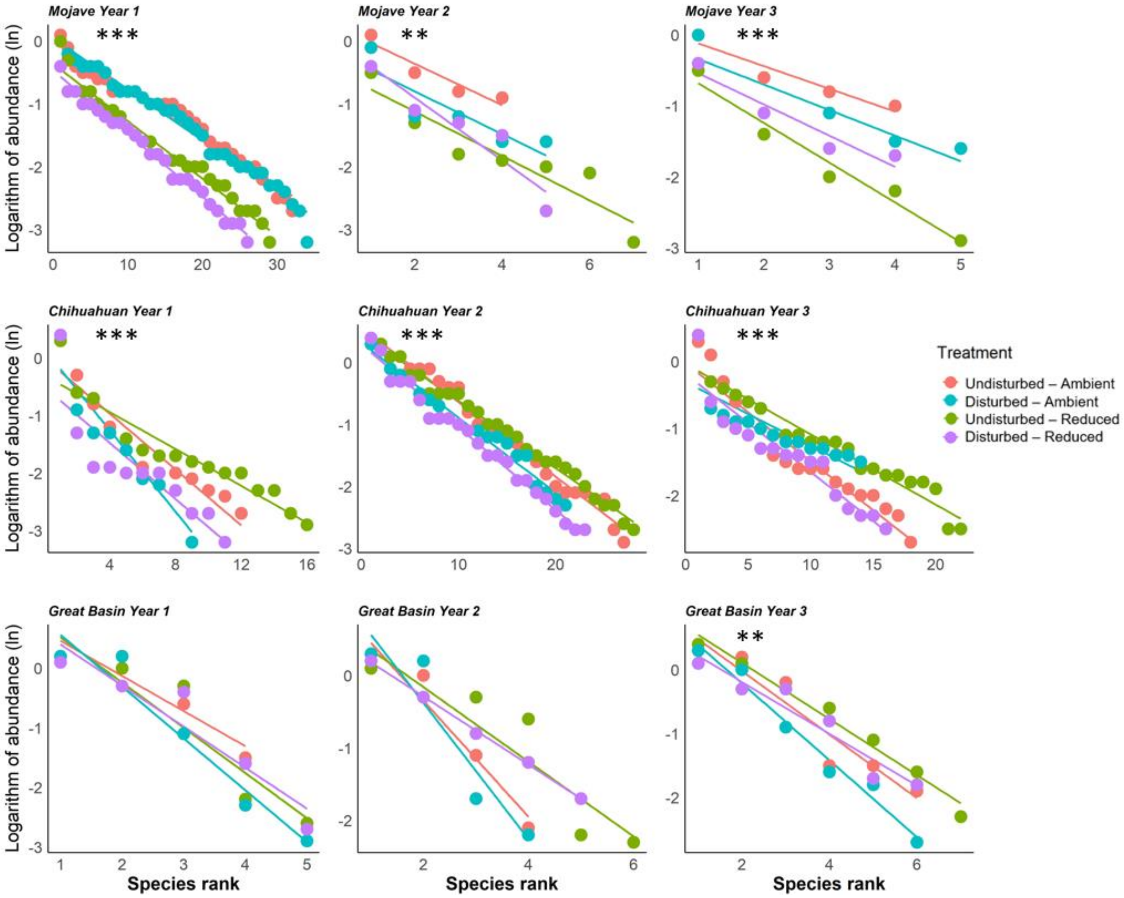

Figure 4.4. Rank-abundance curves for each site, treatment, and year. Log-transformed plant species abundances are plotted against their rank in the community. The steepness of each slope indicates evenness with that community. Differences among treatments as determined by ANCOVA are indicated with asterisks.

Reducing short-term precipitation changed the direction of the relationship between the slopes rank-abundance curves and long-term precipitation, in support of the third hypothesis (Figure S4.1.4). Under the ambient precipitation regime, undisturbed communities had a negative relationship with mean annual precipitation (long-term precipitation) and disturbed communities had a positive relationship. The slopes of rank-abundance curves across a short-term precipitation gradient were most sensitive as long-term precipitation decreased. The Great Basin site, which had the highest long-term precipitation in the experiment, had the least sensitive slopes of rank-abundance curves. The presence of disturbance increased the sensitivity of rank-abundance curve slopes across all three sites (Figure S4.1.3, Figure S4.1.4).

The treatments and the severe natural drought the Mojave site experienced changed the rank abundance curves of the site in several ways (Figure 4.5). In year one, reduced precipitation caused by the rainout shelters in the reduced precipitation and reduced precipitation + disturbance treatments reduced the total abundance of plants in those plots and reduced richness and evenness relative to the control. The effects of severe drought at this site are readily apparent in years 2 and 3 of the experiment as richness is dramatically reduced. All experimental manipulations have reduced abundance relative to the control in years 2 and 3 of the experiment, indicating that physical disturbance reduces resiliency to climate extremes in this system.

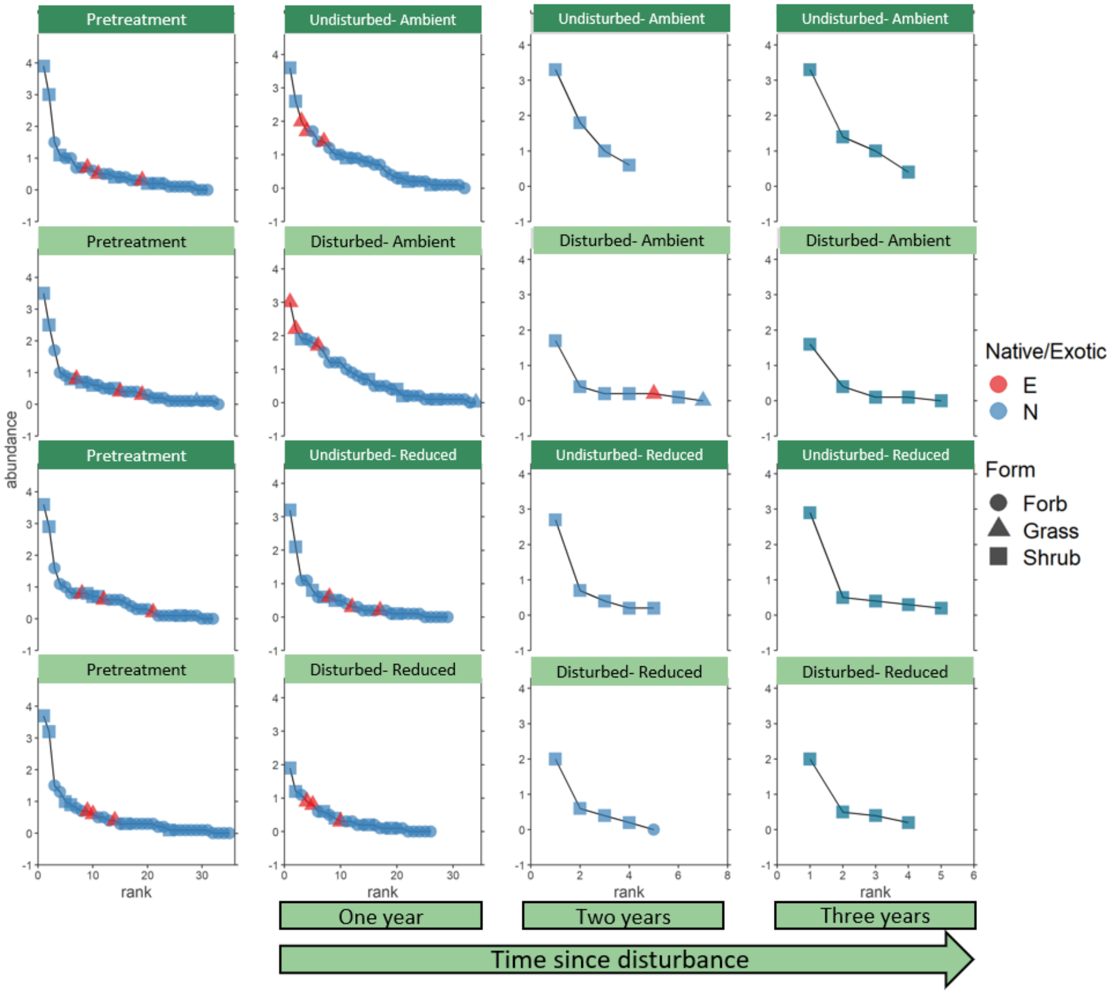

Figure 4.5. Rank abundance curves across years for each treatment in the Mojave site: pretreatment and treatment years 1-3. Plant species abundances are plotted against their rank in the community. Plots represent treatment-year pairings and are identified as either disturbed or undisturbed and receiving either ambient or experimentally reduced precipitation. Plots are arranged by treatment and year: treatments are within rows and years are within columns. Data across all replicates within a treatment are plotted within each panel. Functional types are represented with unique shapes: forbs are plotted as circles, grasses are plotted as triangles, and shrubs are plotted as squares. Species provenances are represented with colors: native species are plotted in blue, and non-native species are plotted in red.

In the Chihuahuan, the dominant shrubs were not affected by either disturbance or precipitation reduction (Figure 4.6, Figure S4.1.7). The dominant grasses decreased in dominance with all the experimental treatments: by the end of the experiment, each treatment except the control had lost black gramma as the second most dominant plant in the plots. These results strongly support existing conceptual frameworks of vegetation dynamics in this ecosystem: disturbance and reductions in precipitation push plant communities towards shrub-dominated alternate stable states.

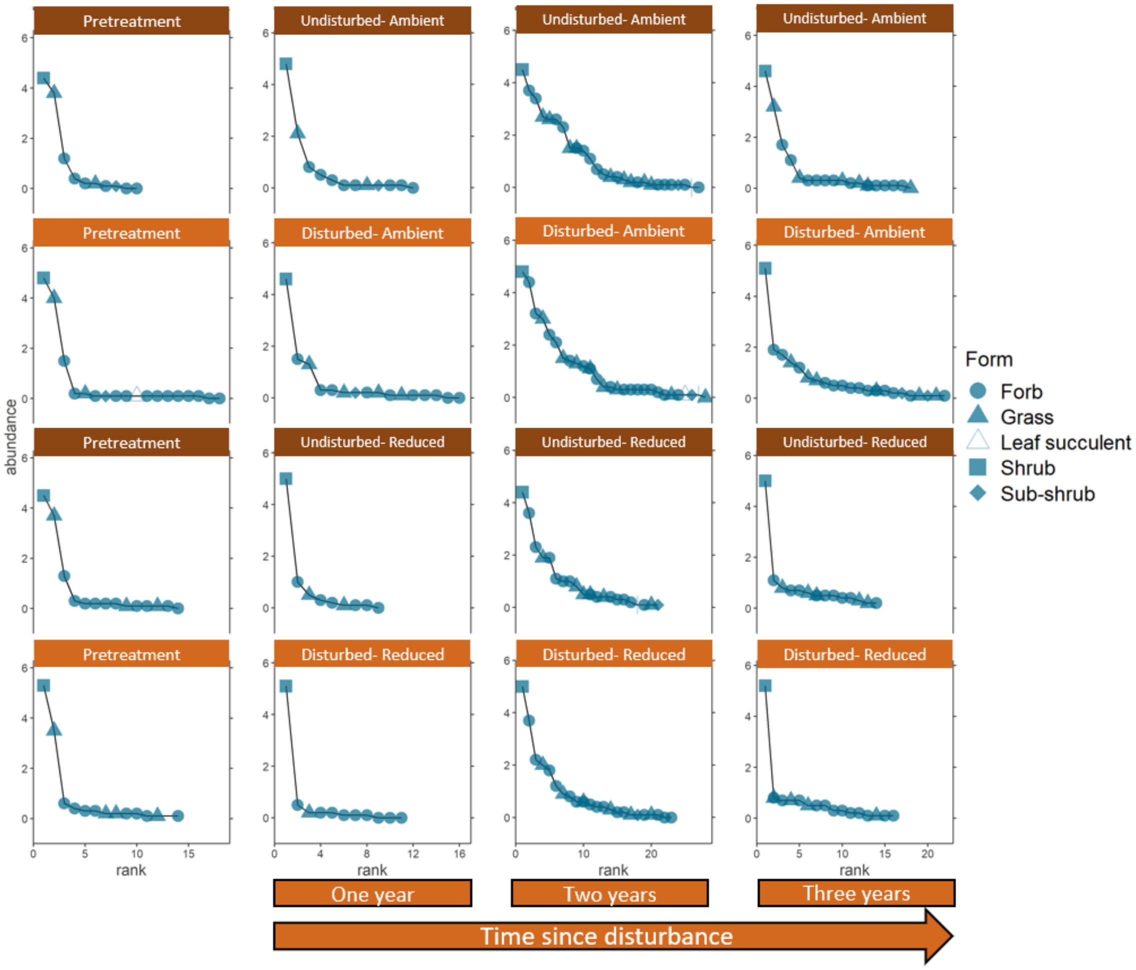

Figure 4.6. Rank abundance curves across years for each treatment in the Chihuahuan site: pretreatment and treatment years 1-3. Plant species abundances are plotted against their rank in the community. Plots represent treatment-year pairings and are identified as either disturbed or undisturbed and receiving either ambient or experimentally reduced precipitation. Plots are arranged by treatment and year: treatments are within rows and years are within columns. Data across all replicates within a treatment are plotted within each panel. Functional types are represented with unique shapes: forbs are plotted as circles, grasses are plotted as solid triangles, leaf succulents are plotted as open triangles, sub-shrubs are plotted as diamonds, and shrubs are plotted as squares. There were no

non-native species present at this site, so there is no color designation of species provenance in this figure.

Changes in the rank-abundance curves relative to the control are evident across all three treatment years at the Great Basin site (Figure 4.7, Figure S4.1.8). Reduced short-term precipitation gradually diverges with control conditions, with the biggest difference in year 3. The disturbance treatment changed the most abundant species from a perennial native shrub to a non-native forb species under ambient short term precipitation; in other words, the disturbance treatment resulted in increased abundance of this non-native plant, and when the disturbance and reduced precipitation treatments were applied together, the reduced precipitation reduced the non-native plants' success relative to when disturbance occurred alone (Figure 4.7).

