BIOLOGICAL INTERACTIONS AND DISTURBANCE IN ARID ECOSYSTEMS: EXAMPLES FROM THE GREAT BASIN, MOJAVE, AND NORTHERN CHIHUAHUAN DESERTS

BY

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ABSTRACT

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In an era where human influence pervades every corner of the natural world, improving our understanding the how ecosystems are structured and function has never been more critical. Dryland ecosystems, occupying over 40% of the plant's land surface area, represent the largest terrestrial biome on earth. Drylands are particularly vulnerable to global change pressures such as rising temperatures, altered precipitation regimes, and the spread of invasive species. The Earth's climate is changing rapidly, exacerbating these pressures and threatening the productivity, biodiversity, and function of dryland ecosystems. The interactions between these shifting pressures and disturbances, both natural and anthropogenic, add layers of complexity that challenge our understanding of these ecosystems.

In my dissertation, I used a combination of observational and experimental studies to investigate the impacts of disturbances on vegetation within dryland ecosystems, focusing particularly on the interactions between climate and biological factors known to influence the structure and function of plants. A rainfall manipulation and mechanical disturbance experiment repeated in three climatically distinct North America dryland ecosystems revealed complex, site-specific responses of dominant shrubs to environmental stressors. Findings indicated that individual traits, such as plant size, significantly influence sensitivity to climate changes, highlighting the need for localized management strategies. A study assessing the trophic impacts from a native twig girdling beetle on the above ground biomass of honey mesquite (*Prosopis glandulosa*) found significant year-to-year variability in beetle activity, with notable reductions in mesquite biomass due to girdling that exceeded estimates for annual net primary production for some years. A study assessing the influence of fire on biodiversity of soil seed bank across the Mojave found increased diversity in burned areas, but highlights the dominance of invasive species, ultimately leading to biodiversity loss and community homogenization. These findings underscore the significant impact of invasive species and the necessity of management practices to mitigate their spread.

Collectively, this dissertation provides a nuanced understanding of how natural and novel disturbance regimes affect dryland ecosystems. The differential responses among species and ecosystems suggest that effective management strategies must consider local ecological contexts to preserve productivity and biodiversity amidst rapidly changing global pressures.

DEDICATION

For Elliot

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CHAPTER 1

INTRODUCTION

Disturbance is widespread in ecosystems, and it helps shape patterns of species abundance, community dynamics, and, ultimately, biodiversity through space and time (Turner, 2010). However, by its very nature, disturbance does not happen as a uniform process. It occurs in discrete events that disrupt current ecosystem function, alter resource availability, and change the structure of populations, and biotic communities (Newman, 2019; Pickett and White, 1985). In the case of natural disturbances, as with other natural processes, they are often characterized in terms of regimes. For example, a fire regime can be described both conceptually and mathematically by frequency, severity, seasonality, spatial complexity, size, and extent (Klinger and Brooks, 2017; McLauchlan et al., 2020; Sugihara et al., 2006). Natural disturbance regimes can establish and operate outside the sphere of human influence. Indeed, evolutionary history tells us that fire regimes existed long before humans came about as a species (Keeley et al., 2011). Yet the global reach of human activities now makes this independence increasingly rare. Human-induced changes such as deforestation, urbanization, pollution, and climate change have altered natural disturbance regimes in profound ways (Geist and Lambin 2002, Turner 2010, Johnstone et al. 2016). For instance, human activities have increased the frequency and intensity of wildfires, changed the hydrology of watersheds, and introduced invasive species that disrupt native ecosystems. Agricultural practices and industrial activities release pollutants that alter soil chemistry and water quality, affecting the health and function of biological systems, and climate change driven by anthropogenic greenhouse gas emissions is modifying temperature and precipitation patterns, leading to shifts in species distributions and the timing of biological events. As a result, human activities are now a significant driver of ecological change, often exacerbating the effects of natural processes and creating new challenges for the resilience and stability of ecosystems worldwide.

Here in western North America, the increase in global temperatures has been linked to larger, more severe drought events (Zhang et al., 2021), and current forecasts suggest they will become more prevalent going forward (Bradford et al., 2020). Along with drought, hotter climate extremes are expected to increase aridity across the region, leading to drier soil conditions, and a fundamental shift in the water availability for vegetation (Overpeck and Udall, 2020). Regional changes in climate are also interacting with disturbance regimes like fire, which drought and aridity tend to increase when fuel (e.g., vegetation) is available (Mueller et al., 2020). In dryland ecosystems, increased disturbance from fire can have second order effects, such as promoting the spread of invasive annual grasses (D'Antonio and Vitousek, Peter M, 2004), which can cause drastic shifts in plant community composition (Abella, 2009), carbon cycling (Nagy et al., 2021; Norton et al., 2004), and even increased fire frequency (Brooks et al., 2004; D'Antonio and Vitousek, Peter M, 2004). However, disturbance is not limited to natural sources. Other sources of disturbance may be caused entirely by human action, such as the introduction of cattle into dryland ecosystems that share little evolutionary history with large grazers (Milchunas et al., 1988), or physical disturbance form vehicles, and heavy machinery use (Groom et al., 2007; Wang et al., 2014). These disturbances tend to be thought of less in terms of natural regimes, and more in terms of human impacts on a system. They are disruptions that restructure ecological communities, and drive change in ecosystem function, but they are outside the historic processes that shape ecosystems (Newman, 2019).