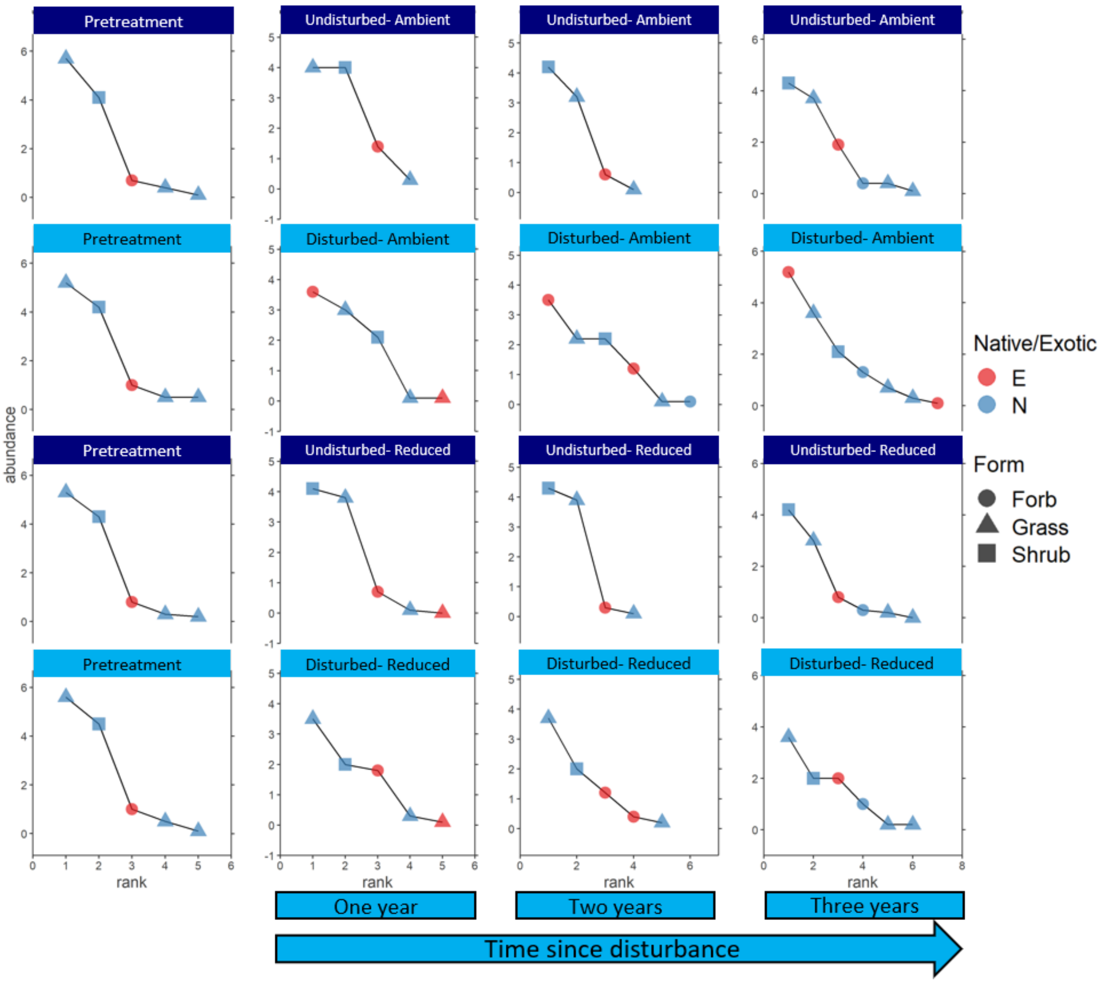

Figure 4.7. Rank abundance curves across years for each treatment in the Great Basin site: pretreatment and treatment years 1-3. Plant species abundances are plotted against their rank in the community. Plots represent treatment-year pairings and are identified as either disturbed or undisturbed and receiving either ambient or experimentally reduced precipitation. Plots are arranged by treatment and year: treatments are within rows and years are within columns. Data across all replicates within a treatment are plotted within each panel. Functional types are represented with unique shapes: forbs are plotted as circles, grasses are plotted as triangles, and shrubs are plotted as squares. Species provenances are represented with colors: native species are plotted in blue, and non-native species are plotted in red.

Disturbance and precipitation effects on non-native species abundance

The within-site rank-abundance curves provide a nuanced view of where non-native species fell into the hierarchy of species within sites, and the mechanisms behind these patterns can be further unpacked by exploring the relationship between non-native species abundance and mean annual precipitation. At the two sites with non-native species present (Mojave and Great Basin), I found that non-native species increased with increasing short-term precipitation, but the magnitude of increase was greatly exaggerated after disturbance (Figure 4.8, Tables S4.2.14 & S4.2.15).

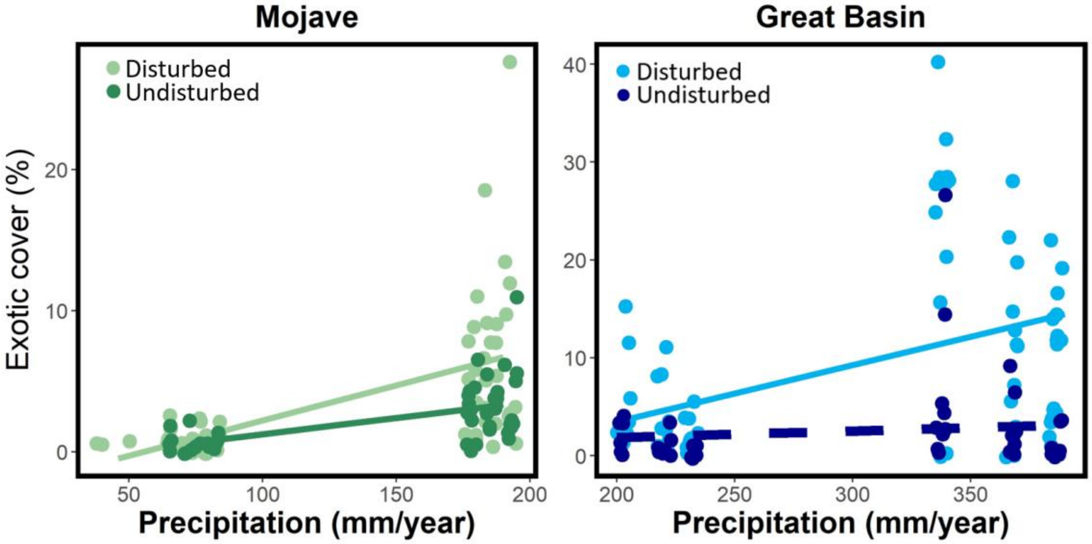

Figure 4.8. Cover of non-native species across short term precipitation gradients at the Mojave and Great Basin sites. Disturbed conditions are plotted in light colors, and undisturbed conditions are plotted in dark colors. Data are from all three treatment years of the field experiment.

Individual and interactive effects of disturbance and precipitation amount on community composition

Disturbance and precipitation reductions interacted to change both mean and variability of plant communities within sites: precipitation reductions and disturbance changed mean composition across all sites and years relative to control conditions (Figure 4.9, Table 2).

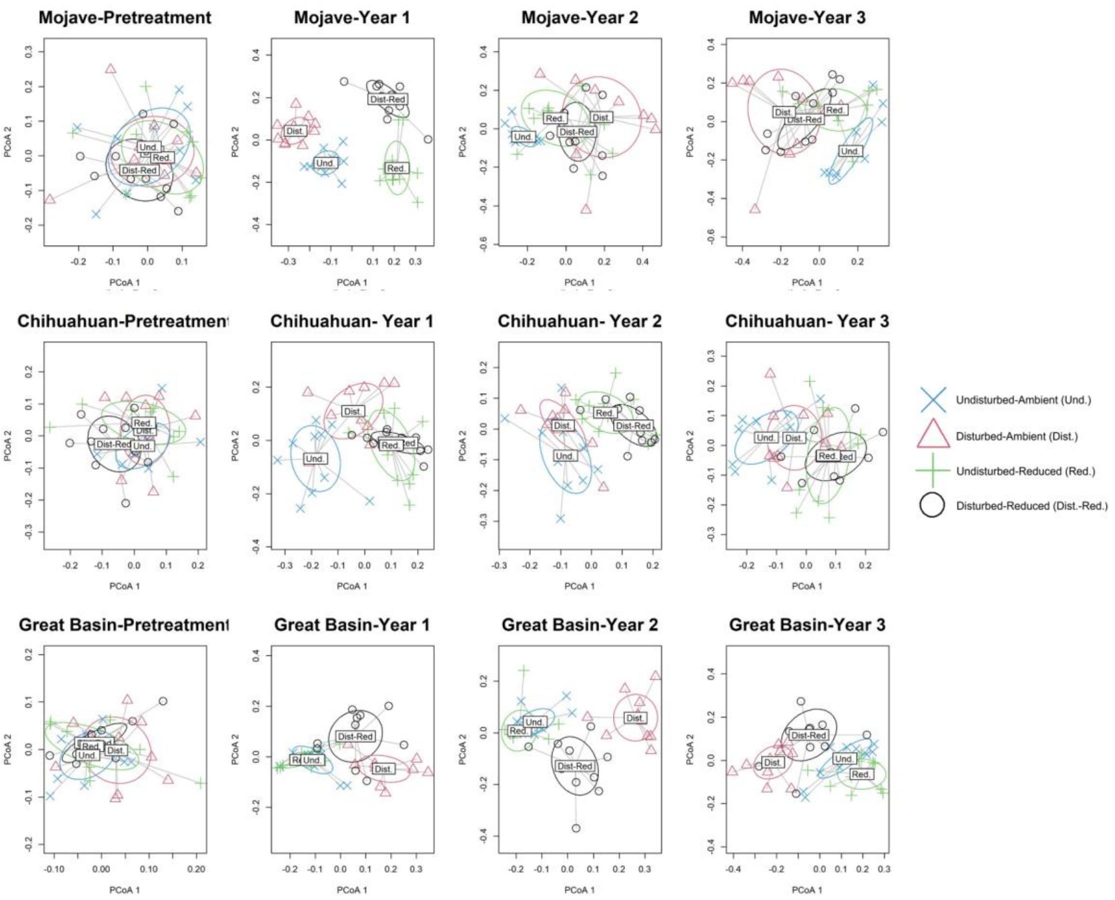

Figure 4.9. Nonmetric multi-dimensional scaling plots for all replicates within each site and year. Within each site, experimental treatments are displayed with different shapes: undisturbed, ambient precipitation plots are plotted as blue Xs and are labeled with the abbreviation “Und.”; disturbed, ambient precipitation plots are plotted as red triangles and are labeled with the abbreviation “Dist.”; undisturbed, reduced precipitation plots are plotted with green pluses and are labeled with the abbreviation “Red.”; and disturbed, reduced precipitation plots are plotted with black circles and are labelled with the abbreviation “Dist-Red”.

Table 4.2. Rank abundance curve and compositional response across experimental treatments at three study locations. Each row in the table represents a comparison between two experimental treatments, here I compare control with reduced precipitation, disturbance, and reduced precipitation + disturbance treatments, as well as comparing reduced precipitation and reduced precipitation x disturbance treatments. In the evenness and richness columns for each site, changes in these community metrics are identified by color and a positive (+) or negative (-) symbol to denote the change from the first treatment identified in each coupling (left side) with the second treatment identified in each coupling (right side). No change between the treatments in a comparison is listed as “na”. In the mean and dispersion columns, shifts in the centroid in multivariate community space as measured by PERMANOVA are displayed in the mean column and differences in variance in multivariate community space as measured by PERMDISP are displayed in the “Disp.” column.

	Mojave				**Great Basin**				**Chihuahuan**			
Treatment/Year Combinations	RAC responses		Composition		RAC responses		Composition		RAC responses		Composition	
	Even	Rich	Mean	Disp	Even	Rich	Mean	Disp	Even	Rich	Mean	Disp
Y1 Control: Reduced PPT	-	-	***		-	+			-	-	***	
Y1 Control: Disturbance	-	+	***		-	+	***		+	+	*	
Y1 Control: Reduced PPT+ Disturbance	-	-	***	.	-	+	***	*	-	-	**	.
Y1 Reduced PPT: Reduced PPT+ Disturbance	+	-	***		+	**na**	**		+	+	***	
Y2 Control: Reduced PPT	-	+	**		-	+			+	-	**	

Y2 Control: Disturbance	-	+	***	**	+	+	***	*	+	+		**
Y2 Control: Reduced PPT+ Disturbance	-	+	***		+	+	***	*	+	-	**	
Y2 Reduced PPT: Reduced PPT+ Disturbance	-	**na**	***		+	+	***	.	-	+	***	
Y3 Control: Reduced PPT	-	+	**		-	**na**			+	-	***	
Y3 Control: Disturbance	-	+	***		-	+	***		+	+	***	
Y3 Control: Reduced PPT+ Disturbance	-	**na**	***		+	**na**	**		+	-	***	
Y3 Reduced PPT: Reduced PPT+ Disturbance	+	-	***		+	**na**	**		-	+	***	

Changes in mean community dispersion had different patterns within each of the three sites (Figure 4.10, Table 4.2). The largest changes in mean dispersion were from disturbance, and disturbance increased dispersion at the Mojave site in ambient conditions only (t = -3.99, df = 58, p < 0.001), decreased dispersion at the Chihuahuan site in reduced rainfall conditions only (t = 2.44, df = 57.02, p-value < 0.05), and increased dispersion at the Great Basin site across both ambient (t = -2.14, df = 57.9, p-value < 0.05) and reduced rainfall conditions (t = -2.78, df = 55.39, p-value < 0.05). At the Mojave and Chihuahuan sites, changes in dispersion were only present within one precipitation treatment, indicating an interaction between disturbance and reduced precipitation.

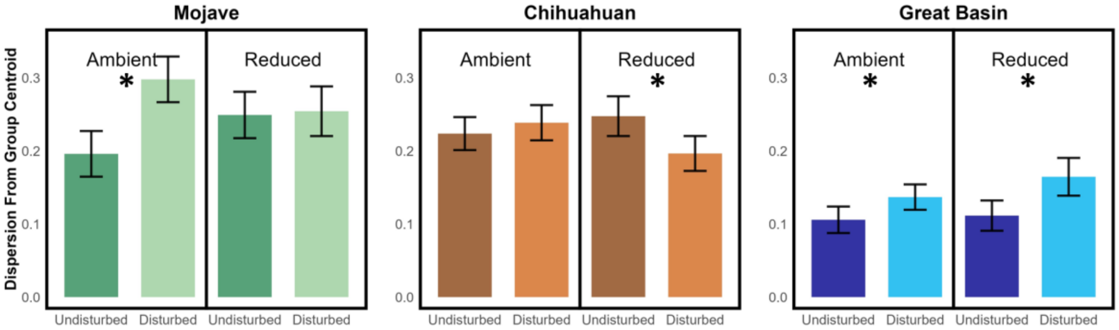

Figure 4.10. Differential effects of disturbance and precipitation on community dispersion (Bray-Curtis distances; mean ± SE). Asterisks indicate significant difference between disturbed and undisturbed conditions within precipitation bins using a t-test ($p < 0.05$).

The mixed models of community dispersion across within-site precipitation indicated that dispersion trended positively or negatively with short-term precipitation at the Chihuahuan and Mojave sites, depending on the presence of disturbance (Figure

S4.1.5, Tables S4.2.16-S4.2.18). Dispersion at the Great Basin was negatively related to short term precipitation in both undisturbed and disturbed conditions.

Discussion

As expected, both physical disturbance and precipitation reductions changed the plant communities at all three dryland sites as indicated by multiple measures of diversity within communities. I detected changes in richness and evenness within sites across sample years, but broadly speaking, these metrics were relatively insensitive to the experimental treatments. Specific aspects of community composition showed much larger responses to the treatments: relative abundance of plant functional types, species rank abundance, and community dispersion. These analyses indicate that in part, changes in community composition were driven by changes in soil water availability, with predictable decreases in soil water from precipitation reductions and increases in soil water resulting from disturbance. I found that these multivariate measures of community composition provide insight as to how global change drivers can affect dryland plant communities.

Precipitation effects on dryland biodiversity

I found that short-term precipitation had strong control over dryland plant species richness, and this effect attenuated as long-term precipitation increased. The sensitivity of dryland richness to precipitation was greatest at the Mojave site, indicating that climate change effects on richness may be strongest in the most water-limited areas. Abiotic factors are likely the most important factor in determining species richness in drylands

(Cleland et al. 2013), and the sites showed decreasing sensitivity to short term precipitation as long term precipitation increased (i.e., in wetter sites). These findings agree with previous experimental approaches and support the idea that compositional changes are typically less severe than the changes exhibited by the most responsive species (Zhang et al. 2020). Stated another way, experimental effects on richness alone should be interpreted in light of the composition of each community. Across long-term precipitation gradients, the relationship between richness and precipitation can be hump-shaped (Smith et al. 2022), and it is possible that the stronger slopes I found between richness and precipitation in the Mojave (the driest site) versus the Great Basin (the wettest site) were capturing this nonlinear change between richness and precipitation across large rainfall gradients.

While the relationship between water availability and richness has received comparatively more attention in the literature (Noy-Meir 1973, Adler et al. 2011, Jordan et al. 2020), evenness has received relatively less attention (Smith et al. 2022), making these results especially useful for extending conceptual frameworks of the drivers of evenness in dryland systems. For any richness, high or low, there can be a broad range of evenness values (Jost 2010). Understanding that evenness differences were large across years because of changes in precipitation, differences in evenness within years provide insight as to what effects the experimental treatments had on plant communities. The strong drop in richness at the Mojave site and the strong increase in richness at the Chihuahuan site driven by below- and above-mean precipitation, respectively, changes how one might consider evenness across years of the experiment (Figures S4.1.3 & S4.1.4). Competitive interactions may be a factor determining the negative relationship between water availability and evenness (Smith et al. 2022), and species richness and evenness likely have different drivers along resource gradients (Stirling and Wilsey 2001). As community metrics, richness and evenness do not clearly capture the changes in plant communities that occurred because of the experimental treatments. Further, evenness is scale-dependent and can be affected by plot size (Weiher and Keddy 1999). I show that community composition did change as the result of the treatments, but these changes are not apparent in richness or evenness patterns: the changes manifest as changes in species abundances and species rank.

Disturbance effects on dryland biodiversity

Sites with higher richness inherently have more species that could be lost from a disturbance, making this metric of plant communities somewhat dependent on initial richness values (i.e., a greater range of variability in the chosen response variable). Thus, we might have expected larger effects of disturbance on richness as species richness increased across these sites (Murphy and Romanuk 2014). Species richness tends to recover from disturbance more quickly than composition in drylands because a large portion of typical species pools in drylands are annual plants, which are able to colonize a site quickly following a disturbance (Abella 2010, Alon and Sternberg 2019). Dryland climate change impacts and responses to human disturbances will likely be controlled at the site scale by soil and topographic properties, which exert key modifying characteristics on available soil water over time (Munson et al. 2015). While this experiment confers some cross-site generalities, broader ecological frameworks indicate that these within-site results could have been modified not only by different climates, but also by differences in soil texture and structure (Peters et al. 2011).

Richness and evenness can respond differently to disturbances, and I found contrasting patterns of richness and evenness responses to disturbance across the sites. These results reinforce that evenness responses to disturbance across precipitation gradients are not well understood by existing theory (Hillebrand et al. 2008, Smith et al. 2022). Evenness can respond more quickly to human caused disturbances than richness, making this a key response variable to consider across ecosystem types in an era of global change (Hillebrand et al. 2008). Within each site, evenness was more responsive to disturbance than richness (Figures S4.1.4-S4.1.8). This change in evenness has important consequences for ecosystems long before any species are driven to extinction. These changes in evenness can have large influences on the structure and function of ecosystems but can remain undetectable if richness is the only response variable. Across drylands globally, evenness peaked at intermediate levels of woody cover (Soliveres et al. 2014). Because the disturbance level reduced woody cover, it drove these systems into a more uneven state, likely reducing ecosystem function following disturbances (see previous chapter).

Longstanding models of disturbance and succession developed for more mesic systems are not always directly applicable in drylands. Theory predicts that the magnitude of change following a pulse disturbance is proportional to the amount of energy flux in that system (Jentsch and White 2019). Energy flux in dryland systems is proportionally less than mesic systems as measured by net primary productivity (Lauenroth 1979), meaning disturbance pushes these low productivity systems to even lower productivity. However, ecologists must consider the relative decrease in ecosystem function and changes in community states following a disturbance in drylands. Traditional concepts of ecological succession are much less predictive in dryland systems, likely because interannual variability in climate only occasionally creates conditions where dominant species are able to reestablish, whereas mesic systems have a more predictable modal climate and many more dominant species possess resprouting ability following a disturbance (Grime 1979, Chapin et al. 2011). I likely would have to observe the plots in this experiment for multiple decades to see a complete return to community structure and composition prior to the disturbance treatment (Abella 2010).

Disturbance and precipitation interactive effects on dryland biodiversity

Short-term changes in precipitation and disturbance interacted across the dryland ecosystems I studied, with implications for how biodiversity should be managed in dryland ecosystems and what ecosystem services can be derived. The changes in richness, evenness, and composition I found indicate large consequences of changing land use and climate patterns across dryland ecosystems. Species richness can modulate a community's ability to resist and recover from a low precipitation period, but this effect tends to be most obvious over multiple-year dry periods (Kreyling et al. 2017). Species richness is linked to the total amount of resources and their temporal stability (Storch and Okie 2019), leading to higher richness in disturbed conditions because of less competition from the dominant plant species removed by the disturbance. Previous studies in water-limited ecosystems have found that precipitation affects richness more strongly than disturbance (Rito et al. 2017). Additionally, evenness has been shown to be unaffected by single environmental stressors across experimental communities but responsive to multiple environmental stressors across communities (Speißer et al. 2022). Cross-site analyses have found that grazing and precipitation can have both additive and interactive effects, and that low precipitation following a disturbance as was done in this experiment can favor perennial plants over annual plants and modify communities over time (Ruppert et al. 2015).

Disturbance reordered plant communities, changing dominance and relative abundances of key plant species and functional types**.** Rank abundance curves allow us to see patterns of change across the three plant communities that I sampled that I would not have otherwise detected through richness and evenness alone. Shifts in ranks may be a more important process on shorter time scales than shifts in species identities (Hillebrand et al. 2008), and community changes in drylands have been shown to be driven more by changes in species abundances than by changes in richness (Jones et al. 2017). Differences between control and treatment communities in manipulative experiments are rarely the result of species identity differences, and these observations support that, indeed, rank shifts drove much of the compositional differences that I observed (Avolio et al. 2022). Close examination of individual components of change within rank-abundance curves within replicates reflects how these treatments changed plant communities. Specifically, changes in rank, species gains, and species losses within each sample year reveal contrasting patterns across the individual and combined global change drivers in this experiment, highlighting that a single metric like richness often fails to capture community dynamics (Figure S4.1.6-S4.1.8). Importantly, cross-site evidence suggests that rank-abundance relationships can be driven by site-scale differences in soil properties in drylands (Ulrich et al. 2016), suggesting that further work could explore how soil properties modulate responses to the drivers I tested here within ecosystem types.

These results show that reducing short-term precipitation and disturbance can have pronounced individual and interactive effects on community dispersion in each of these drylands, but interestingly, each dryland ecosystem responded uniquely to these individual and combined drivers. I found three different patterns of community dispersion responses to the interactive effects of reduced precipitation and disturbance. Variability in community to similar environmental stressors can be considered a meaningful response in its own right (Houseman et al. 2008). The effect of disturbance on community dispersion is likely to be more variable than that of changes in short-term precipitation. This is because the type of disturbance I applied may have differential effects on species because of their aboveground structures' inherent resistance to disturbance. The strong disturbance treatment temporarily reduced the standing stock of the existing community at the Mojave and Great Basin sites, increasing invasion from the surrounding local community and the seed bank. This treatment could have led to an increase in community dispersion if there was local variation in species composition and/or the seed bank, and I found this was true for both sites under ambient precipitation regimes, but only for the Great Basin site under the reduced precipitation regime.

These interactions arose from stressors having inconsistent impacts across the landscape, which appeared capable of generating larger ecological effects than from individual stressors deployed in this experiment. Other studies have shown that the singular effect of stressors can vary across climate gradients (Guo et al. 2018, Peters et al. 2019), experimentally imposed drought gradients (Smith et al. 2024), and in relation to community composition (Luo et al. 2020). This study's novelty is in demonstrating that the cumulative effects of multiple stressors can also be inconsistent across the landscape.

Mechanisms driving sensitivity to precipitation and disturbance

Soil water could have been a major driver of dryland biodiversity responses to the experimental manipulations and understanding soil water–disturbance dynamics has landscape-scale implications for management. Because disturbance interacts with soil water availability across short- and long-term precipitation gradients, disrupting soil structure has been shown to have large effects on hydraulic properties of the soil profile and soil water resources available to plants (Caldwell et al. 2006). At low precipitation values, disturbance destroyed existing shrub architecture, likely increased bare soil evaporation by reducing shrub canopy shading and ultimately reducing available soil water. At high precipitation values, disturbance caused an increase in available soil water by reducing evapotranspiration. The reduction of resource use efficiency and available soil water likely drove the differences in synergism I observed across the three sites. Models suggest biomass has greater effects on soil moisture than either functional group or climate change, underscoring the need to recognize vegetation structural changes that emerge from human disturbances beyond the compositional changes I observed in this study (Wilson et al. 2018). Further, these results suggest that physical disturbance can be used to manipulate soil water availability. Specifically, I found that in surface soil layers (0-30 cm), disturbance alone tended to increase available soil moisture over controls (Figure S4.1.9). This pattern was also present during the wettest month with each sample year (Figure S4.1.10), which likely affected the changes in richness and non-native abundance that I observed.

Across dryland ecosystems, the amount of precipitation that follows a disturbance is a key modulating factor for how the effects of disturbance manifest in plant communities. In each of these study systems, total energy flux is tightly linked to available soil water (Noy-Meir 1973, Jentsch and White 2019). Disturbance interacted with precipitation amount at each of the three sites, and the ways that these drivers interacted changed along a gradient of mean annual precipitation. Models of disturbance and diversity, relationships between richness and evenness, concepts of succession, and concepts of biodiversity-ecosystem functioning were usually developed in more mesic systems with less severe shortages of soil water, higher species richness, and less interannual variability in climate than the desert shrublands in this field experiment (Connell 1978, Huston 1979, Tilman 1982). These results suggest that conceptual models of climate and disturbance effects in drylands must account for the precipitation following disturbance and how this precipitation modulates plant community recovery from disturbance over time (Jentsch and White 2019).

Non-native species responses to precipitation and disturbance

I found that the amount of short term precipitation following disturbance is a major control over non-native species abundance, with implications for land management and controlling invasion dynamics. Specifically, the timing of land management activities that cause disturbances can be manipulated to reduce the subsequent increase in non-native species abundance. In drylands, a disturbance may remove or reduce dominant, disturbance-intolerant plants (shrubs) from a community, and combined with changes in short term precipitation, create the opportunity for non-native species to take advantage of available resources (Buma 2015). Meta-analysis revealed that anthropogenic disturbances like the one I imposed tend to facilitate invasion (non-native richness and abundance) more than other types of disturbance (Jauni et al. 2015). Further, ecological effects of invasion tend to be greater when they co-occur with reductions in short term rainfall (Lopez et al. 2022). Non-native species are commonly species that benefit from disturbance, but the worst invaders can have larger increases following disturbance in the invaded ranges, as opposed to their home ranges (Hierro et al. 2006).

In ecosystems where non-native species are present, high resource availability following disturbance can lead to large increases in the abundance of non-native species, with propagule presence a key modulating factor. One of the sites, the Chihuahuan, had no non-native species present before the disturbance treatment, and no non-native species appeared in communities even after the disturbance treatment. In contrast, the other two sites saw large increases in non-native species abundance following disturbance because these sites had non-native propagules present before the disturbance occurred.

Disturbance and precipitation as drivers of shrub encroachment

In ecosystems where the dominant plants are resistant to disturbance, low resource availability following disturbance can enhance the dominance disturbance-resistant plants. Disturbance increased the dominance of shrubs at the Chihuahuan site and decreased the dominance of shrubs at the Mojave and Great Basin sites. An increase in the abundance of woody plants can cause decreases in ecosystem function in certain dryland systems, like the Chihuahuan (Havstad et al. 2006), while in other dryland systems, decreases in woody plants cause decreases in ecosystem function, such as in the Mojave and Great Basin Deserts (Walker et al. 2001, Chambers et al. 2014). Thus, I found that disturbance pushed all three of the sites towards less functional states.

These findings have concerning implications for the two ecosystems in this study where keeping mature shrubs on the landscape is often a conservation goal: the Mojave and Great Basin. Because favorable germination years for the dominant shrub species do not occur every year, the legacy of disturbance events in the Mojave and Great Basin systems could persist for decades. Current management of both of these systems broadly prioritizes keeping mature shrubs on the landscape (Steiger and Webb 2000, Webb 2002, Knick et al. 2003), and I showed that a one-time disturbance event can greatly reduce or eliminate shrub cover at the plot scale. In the Great Basin, sagebrush-obligate wildlife species require sagebrush cover, sagebrush is slow to recover, and evidence suggest that more intact communities in this system are more resistant to invasion (Davies et al. 2011). In the Mojave, facilitative effects may increase net productivity and plant community diversity in the presence of shrubs (Walker et al. 2001, Whitford and Duval 2020). In both systems, especially in an uncertain climate, keeping mature shrubs on the landscape reduces dust emissions, lowers albedo, improves habitat quality, and enhances the resiliency and resistance of a site (Duniway et al. 2019). Thus, preventing physical disturbances and the subsequent loss of shrubs should be a management priority.

Unlike the Mojave and Great Basin Deserts, the disturbance treatment increased the dominance of mesquite in the Chihuahuan site. The brush management literature supports these findings in the Chihuahuan and range managers have understood the challenges of mesquite management for a long time- those shrubs are tough (Fisher 1950, Glendening 1952). Previous experimental work has shown the same pattern I observed- an increase in mesquite cover following a mechanical disturbance (Ruthven and Krakauer 2004). Ecologists have been concerned about desertification in this system, and I can contextualize the loss of black gramma from the plots in existing frameworks about the balance of grasses and shrubs in this system (Schlesinger et al. 1990, Peters et al. 2012).