In drylands, physical disturbances can cause long-lasting changes to vegetation that can persists for decades after the initial event (Terry and Adler, 2024). For individual plants, physical disturbance can damage the physical structure and architecture of a plant, which can alter plant physiological function, remove biomass (Pickett et al., 1989), and lead to less photosynthetically active area, and less productivity (White, 1979). But these interactions can be complex. Physical disturbance of soil can lead to increased availability of soil nutrients and an associated increase of photosynthetic activity in plants, while simultaneously disrupting longer term N fixation leading to overall N loss and reduced photosynthetic capacity of a location (Evens and Belnap 1999). At larger spatial scales, disturbance may reduce the abundance of key species, such as desert shrubs, leading to drastic changes in productivity of entire plant communities (Coffin and Lauenroth, 1989; Koerner and Collins, 2014).

This dissertation is a story about interactions. My overall and initial research objective was to assess the effects of disturbance and climate drivers on desert plants. Deserts, by nature, are inherently harsh environments for biological organisms, including plants, due to extreme water scarcity, temperature fluctuations, nutrient-poor soils, intense solar radiation, wind erosion, sparse vegetation, and isolation. These conditions amplify stressors, both natural and human-induced, making survival and growth challenging. What emerged here is simple story: that ecological context is important and biological interactions between plant species, across trophic levels, or at the level of the individual, can shape ecosystems responses in novel ways. Because precipitation is the dominant control of biological processes in deserts, my analysis begins there with Chapter 2.

Thesis Objectives

Chapter 2, titled “Growth limitations for drought and disturbance interactions in dryland shrubs: An experiment from three North American desert ecosystems”, addresses two main questions: 1) how do altered precipitation regimes interact with physical disturbance to affect plant growth; and, 2) how does the relationship between plant growth and altered precipitation and physical disturbance vary across different dryland ecoregions, each with very different vegetation communities, and climatic signatures. Here I utilize an experimental approach that combines rainfall manipulation with direct physical disturbance at sites in the northern Great Basin, Mojave, and northern Chihuahuan deserts. I then assess the independent and interactive effects of these treatments on integrated measures of plant growth over 4 years and contrast them with snapshot data of ecophysiological function.

Chapter 3, titled “Interaction of cerambycid twig girdling beetles on above ground biomass of Honey mesquite in the Northern Chihuahuan Desert”, is the result of an eruptive pruning event by a native wood boring beetle that occurred at the northern Chihuahuan experimental site detailed in Ch. 2. This was a natural phenomenological disturbance by the Mesquite twig girdler (*Oncideres rhodosticta*) that occurs episodically as part of the beetle’s population and life history dynamics. Above ground estimates of biomass are the standard field based methods for estimating Net Primary Productivity (NPP) in dryland systems (Jordan 2024), and considerable efforts have been made to understand the relationships of NPP to climate, vegetation community dynamics and edaphic factors at our study area (Gherardi and Sala, 2015;

Huenneke and Schlesinger, 2006; Peters, 2021). However, cross trophic variability is rarely incorporated into measures of biomass change over time for the dominant shrub Honey Mesquite (*Prosopis glandulosa*). Here I assess the trophic interaction of the Mesquite twig girdler with annual estimates of biomass over four years. I develop site specific allometric models for living biomass at the full shrub size, and biomass at the size of the selection by the beetles.

In chapter 4, titled "Homogenization of soil seed bank communities by fire and invasive species in the Mojave Desert", I transition away from the individual and trophic level interactions, to look at the relationship of full species assemblages and disturbance from fire. The Mojave Desert is the most arid of the three experimental deserts represented in Ch. 2. Because of this, it may be the most sensitive to interacting climate and disturbance stressors. Adding to this sensitivity are the life history traits of the plants themselves that grow there. Desert annual plants utilize the dormancy (seed) phase of their lifecycle as part of an adaptive bet hedging strategy in response to highly variable annual rainfall patterns (Gremer and Venable, 2014). The main objective of this study was to look at plant assemblages through the lens of soil seed banks in an effort to better understand patterns of plant diversity in relation to disturbance (fire) and climate. This study was designed to leverage the distinct descriptive variables of a natural disturbance regime (time, severity, frequency, and extent) and understand their importance in relation to patterns of diversity. Adding to the complexity of the disturbance regime are the post disturbance patterns of invasion by non-native annual plants.