These findings suggest that the combination of changes in precipitation and disturbance will further push these systems into a shrub-encroached state. This follows longstanding conceptual models of dryland community dynamics in a changing climate: reduced water inputs will reduce communities to a more shrub-dominated state (Bestelmeyer et al. 2013). Notably, all treatments at the Chihuahuan site began with black gramma as the second most dominant species. By the end of the experiment, only the controls retained black gramma as the second most abundant species, indicating that both reduced precipitation and disturbance can reduce the abundance of this historically prevalent species.

Management implications

Despite decades of research, communicating and managing for plant biodiversity is still a major challenge in natural resource management. Drylands in particular, with ephemeral species, spatial heterogeneity, and vast expanses, lag behind other systems in recognition of biodiversity values (Hoover et al. 2020). If land management is to account for patterns of biodiversity, clearly documenting when and where to expect diversity to be present in a dryland system and how that diversity may respond to drivers is paramount. Specifically, land management goals often integrate plant species diversity and abundance when managing for wildlife, but these goals are typically static and do not account for variation due to climate or disturbance (Pennington et al. 2016). These results suggest that for adaptive management to be successful, biodiversity goals should be tailored to regional climate events and disturbance history. Beyond patterns of biodiversity, the findings on non-native species' responses and potential drivers of shrub encroachment have direct implications for management of those particular ecosystems.

Conclusions

I conclude that a multi-year reduction in ambient precipitation and a one-time physical disturbance at each site were extreme enough to invoke a significant and multilevel response in each of these ecosystems. In two of the sites, the combined effects of these drivers dramatically reduced the dominant shrubs of the system, creating opportunities for increases in non-native annual species. In the third site, shrubs were especially disturbance-resistant, but the dominant native perennial grass was sharply reduced by both simulated global change drivers. Across these sites, these changes represent undesirable changes in community identity for biodiversity and the provisioning of ecosystem services. Additional research and concerted effort from the scientific and management communities to prevent further degradation of the world's drylands is warranted.

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S. Larsen, J. Larson, J. Lawson, C. V. Leder, A. Linstädter, J. Liu, S. Liu, A. G. Lodge, G. Longo, A. Loydi, J. Luan, F. Curtis Lubbe, C. Macfarlane, K. Mackie-Haas, A. V. Malyshev, A. Maturano-Ruiz, T. Merchant, D. B. Metcalfe, A. S. Mori, E. Mudongo, G. S. Newman, U. N. Nielsen, D. Nimmo, Y. Niu, P. Nobre, R. C. O'Connor, R. Ogaya, G. R. Oñatibia, I. Orbán, B. Osborne, R. Otfinowski, M. Pärtel, J. Penuelas, P. L. Peri, G. Peter, A. Petraglia, C. Picon-Cochard, V. D. Pillar, J. M. Piñeiro-Guerra, L. W. Ploughe, R. M. Plowes, C. Portales-Reyes, S. M. Prober, Y. Pueyo, S. C. Reed, E. G. Ritchie, D. A. Rodríguez, W. E. Rogers, C. Roscher, A. M. Sánchez, B. A. Santos, M. Cecilia Scarfó, E. W. Seabloom, B. Shi, L. Souza, A. Stampfli, R. J. Standish, M. Sternberg, W. Sun, M. Sünnemann, M. Tedder, P. Thorvaldsen, D. Tian, K. Tielbörger, A. Valdecantos, L. van den Brink, V. Vandvik, M. R. Vankoughnett, L. Guri Velle, C. Wang, Y. Wang, G. M. Wardle, C. Werner, C. Wei, G. Wiehl, J. L. Williams, A. A. Wolf, M. Zeiter, F. Zhang, J. Zhu, N. Zong, and X. Zuo. 2024. Extreme drought impacts have been underestimated in grasslands and shrublands globally. Proceedings of the National Academy of Sciences 121:e2309881120.

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Supplementary Material for Chapter 4

Supplemental 4.1: Information about sites, climate patterns, community abundance, environmental sensors, and supporting analyses

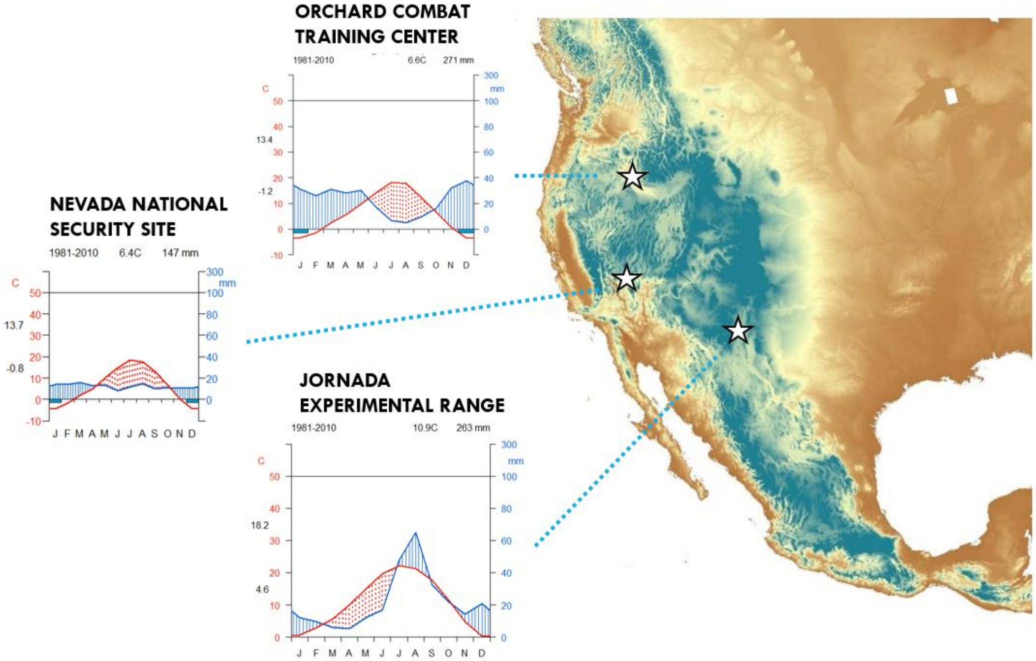


Figure S4.1.1. Experimental site locations in North America and Walter-Leith diagrams of climate at each site. Shading on map represents elevation: tan colors represent lower elevations, yellows intermediate elevations, and blues high elevations.

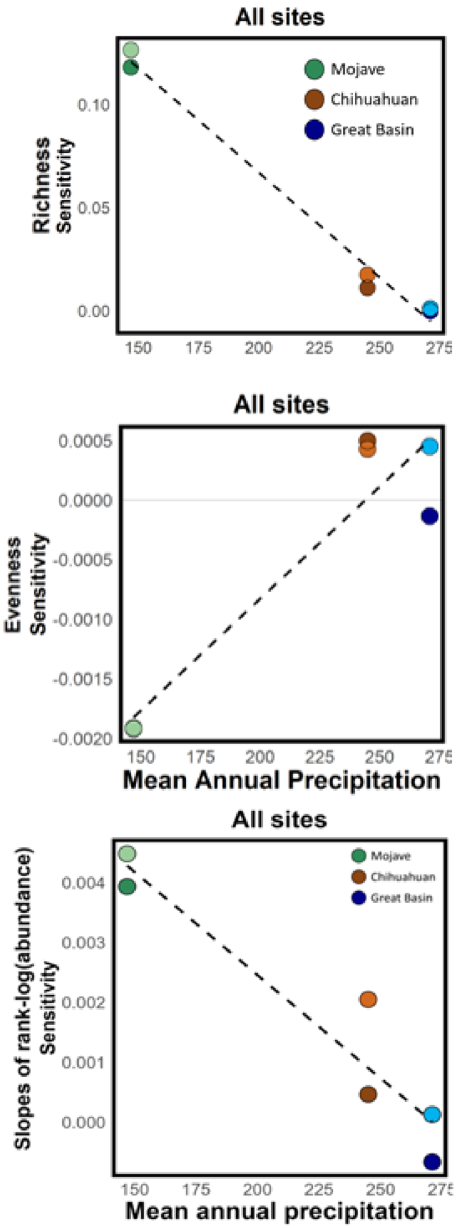


Figure S4.1.2. Sensitivity of relationship between mean annual precipitation and richness, evenness, and slopes of log-transformed rank-abundance curves across all three sites in disturbed (light colors) and undisturbed conditions (dark colors; Mojave = green, Chihuahuan = brown, Great Basin = blue). I calculated sensitivity as the slope of the each one of these relationships (Figures 1 & 4). Dotted lines represent non-significant relationships and are meant to suggest that these relationships may be linear across precipitation gradients.

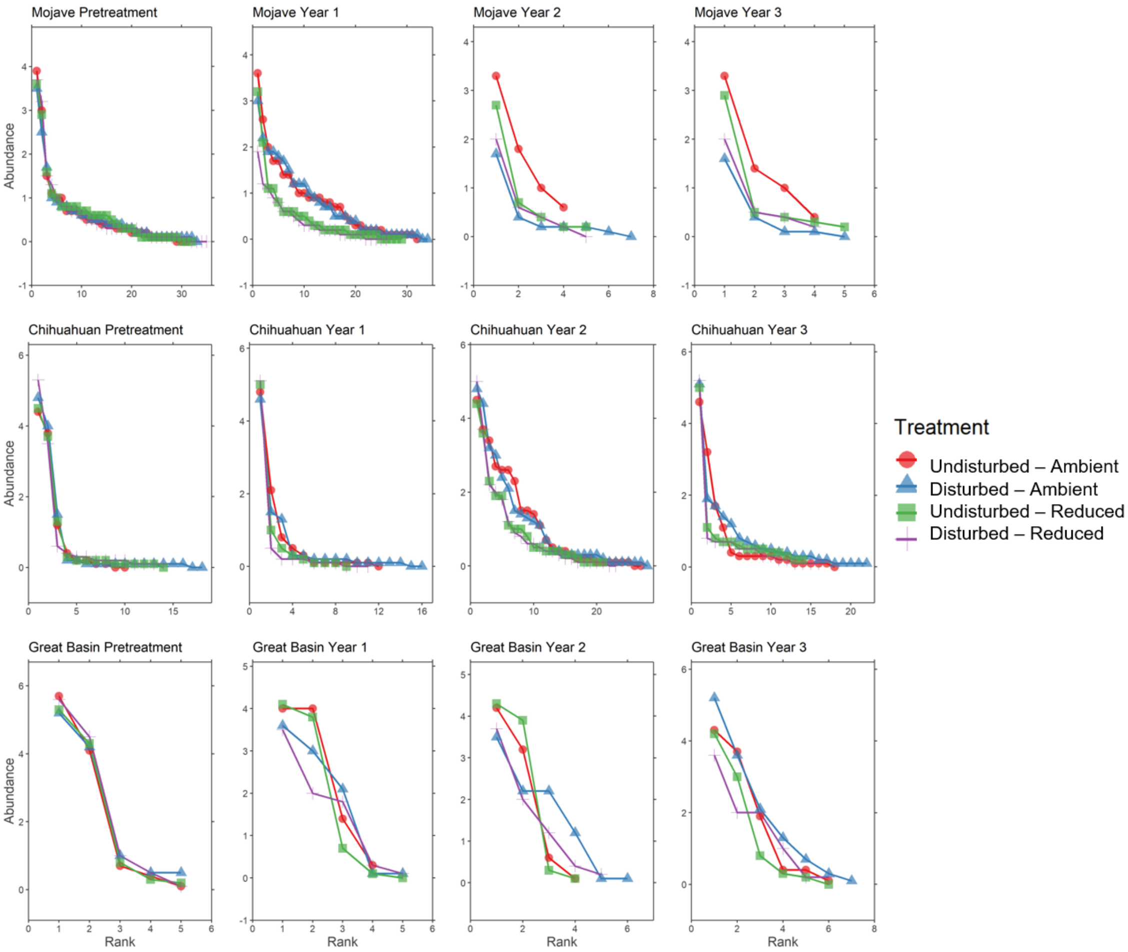


Figure S4.1.3. Rank abundance curves for each site, treatment, and year. Plant species abundances are plotted against their rank in the community. Data across all replicates within a treatment are plotted with unique colors and shapes: control plots are red with circles, disturbance plots that received ambient precipitation are blue with triangles, reduced precipitation plots are plotted in green with squares, and disturbance plots that had reduced precipitation and are plotted in purple with pulses.

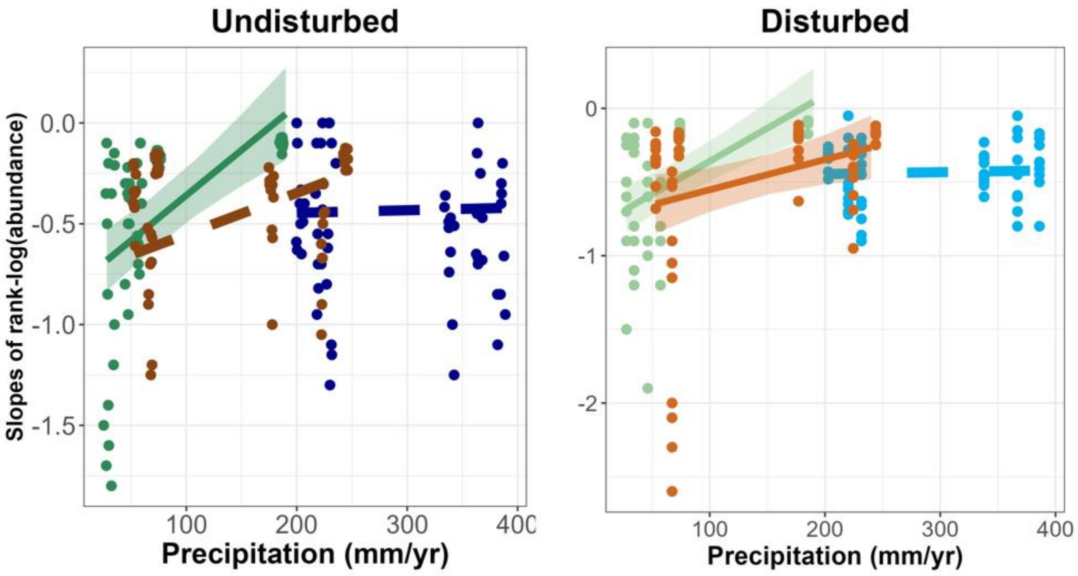


Figure S4.1.4. Slopes of log transformed rank-abundance curves in disturbed and undisturbed conditions across long and short term precipitation gradients. Green = Mojave, Brown = Chihuahuan, Blue = Great Basin. Data are from all three treatment years of the field experiment.

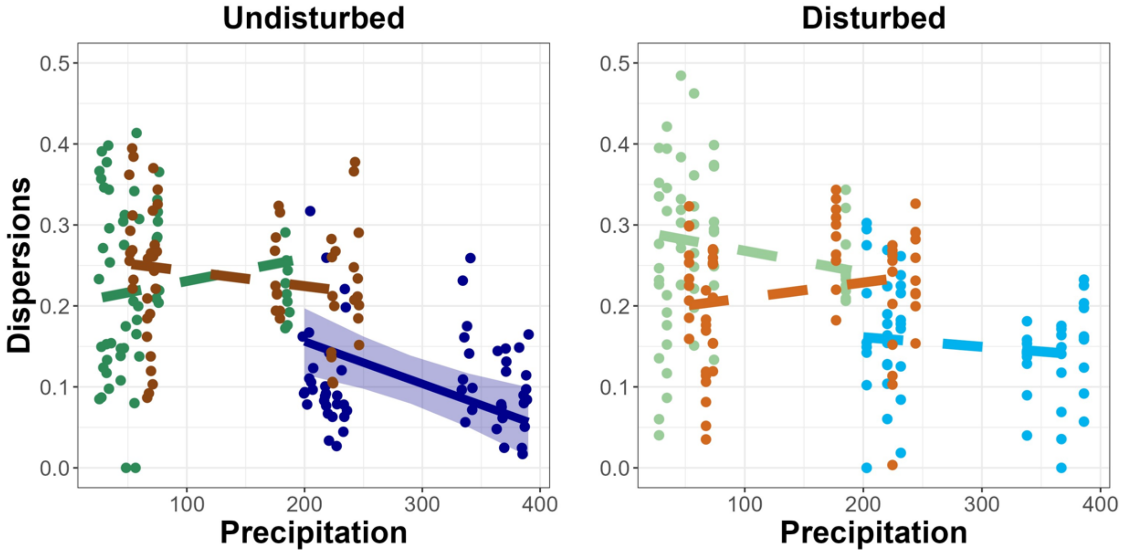
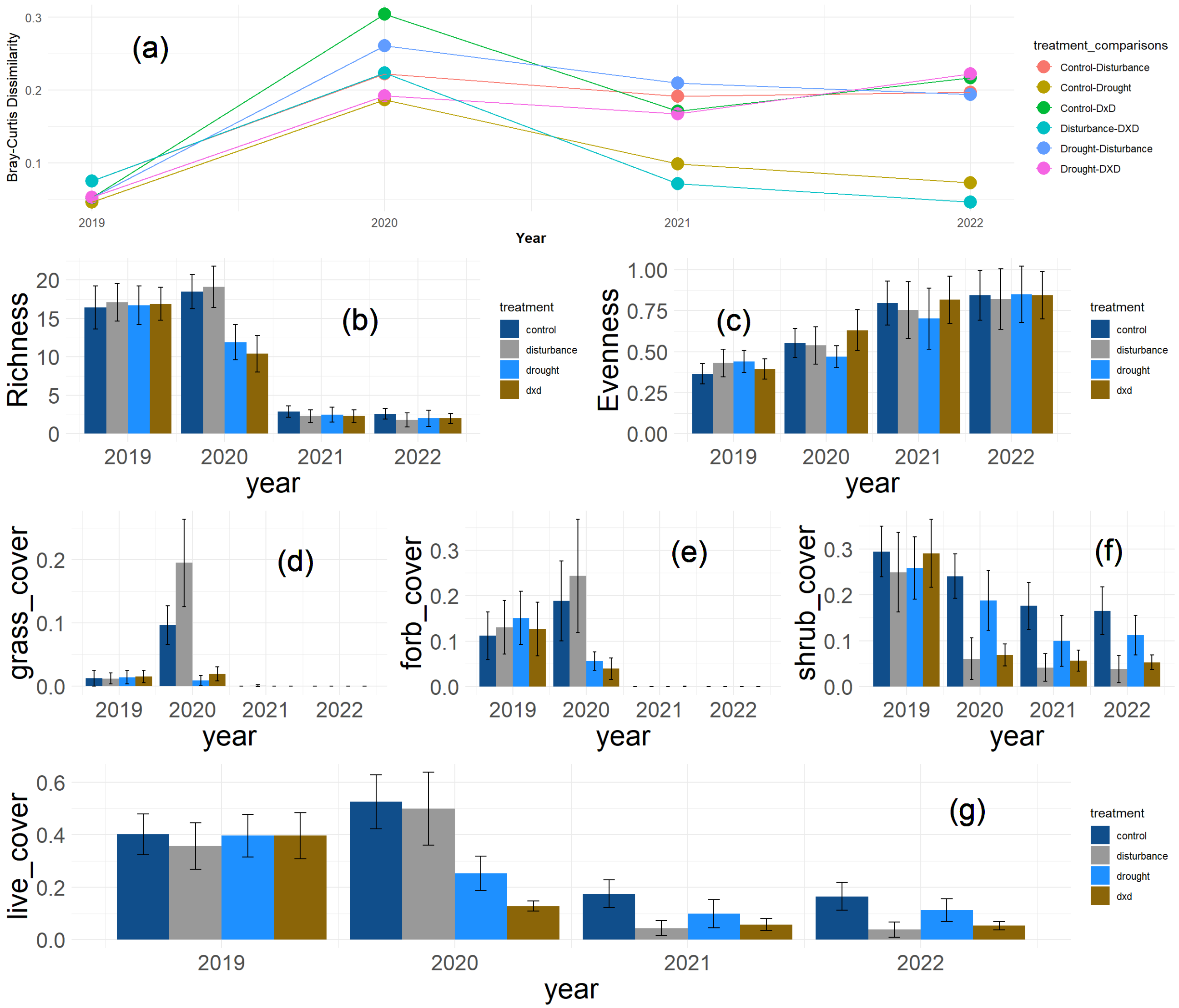


Figure S4.1.5. Community dispersions (Bray-Curtis distances) in disturbed and undisturbed conditions across long and short term precipitation gradients. Green = Mojave, Brown = Chihuahuan, Blue = Great Basin. The figure in the right column display the sensitivity of dispersions across short term precipitation gradients across each site's mean annual precipitation value, with undisturbed conditions plotted in dark colors, and disturbed conditions plotted in light colors. Data are from all three treatment years of the field experiment.



(a)
Bray-Curtis Dissimilarity
0.3
0.2
0.1
2019
2020
2021
2022
Year
treatment_comparisons
Control-Disturbance
Control-Drought
Control-DxD
Disturbance-DXD
Drought-Disturbance
Drought-DXD
(b)
Richness
20
15
10
5
0
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd
(c)
Evenness
1.00
0.75
0.50
0.25
0.00
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd
(d)
grass_cover
0.2
0.1
0.0
2019
2020
2021
2022
year
(e)
forb_cover
0.3
0.2
0.1
0.0
2019
2020
2021
2022
year
(f)
shrub_cover
0.3
0.2
0.1
0.0
2019
2020
2021
2022
year
(g)
live_cover
0.6
0.4
0.2
0.0
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd

Figure S4.1.6. The effects of reduced precipitation and disturbance on a suite of plant community metrics at the Mojave Desert site:

a. Species composition as measured by Bray-Curtis dissimilarity. Each color of points & lines represents a unique comparison across treatments within a site.

b. Species richness

c. across treatments and years. The effects of severe meteorological drought are seen in 2021 and 2022.

d. Evenness across treatments and years. Evenness increased when annual life forms failed to germinate in the severe drought of 2021 and 2022.

e. Grass cover across treatments and years. There was a strong non-native annual grass response to disturbance seen in 2020.

f. Forb cover across treatments and years. The effects of reduced precipitation is notable in the treatments in 2020 as well as the effects of the 2021-2022 drought.

g. Shrub cover across treatments and years. The disturbance treatment reduced shrub cover across years.

h. Live cover of all plant functional types across treatments and years.

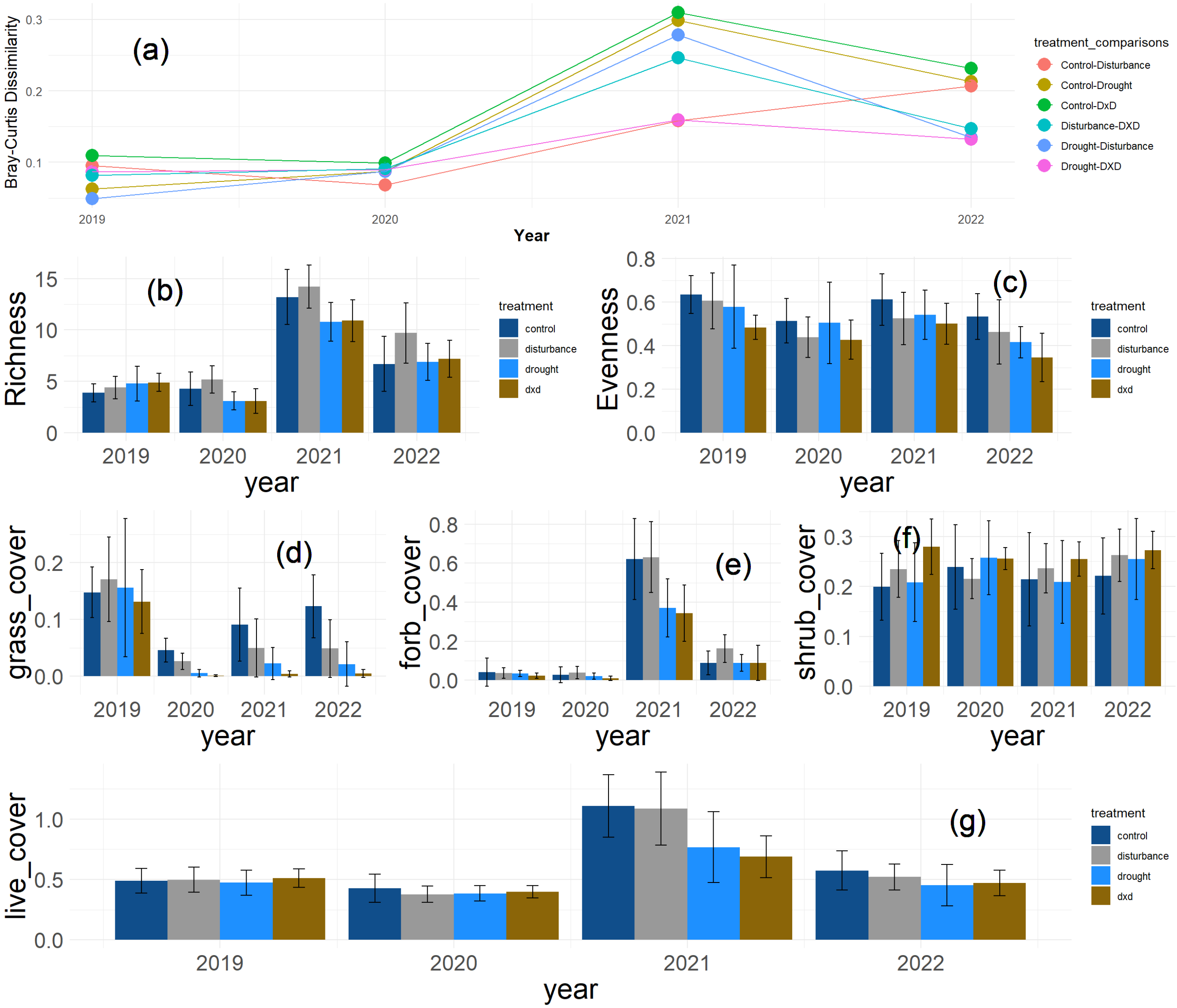

(a)
Bray-Curtis Dissimilarity
0.1
0.2
0.3
2019
2020
2021
2022
Year
treatment_comparisons
Control-Disturbance
Control-Drought
Control-DxD
Disturbance-DXD
Drought-Disturbance
Drought-DXD
(b)
Richness
0
5
10
15
year
treatment
control
disturbance
drought
dxd
(c)
Evenness
0.0
0.2
0.4
0.6
0.8
year
(d)
grass_cover
0.0
0.1
0.2
(e)
forb_cover
0.0
0.2
0.4
0.6
0.8
(f)
shrub_cover
0.0
0.1
0.2
0.3
(g)
live_cover
0.0
0.5
1.0
2019
2020
2021
2022
year

Figure S4.1.7. The effects of reduced precipitation and disturbance on a suite of plant community metrics at the Chihuahuan Desert site:

a. Species composition as measured by Bray-Curtis dissimilarity. Each color of points & lines represents a unique comparison across treatments within a site.

b. Species richness across treatments and years. 2021 had above-mean forb germination, driving species richness.

c. Evenness across treatments and years.

d. Grass cover across treatments and years. The precipitation reductions and disturbance treatment reduced grass cover across years.

e. Forb cover across treatments and years. 2021 had above-mean forb cover.

f. Shrub cover across treatments and years. None of the treatments reduced shrub cover.

g. Live cover of all plant functional types across treatments and years.

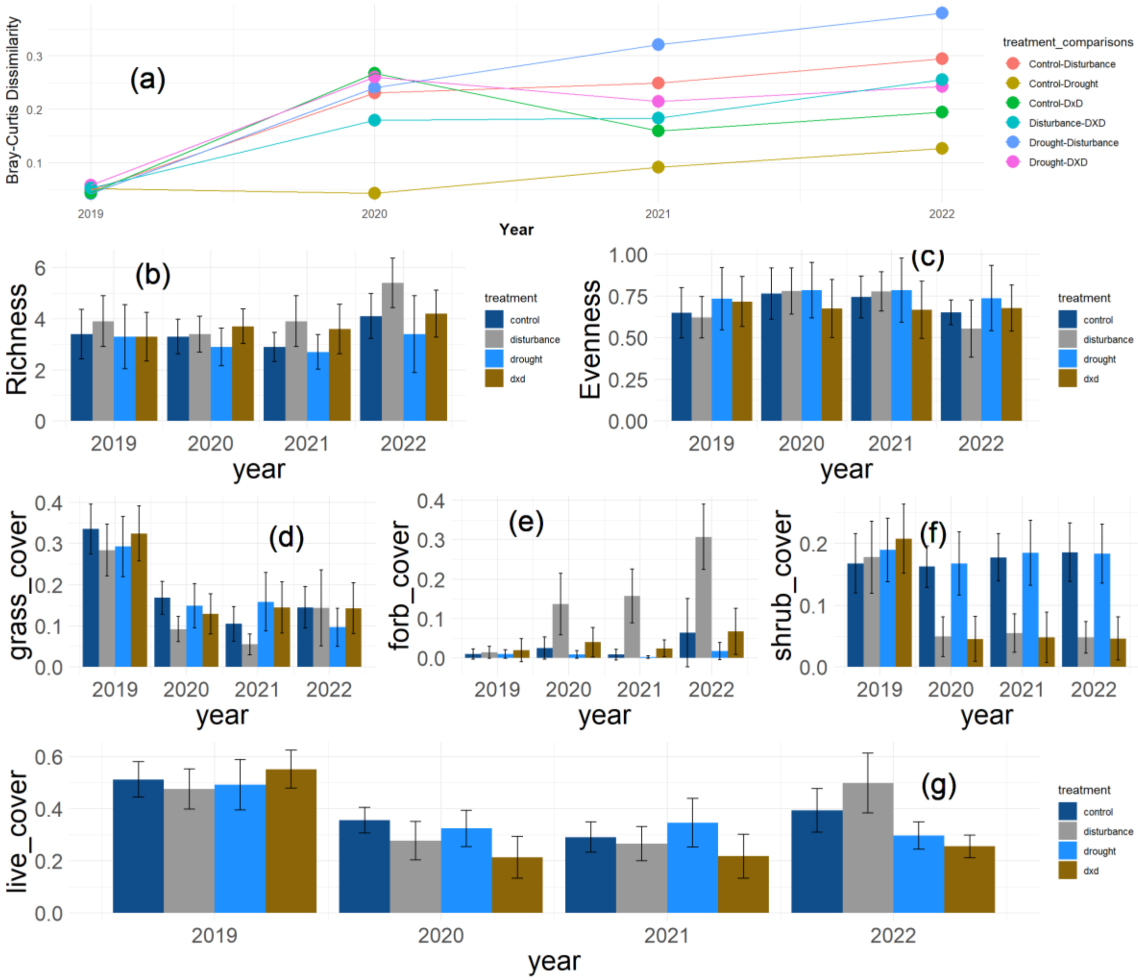

(a)
Bray-Curtis Dissimilarity
0.1
0.2
0.3
2019
2020
2021
2022
Year
treatment_comparisons
Control-Disturbance
Control-Drought
Control-DxD
Disturbance-DXD
Drought-Disturbance
Drought-DXD
(b)
Richness
0
2
4
6
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd
(c)
Evenness
0.00
0.25
0.50
0.75
1.00
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd
(d)
grass_cover
0.0
0.1
0.2
0.3
0.4
2019
2020
2021
2022
year
(e)
forb_cover
0.0
0.1
0.2
0.3
0.4
2019
2020
2021
2022
year
(f)
shrub_cover
0.0
0.1
0.2
2019
2020
2021
2022
year
(g)
live_cover
0.0
0.2
0.4
0.6
2019
2020
2021
2022
year
treatment
control
disturbance
drought
dxd

Figure S4.1.8. The effects of reduced precipitation and disturbance on a suite of plant community metrics at the Great Basin Desert site:

a. Species composition as measured by Bray-Curtis dissimilarity. Each color of points & lines represents a unique comparison across treatments within a site.

b. Species richness across treatments and years. This site had very low species richness overall.

c. Evenness across treatments and years.

d. Grass cover across treatments and years.

e. Forb cover across treatments and years. The high cover values in 2020, 2021, and 2022 are primarily driven by an non-native forb.

f. Shrub cover across treatments and years. The disturbance treatment reduced shrub cover across years.

g. Live cover of all plant functional types across treatments and years.

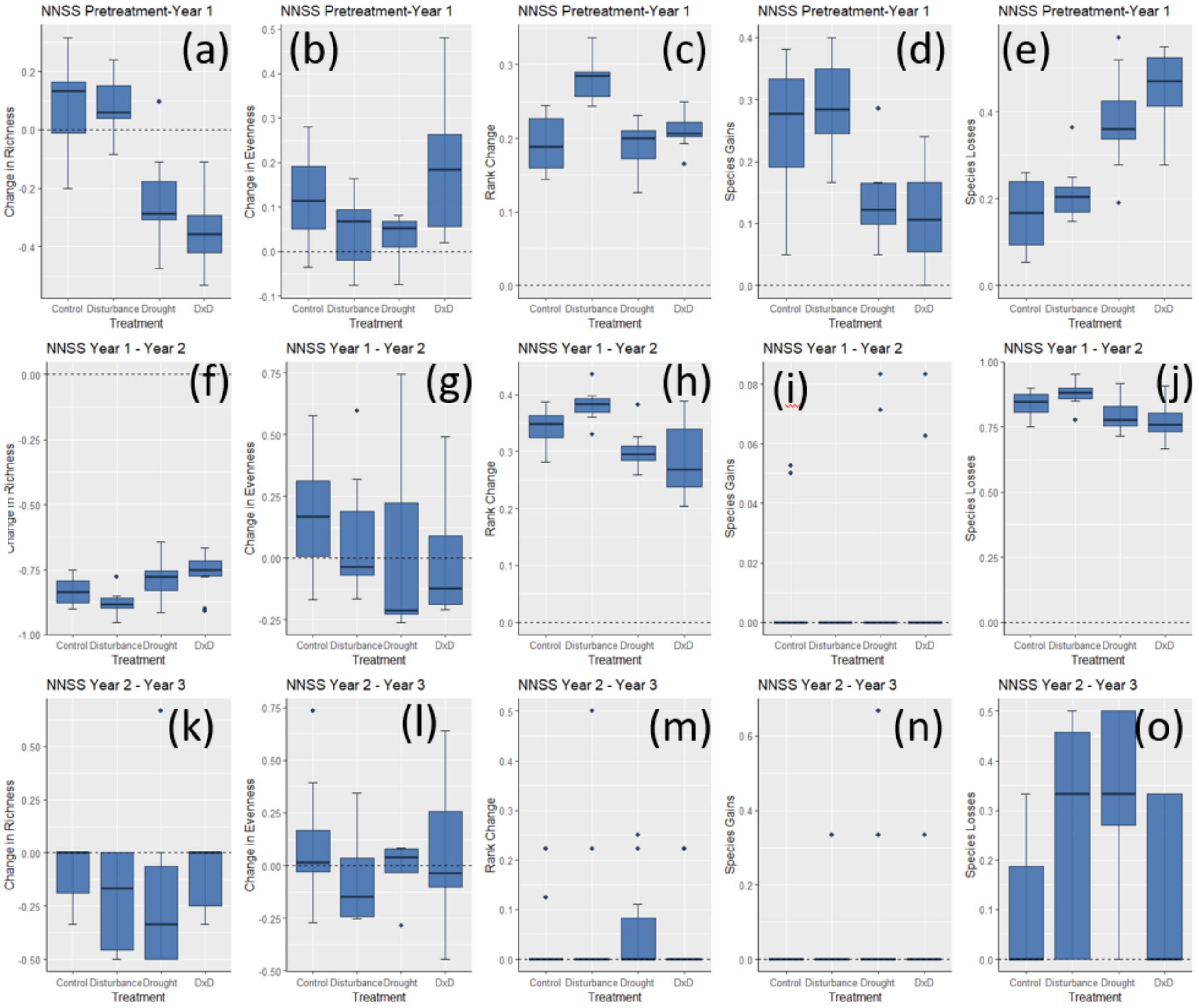

NNSS Pretreatment-Year 1
(a)
Change in Richness
(b)
Change in Evenness
(c)
Rank Change
(d)
Species Gains
(e)
Species Losses
NNSS Year 1 - Year 2
(f)
(g)
(h)
(i)
(j)
NNSS Year 2 - Year 3
(k)
(l)
(m)
(n)
(o)
Control
Disturbance
Drought
DxD
Treatment

Figure S4.1.9. Boxplots of community changes across experiment years at the Mojave site. Plots are arranged with year comparisons within rows and community responses in columns. To generate change values, I compared plot-level values each year to the previous year's values from the same plot: pretreatment (2019) to treatment year 1 (2020), treatment year 1 (2020) to treatment year 2 (2021), and treatment year 2 (2021) to treatment year 3 (2022). Variables quantified here include **change in richness**, or the range of change values in the number of species detected in sampling within each replicate divided by the total number of unique species in both time periods. A positive value occurs when a there is an increase in species richness over time, and a negative value when there is a decrease in species richness over time (A-F-K); **change in evenness,** change in evenness between the two time periods for a replicate. A positive value occurs when evenness increases over time, and a negative value when evenness decreases in over time (B-G-L); **rank change**, the absolute value of the mean change in species ranks between the two time periods for a replicate divided by the total number of unique species in both time periods (C-H-M); **species gains**: the number of species that are present at time period 2 that were not present at time period 1 for a replicate divided by the total number of unique species in both time periods (D-I-N); **species losses**: the number of species that are not present at time period 2 but were present at time period 1 for a replicate divided by the total number of unique species in both time periods (E-J-O; Hallett et al. 2020). Each box displays the interquartile range (IQR), or the range of values that cover the 25 percentile (Q1) to 75 percentile (Q3), with the solid line in the middle of the boxplot indicating median values. The whiskers show the minimum (Q1 - 1.5 * IQR) and maximum (Q3 + 1.5 * IQR). Any points that fall outside these whiskers are outliers.

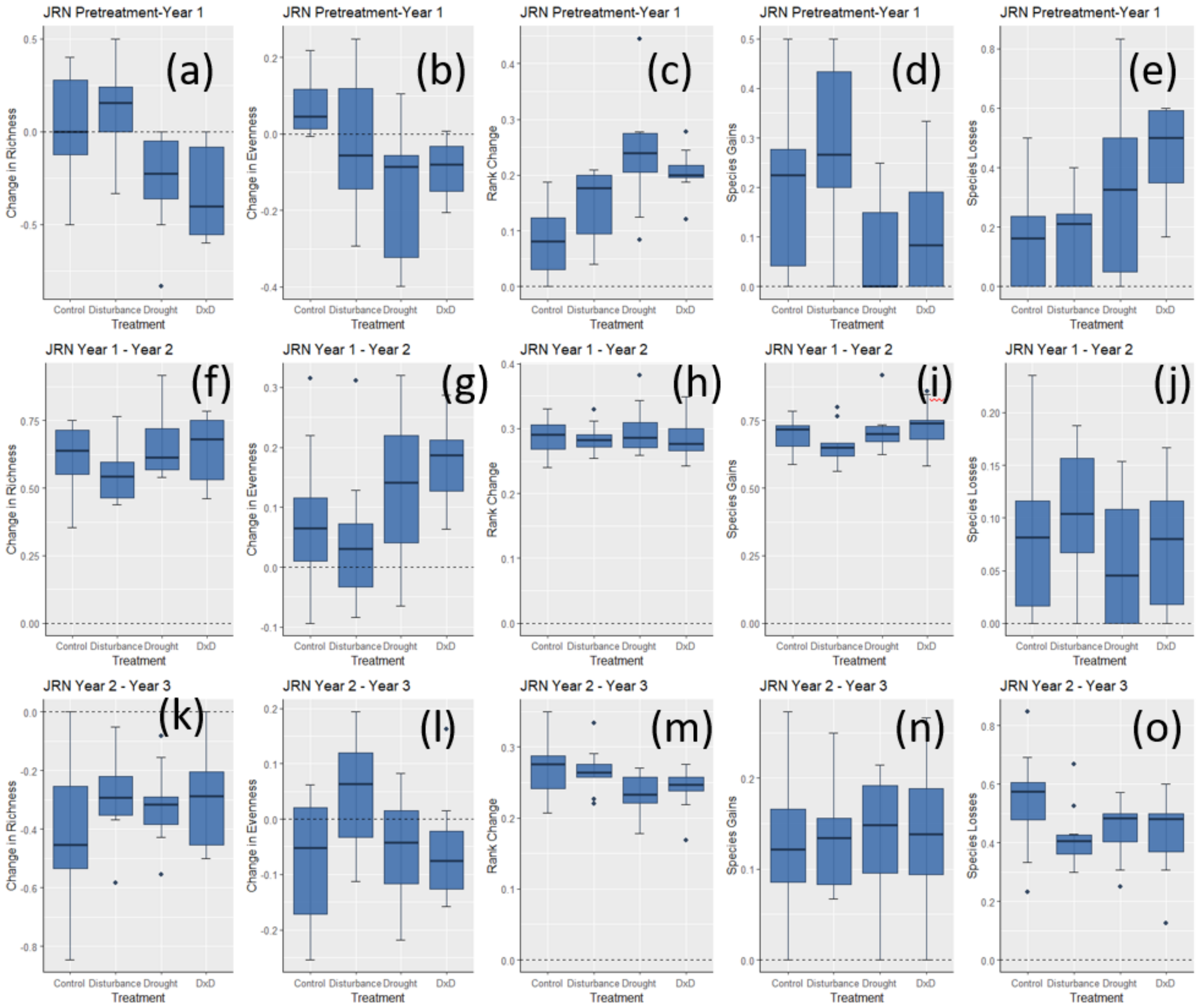

JRN Pretreatment-Year 1
(a)
Change in Richness
(b)
Change in Evenness
(c)
Rank Change
(d)
Species Gains
(e)
Species Losses
JRN Year 1 - Year 2
(f)
(g)
(h)
(i)
(j)
JRN Year 2 - Year 3
(k)
(l)
(m)
(n)
(o)
Control
Disturbance
Drought
DxD
Treatment

Figure S4.1.10. Boxplots of community changes across experiment years at the Chihuahuan site. Plots are arranged with year comparisons within rows and community responses in columns. To generate change values, I compared plot-level values each year to the previous year's values from the same plot: pretreatment (2019) to treatment year 1 (2020), treatment year 1 (2020) to treatment year 2 (2021), and treatment year 2 (2021) to treatment year 3 (2022). Variables quantified here include **change in richness**, or the range of change values in the number of species detected in sampling within each replicate divided by the total number of unique species in both time periods. A positive value occurs when a there is an increase in species richness over time, and a negative value when there is a decrease in species richness over time (A-F-K); **change in evenness,** change in evenness between the two time periods for a replicate. A positive value occurs when evenness increases over time, and a negative value when evenness decreases in over time (B-G-L); **rank change**, the absolute value of the mean change in species ranks between the two time periods for a replicate divided by the total number of unique species in both time periods (C-H-M); **species gains**: the number of species that are present at time period 2 that were not present at time period 1 for a replicate divided by the total number of unique species in both time periods (D-I-N); **species losses**: the number of species that are not present at time period 2 but were present at time period 1 for a replicate divided by the total number of unique species in both time periods (E-J-O; Hallett et al. 2020). Each box displays the interquartile range (IQR), or the range of values that cover the 25 percentile (Q1) to 75 percentile (Q3), with the solid line in the middle of the boxplot indicating median values. The whiskers show the minimum (Q1 - 1.5 * IQR) and maximum (Q3 + 1.5 * IQR). Any points that fall outside these whiskers are outliers.

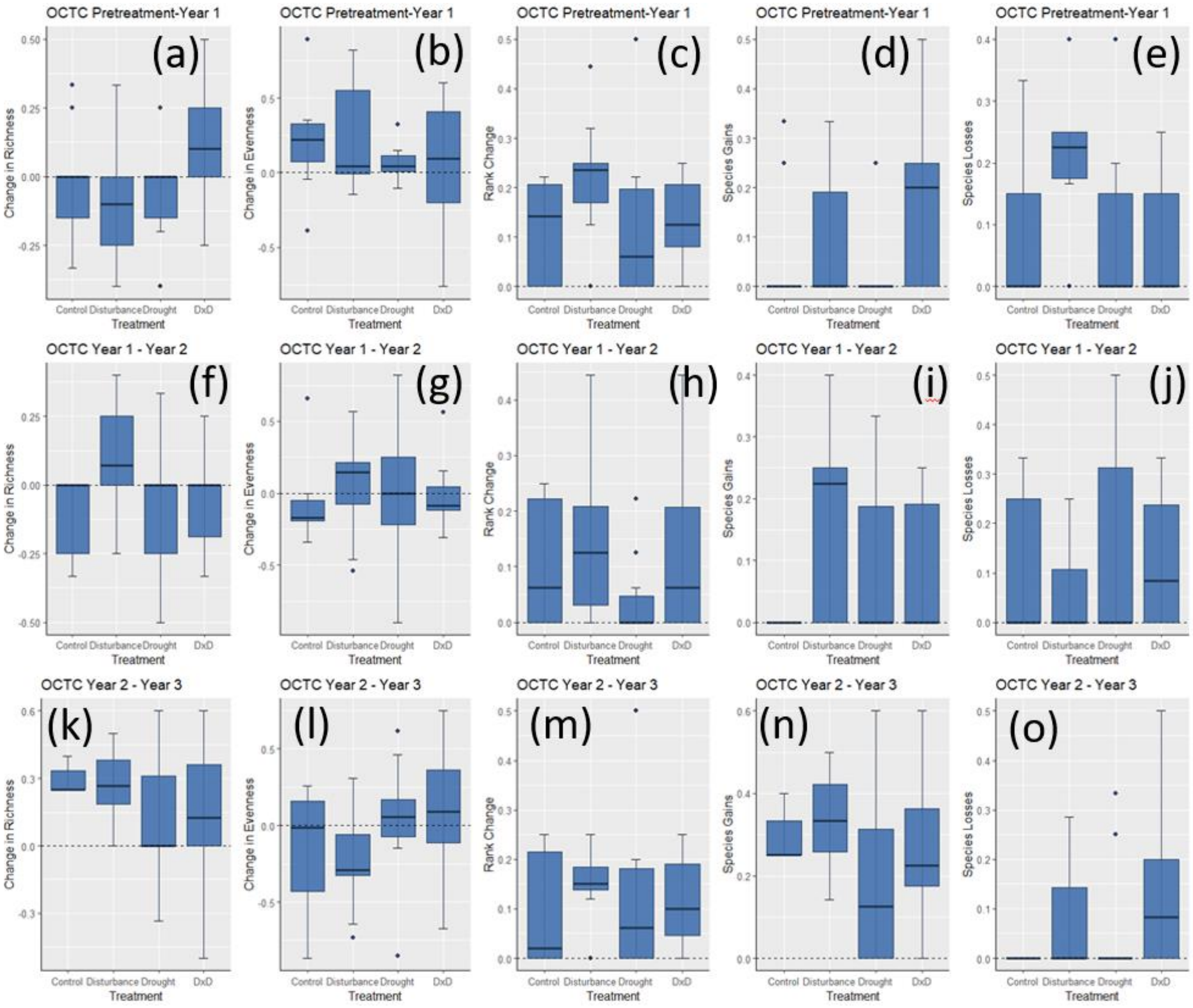

OCTC Pretreatment-Year 1
(a)
Change in Richness
(b)
Change in Evenness
(c)
Rank Change
(d)
Species Gains
(e)
Species Losses
OCTC Year 1 - Year 2
(f)
(g)
(h)
(i)
(j)
OCTC Year 2 - Year 3
(k)
(l)
(m)
(n)
(o)
Control
Disturbance
Drought
DxD
Treatment

Figure S4.1.11. Boxplots of community changes across experiment years at the Great Basin site. Plots are arranged with year comparisons within rows and community responses in columns. To generate change values, I compared plot-level values each year to the previous year's values from the same plot: pretreatment (2019) to treatment year 1 (2020), treatment year 1 (2020) to treatment year 2 (2021), and treatment year 2 (2021) to treatment year 3 (2022). Variables quantified here include **change in richness**, or the range of change values in the number of species detected in sampling within each replicate divided by the total number of unique species in both time periods. A positive value occurs when a there is an increase in species richness over time, and a negative value when there is a decrease in species richness over time (A-F-K); **change in evenness,** change in evenness between the two time periods for a replicate. A positive value occurs when evenness increases over time, and a negative value when evenness decreases in over time (B-G-L); **rank change**, the absolute value of the mean change in species ranks between the two time periods for a replicate divided by the total number of unique species in both time periods (C-H-M); **species gains**: the number of species that are present at time period 2 that were not present at time period 1 for a replicate divided by the total number of unique species in both time periods (D-I-N); **species losses**: the number of species that are not present at time period 2 but were present at time period 1 for a replicate divided by the total number of unique species in both time periods (E-J-O; Hallett et al. 2020). Each box displays the interquartile range (IQR), or the range of values that cover the 25 percentile (Q1) to 75 percentile (Q3), with the solid line in the middle of the boxplot indicating median values. The whiskers show the minimum (Q1 - 1.5 * IQR) and maximum (Q3 + 1.5 * IQR). Any points that fall outside these whiskers are outliers.

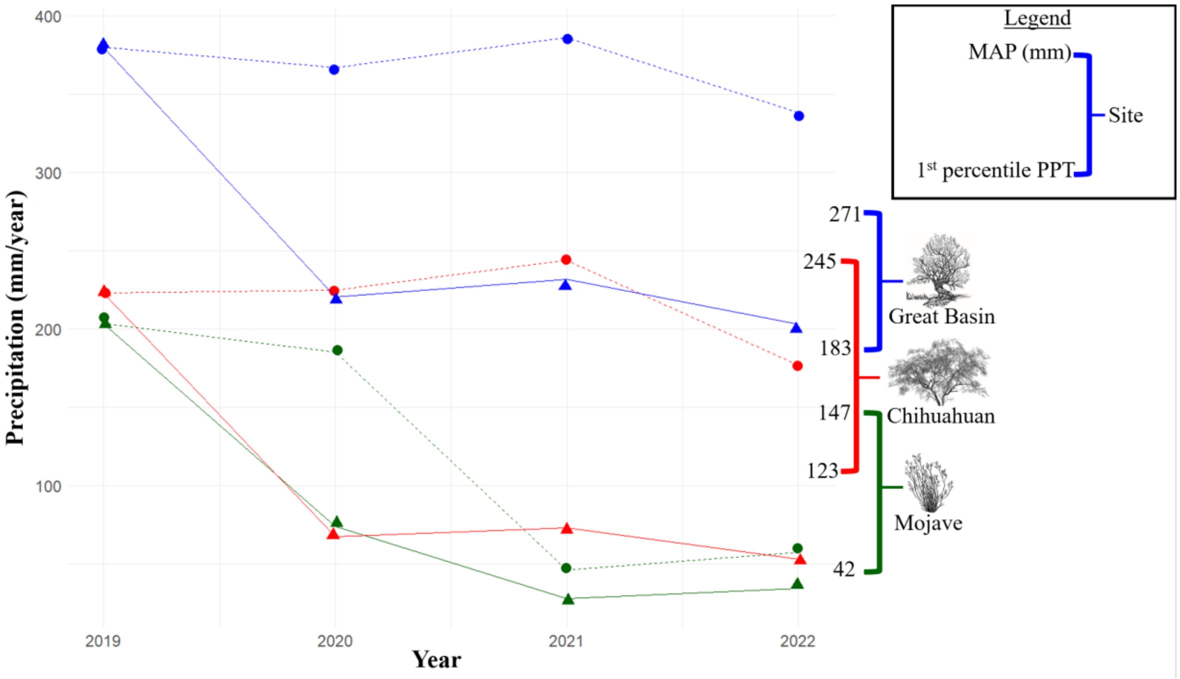


Figure S4.1.12. Ambient and reduced precipitation during field experiment for the three sites: Mojave (green points and lines), Great Basin (blue points and lines), and Chihuahuan (red points and lines). Circles display ambient precipitation at each site over the experiment, while triangles display reduced precipitation in experimental treatments with rainfall exclusion shelters. On the right margin of the figure, brackets indicate the mean annual precipitation at each site and the 1st percentile in precipitation over a 100-year period for each site. The upper bracket and value for each site displays mean annual precipitation in millimeters, while the lower bracket and value displays the 1st percentile precipitation amount in millimeters.

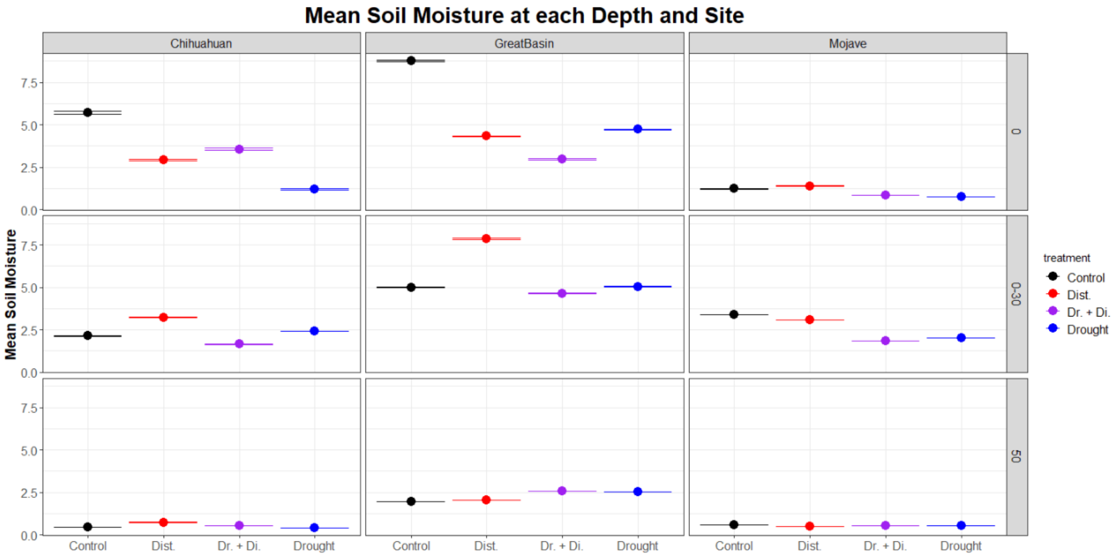


Figure S4.1.13. Mean soil moisture (% Volumetric water content) for each experimental treatment at different depths (0 cm, 0-30 cm, 50 cm) for the duration of the experiment.

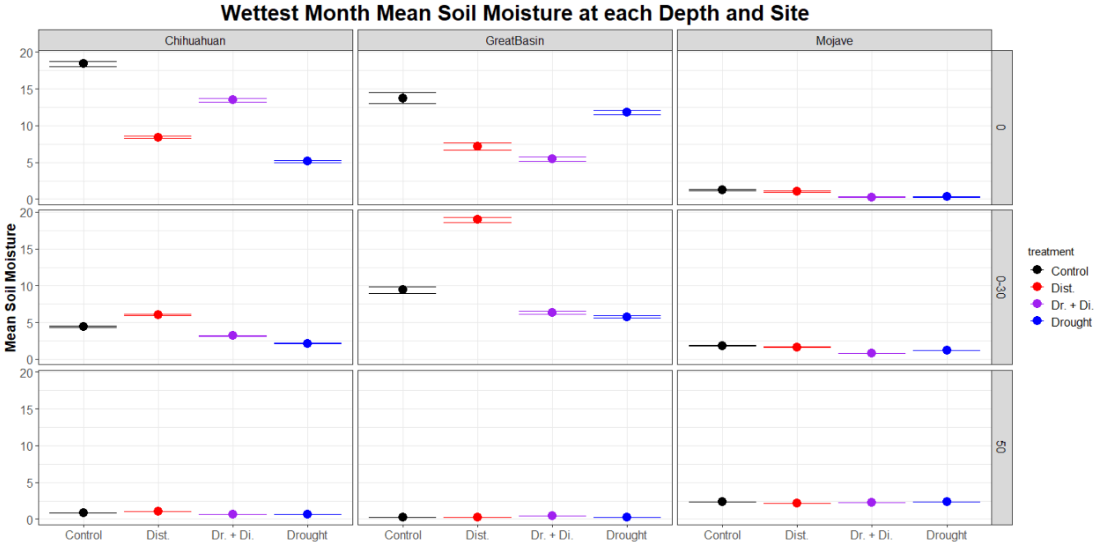


Figure S4.1.14. Mean soil moisture for the wettest month of the year (% Volumetric water content) for each experimental treatment at different depths (0 cm, 0-30 cm, 50 cm) for the duration of the experiment.

Supplemental 4.2: Mixed model tables; PERMANOVA and PERMDISP tables

Table S4.2.1. Mixed model results of richness-precipitation relationship at the Mojave site.

	UNDISTURBED richness			**DISTURBED richness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-1.62	-2.89 – -0.35	**0.013**	-2.64	-3.85 – -1.44	**<0.001**
ppt	0.12	0.11 – 0.13	**<0.001**	0.13	0.12 – 0.14	**<0.001**
Random Effects						
σ^2	5.68			3.97		
τ_{00}	2.29_{plot}			3.10_{plot}		
ICC	0.29			0.44		
N	20_{plot}			20_{plot}		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.834 / 0.882			0.867 / 0.925		

Table S4.2.2. Mixed model results of richness-precipitation relationship at the Chihauhuan site.

	UNDISTURBED richness			**DISTURBED richness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	6.59	4.33 – 8.84	**<0.001**	6.26	4.10 – 8.42	**<0.001**
ppt	0.01	-0.00 – 0.03	0.125	0.02	0.00 – 0.03	**0.012**
Random Effects						
σ^2	18.11			16.61		
τ_{00}	0.00_{plot}			0.00_{plot}		
N	20_{plot}			20_{plot}		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.039 / NA			0.102 / NA		

Table S4.2.3. Mixed model results of richness-precipitation relationship at the Great Basin site.

	UNDISTURBED richness			**DISTURBED richness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	3.30	1.98 – 4.63	**<0.001**	3.64	2.52 – 4.77	**<0.001**
ppt	-0.00	- 0.00 – 0.00	0.875	0.00	- 0.00 – 0.00	0.555
Random Effects						
σ^2	0.61			1.16		
τ_{00}	0.38 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
ICC	0.38					
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.001 / 0.383			0.006 / NA		

Table S4.2.4. Mixed model results of evenness-precipitation relationship at the Mojave site.

	UNDISTURBED evenness			**DISTURBED evenness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.84	0.76 – 0.92	**<0.001**	0.87	0.80 – 0.94	**<0.001**
ppt	-0.00	-0.00 – -0.00	**<0.001**	-0.00	-0.00 – -0.00	**<0.001**
Random Effects						
σ^2	0.03			0.02		
τ_{00}	0.01 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
ICC	0.21			0.11		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		

Observations	60	60
Marginal R^2 / Conditional R^2	0.245 / 0.403	0.311 / 0.387

Table S4.2.5. Mixed model results of evenness-precipitation relationship at the Chihuahuan site.

	UNDISTURBED evenness			**DISTURBED evenness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.45	0.38 – 0.52	**<0.001**	0.39	0.32 – 0.46	**<0.001**
ppt	0.00	0.00 – 0.00	**0.020**	0.00	-0.00 – 0.00	0.055
Random Effects						
σ^2	0.02			0.01		
τ_{00}	0.00 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
ICC	0.00			0.14		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.089 / 0.091			0.075 / 0.202		

Table S4.2.6. Mixed model results of evenness-precipitation relationship at the Great Basin site.

	UNDISTURBED evenness			**DISTURBED evenness**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.78	0.59 – 0.98	**<0.001**	0.56	0.36 – 0.75	**<0.001**
ppt	-0.00	-0.00 – 0.00	0.677	0.00	-0.00 – 0.00	0.173
Random Effects						
σ^2	0.02			0.02		

τ_{00}	0.01_{plot}	0.00_{plot}
ICC	0.23	0.16
N	20_{plot}	20_{plot}
Observations	60	60
Marginal R^2 / Conditional R^2	0.004 / 0.235	0.040 / 0.190

Table S4.2.7. Chi-squared test of proportions results for across plant functional types and cover class elements. Each site-year pairing is reported in the left column, from pretreatment (2019) to treatment year 3 (2022).

Mojave pretreatment	χ-squared = 2.27359	df = 15	p-value = 0.99993
Mojave Year 1	χ-squared = 77.3231	df = 15	**p-value < 0.0001**
Mojave Year 2	χ-squared = 30.9344	df = 12	**p-value = 0.002**
Mojave Year 3	χ-squared = 34.2394	df = 9	**p-value < 0.0001**
Chihuahuan pretreatment	χ-squared = 9.5632	df = 21	p-value = 0.98405
Chihuahuan Year 1	χ-squared = 12.8943	df = 18	p-value = 0.79782
Chihuahuan Year 2	χ-squared = 55.601	df = 21	**p-value < 0.0001**
Chihuahuan Year 3	χ-squared = 59.2724	df = 21	**p-value < 0.0001**
Great Basin pretreatment	χ-squared = 3.342	df = 15	p-value = 0.99922
Great Basin Year 1	χ-squared = 53.1203	df = 15	**p-value < 0.0001**
Great Basin Year 2	χ-squared = 62.3855	df = 15	**p-value < 0.0001**
Great Basin Year 3	χ-squared = 71.5992	df = 15	**p-value < 0.0001**

Table S4.2.8. ANCOVA results for differences in log-transformed slopes of rank-abundance curves between experimental treatments within years at the Mojave site.

	Year 1 logabun	**Year 2 logabun**	**Year 3 logabun**
Predictors	*p*	*p*	*p*
rank	**<0.001**	**<0.001**	**<0.001**
Grouping	**<0.001**	**0.009**	**<0.001**
R^2 / R^2 adjusted	0.969 / 0.968	0.893 / 0.866	0.913 / 0.886

Table S4.2.9. ANCOVA results for differences in log-transformed slopes of rank-abundance curves between experimental treatments within years at the Chihuahuan site.

	Year 1 logabun	**Year 2 logabun**	**Year 3 logabun**
Predictors	*p*	*p*	*p*
rank	**<0.001**	**<0.001**	**<0.001**
Grouping	**<0.001**	**<0.001**	**<0.001**
R^2 / R^2 adjusted	0.796 / 0.777	0.979 / 0.979	0.868 / 0.860

Table S4.2.10. ANCOVA results for differences in log-transformed slopes of rank-abundance curves between experimental treatments within years at the Great Basin site.

	Year 1 logabun	**Year 2 logabun**	**Year 3 logabun**
Predictors	*p*	*p*	*p*
rank	**<0.001**	**<0.001**	**<0.001**
Grouping	0.620	0.301	**0.006**
R^2 / R^2 adjusted	0.894 / 0.864	0.835 / 0.788	0.934 / 0.921

Table S4.2.11. Mixed model results of log-transformed rank-abundance slopes and precipitation relationship at the Mojave site.

	UNDISTURBED slopes			**DISTURBED slopes**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*

(Intercept)	-0.73	-0.92 – -0.55	**<0.001**	-0.81	-0.99 – -0.62	**<0.001**
ppt	0.00	0.00 – 0.01	**<0.001**	0.00	0.00 – 0.01	**<0.001**
Random Effects						
σ^2	0.15			0.10		
τ_{00}	0.02 $_{\text{plot}}$			0.04 $_{\text{plot}}$		
ICC	0.10			0.31		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	55			51		
Marginal R^2 / Conditional R^2	0.223 / 0.301			0.319 / 0.527		

Table S4.2.12. Mixed model results of log-transformed rank-abundance slopes and precipitation relationship at the Chihuahuan site.

	UNDISTURBED slopes			**DISTURBED slopes**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-0.48	-0.63 – -0.33	**<0.001**	-0.76	-1.03 – -0.48	**<0.001**
ppt	0.00	- 0.00 – 0.00	0.321	0.00	0.00 – 0.00	**0.019**
Random Effects						
σ^2	0.08			0.27		
τ_{00}	0.00 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	59			60		
Marginal R^2 / Conditional R^2	0.017 / NA			0.090 / NA		

Table S4.2.13. Mixed model results of log-transformed rank-abundance slopes and precipitation relationship at the Great Basin site.

	UNDISTURBED slopes			DISTURBED slopes		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-0.34	-0.68 – -0.00	**0.049**	-0.47	-0.72 – -0.22	**<0.001**
ppt	-0.00	-0.00 – 0.00	0.247	0.00	-0.00 – 0.00	0.757
Random Effects						
σ^2	0.11			0.03		
τ_{00}	0.00 $_{\text{plot}}$			0.01 $_{\text{plot}}$		
ICC				0.23		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.023 / NA			0.002 / 0.235		

Table S4.2.14. Mixed model results of non-native species cover-precipitation relationship at the Mojave site.

	UNDISTURBED non-native_cover			DISTURBED non-native_cover		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-1.08	-2.70 – 0.54	0.184	-2.76	-5.64 – 0.11	0.059
ppt	0.02	0.01 – 0.03	**<0.001**	0.05	0.03 – 0.07	**<0.001**
Random Effects						
σ^2	3.22			18.85		
τ_{00}	0.00 $_{\text{plot.x}}$			0.00 $_{\text{plot.x}}$		
N	19 $_{\text{plot.x}}$			20 $_{\text{plot.x}}$		
Observations	45			57		
Marginal R^2 / Conditional R^2	0.320 / NA			0.306 / NA		

Table S4.2.15. Mixed model results of non-native species cover-precipitation relationship at the Great Basin site.

	UNDISTURBED non-native_cover			**DISTURBED non-native_cover**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.51	-6.14 – 7.16	0.877	-8.12	-16.83 – 0.59	0.067
ppt	0.01	-0.01 – 0.03	0.536	0.06	0.03 – 0.09	**<0.001**
Random Effects						
σ^2	17.07			74.52		
τ_{00}	4.36 $_{\text{plot.x}}$			2.68 $_{\text{plot.x}}$		
ICC	0.20			0.03		
N	19 $_{\text{plot.x}}$			20 $_{\text{plot.x}}$		
Observations	44			75		
Marginal R^2 / Conditional R^2	0.011 / 0.212			0.197 / 0.224		

Table S4.2.16. Mixed model results of community dispersion-precipitation relationship at the Mojave site.

	UNDISTURBED dispersions			**DISTURBED dispersions**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.20	0.16 – 0.25	**<0.001**	0.30	0.25 – 0.34	**<0.001**
ppt	0.00	-0.00 – 0.00	0.150	-0.00	-0.00 – 0.00	0.196
Random Effects						
σ^2	0.01			0.01		
τ_{00}	0.01 $_{\text{plot}}$			0.01 $_{\text{plot}}$		
ICC	0.52			0.46		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		

Observations	60			60		
Marginal R^2 / Conditional R^2	0.021 / 0.525			0.018 / 0.471		

Table S4.2.17. Mixed model results of community dispersion-precipitation relationship at the Chihuahuan site.

	UNDISTURBED dispersions			**DISTURBED dispersions**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.26	0.21 – 0.31	**<0.001**	0.19	0.15 – 0.23	**<0.001**
ppt	-0.00	-0.00 – 0.00	0.226	0.00	-0.00 – 0.00	0.143
Random Effects						
σ^2	0.01			0.01		
τ_{00}	0.00 $_{\text{plot}}$			0.00 $_{\text{plot}}$		
ICC	0.19			0.01		
N	20 $_{\text{plot}}$			20 $_{\text{plot}}$		
Observations	60			60		
Marginal R^2 / Conditional R^2	0.032 / 0.216			0.037 / 0.045		

Table S4.2.18. Mixed model results of community dispersion-precipitation relationship at the Great Basin site.

	UNDISTURBED dispersions			**DISTURBED dispersions**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.26	0.17 – 0.36	**<0.001**	0.18	0.09 – 0.28	**<0.001**
ppt	-0.00	-0.00 – -0.00	**0.001**	-0.00	-0.00 – 0.00	0.448
Random Effects						
σ^2	0.00			0.00		
τ_{00}	0.00 $_{\text{plot}}$			0.00 $_{\text{plot}}$		

ICC	0.82	0.35
N	20_{plot}	20_{plot}
Observations	60	60
Marginal R^2 / Conditional R^2	0.236 / 0.861	0.015 / 0.362

CHAPTER 5

CONCLUSIONS AND SYNTHESIS

This dissertation used complimentary approaches to ask how drylands are shaped by widespread and influential drivers of change as well as an evaluation of how a large land-managing federal agency approaches the flow of ecosystem services from drylands. This work contributes useful field-derived data, carefully collected over multiple years, to add to our understanding of how global change drivers will influence ecosystems over the coming decades and centuries.

Specific objective 1 was to assess effects and interactions of precipitation and disturbance in dryland ecosystems. I accomplished this objective by deploying and maintaining a manipulative field experiment with a high degree of replication (n=10 replicates per treatment per site) over four years and during an ongoing global pandemic. Physical disturbance had a negative effect on aboveground net primary productivity, and this effect was most pronounced at low precipitation values within and across sites. Specific objective 2 was to assess how effects and interactions of precipitation and disturbance vary along a gradient of aridity. I accomplished this objective by deploying and maintaining a manipulative field experiment over a >1000km latitudinal gradient over four years. The gradient of aridity covered in this field experiment revealed idiosyncratic and general responses to disturbance. In general, the effects of disturbance on richness and evenness were most pronounced at low precipitation values within and across sites.

Across specific objective 1 and 2, this work presents several salient ideas that are relevant to practicing ecologists, land managers, and the earth system modelling community. First and most importantly, this factorial field experiment shows how two widespread drivers, physical disturbance and precipitation reductions, can interact in complex ways to reduce ecosystem functioning and drive plant communities to less desirable states. In the Mojave and Great Basin Deserts, disturbance replaced the native shrubs with non-native species, and while precipitation reductions slowed these invasions slightly, the reduced precipitation also inhibited native plant growth, suggesting that a more invaded state is inevitable with a return of more precipitation. In the Chihuahuan, disturbance and precipitation interacted to drive perennial native grasses out of the system and facilitated a more shrub-invaded state, precisely what land managers in the region have been trying to avoid for decades. Considering these results at a regional scale, these dynamics vary across the three dryland ecosystems in this study, with large implications for how researchers might predict carbon cycle responses to climate change and human action. Specifically, the patterns identified in this work can inform how to account for the standing carbon stock of particular areas and be useful to estimate how changes in carbon stocks may occur from management actions.

These results offer information to inform ecological theory. Although following classic development of theory, these conclusions may open more questions than they answer. Disturbance theory in more mesic systems has been focused on concepts of succession. Though some ideas reasonably extend these concepts to dryland systems, such as cyclical succession, a large portion of ecological theory of disturbance was not developed for the desert shrublands studied here. These results show that changes in productivity over time following a disturbance are highly dependent on how much precipitation occurs following a disturbance. This dissertation suggests that desert shrublands do not conform to models of ecological processes related to disturbance, such as how productivity and diversity vary over time following a disturbance. As an additional case in point, even within research on dryland ecosystems, the majority of work has been in grasslands. Dryland ecologists often highlight the lack of attention on dryland systems, and I suggest that if one filters this concern to specifically desert shrublands, the lack of basic ecology is a major barrier to fundamental scientific understanding and effective land management.

For both specific objective 1 and 2, I reached several broad conclusions that support this approach and findings. By testing disturbance effects along diversity gradients this dissertation offers useful field-derived data and analyses for dryland systems. This work is also useful because of the three ecosystems represented. There are many more experiments in subhumid and dry subhumid grasslands than in deserts. Further, there are many more experiments about precipitation effects than disturbance effects. This study is unique in combining disturbance and precipitation manipulations in three desert systems. Lastly, there are very few disturbance experiments in deserts, with many more experiments of this nature occurring in grasslands. While novelty is not itself a metric of research quality, the insight and data provided by a cross-site assessment of multiple global change factors for four years in a globally important set of ecosystems (i.e., drylands) does have particular importance when so few similar studies exist.

Specific objective 3 was to assess the effect of management decisions on the supply of ecosystem services demanded from military lands in the United States. For perspective of demand from these areas, I evaluated over 40 environmental management plans from DoD installations across the arid western US and determined that, while they have some focus on managing the environment at the ecosystem scale, the plans largely fail to incorporate the ecosystem services conceptual framework. The management of these areas is largely driven by top-down, sweeping regulatory policy at the federal level, and are subject to relatively less regulatory influence at local scales. From a supply perspective, the DoD land base has a disproportionately high number of vertebrate diversity and rare species. Further, they support ecosystem function (represented by primary productivity) at a scale comparable to dryland areas managed by the National Park Service, US Forest Service, and Bureau of Land Management. In order to embody the ecosystem services concept in DoD land management, the most effective approach would likely be driven by top-down, federal level legislative directives.

As a whole, this thesis consolidates the final product of my PhD work with every chapter complementing each other. My second chapter broadly considered the consequences of dryland ecosystem management, the stakeholder groups that gain or lose access to ecosystem services because of management, and the legislative legacy of the DoD land base. Going beyond management, my third chapter used novel methods to ask fundamentally important questions in ecosystem ecology and uncovered that the presence of disturbance modulates the slope of the precipitation–productivity relationship. My fourth chapter focused more finely on community dynamics than ecosystem ecology per se and allowed important insight into the biodiversity consequences of disturbance and changing precipitation in dryland ecosystems. Each chapter offers a novel contribution to the field and adds important contributions to a body of literature about Earth's largest biome.

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