Collectively, the chapters of this dissertation provide a nuanced view of how historically natural, altered, and novel disturbance regimes may affect the productivity and biodiversity of dryland systems. In chapter 1, I found that dominant shrubs of the western U.S. were found to have different responses to drought and physical disturbances, likely due to their differing evolutionary histories. Meanwhile, in chapter 2 I relay that the impact of natural population cycles of a native phytophagous insect was revealed to have the potential to reduce aboveground shrub biomass by levels equivalent to or exceeding severe drought conditions, while in chapter 3 I describe the influence of abiotic and biotic factors (specifically exotic plant invasion) was also found to be reshaping native plant communities in response to changing fire regimes in the Mojave. Taken together, these chapters highlight the importance of considering ecological and evolutionary histories alongside simultaneous efforts to assess the impacts of biotic and abiotic drivers of change in dryland productivity in light of anticipated global change pressures and processes.

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CHAPTER 2

GROWTH LIMITATION FOR DROUGHT AND DISTURBANCE INTERACTIONS IN DRYLAND SHRUBS: AN EXPERIMENT FROM THREE NORTH AMERICAN DESERT ECOSYSTEMS

Abstract

Understanding how climate change and anthropogenic disturbances affect dryland ecosystems is crucial for predicting future ecological dynamics. This study investigates the impacts of sustained multi-year drought (4 years), mechanical disturbance (single event), and their interactions on the growth of dominant shrubs in three climatically distinct North American deserts: the Great Basin, Mojave, and Chihuahuan deserts. Through a combination of experimental rainfall manipulation and physical disturbance treatments, I assessed annual shrub growth and instantaneous ecophysiological responses. In my assessment, I also include biological factors of neighborhood cover, and size of experimental shrubs.

My findings reveal significant reductions in shrub volume for *Artemisia tridentata* (sagebrush) and *Larrea tridentata* (creosote bush) under disturbance treatments, while *Prosopis glandulosa* (honey mesquite) exhibited notable resistance. Drought marginally reduced sagebrush growth, and annual precipitation positively influenced its growth. Positive growth was associated with neighborhood vegetation cover for both sagebrush and creosote bush, while honey mesquite was unaffected by most variables. I did find an overall negative relationship between annual growth, and previous years volume, indicating potential size limitations for each study location. Photosynthetic rates (A_{net}) varied by species and treatment, with sagebrush

showing a negative response to drought and mesquite displaying increased photosynthesis in the first-year post-disturbance.

These results underscore the complex, site-specific nature of shrub responses to environmental stressors in drylands. Effective management strategies should account for local ecological contexts to mitigate climate change and disturbance impacts on these ecosystems. This study contributes to a deeper understanding of how different dryland shrubs respond to changing environmental conditions, informing conservation and management practices in arid regions.

Introduction

Warming global temperatures are disrupting historic climate patterns and altering ecosystems. In parts of western North America, rising temperatures are expected to be accompanied by longer and more severe droughts over large sections of the landscape (Balting et al., 2021; Bradford et al., 2020). A vast majority of the land surface area in western North America is composed of dryland ecosystems (Prăvălie, 2016). These are water limited areas that experience low and variable rainfall with demands of potential evapotranspiration (PET) over 1.5 times the inputs from mean annual precipitation (MAP/PET ratio, i.e. Aridity Index < 0.65; Maestre et al., 2021). The presence of such a persistent water deficit directly shapes the ecological processes that maintain these ecosystems resulting in lower plant productivity and biomass, and associated reduced soil fertility (Bestelmeyer et al., 2015; Whitford and Duval, 2019). This is an arid land and adaptations related to water conservation, drought tolerance, and intermittent rainfall are widespread among plant species (Wood, 2005). Vegetation responses to increases in drought severity in dryland systems will involve individual and plant community level interactions (e.g., competition for water) that are expected to drive functional shifts in species composition and productivity (Biederman et al., 2016; Palmquist et al., 2021).

Because water limitations in dryland ecosystems generally lead to reduced functionality including low primary production, other stressors, such as impacts from disturbance, have a greater potential to cause shifts in vegetation structure and function that can persist long after the stressor has been removed (Kasischke et al., 2013; Maestre et al., 2016). For example, in many locations across western North American, the introduction of cattle into systems that have no evolutionary history or native grazing analogues (Milchunas et al., 1988) has resulted in drastic changes in plant community composition that have persisted for decades after the grazing practice has stopped (Ripplinger et al., 2015). Similarly, infrequent exposure to fire over evolutionary time in some dryland regions, particularly desert ecosystems, means that native vegetation in these locations may be less adapted and more vulnerable to disturbance from fire than more mesic habitats (Brooks et al. 2018, Chambers and Wisdom 2009). In parts of the Great Basin and Mojave Deserts, fire, combined with the introduction of non-native annual plants associated with historic cattle grazing (e.g., cheatgrass), has created a positive feedback relationship, called “the grass fire cycle”, between an altered disturbance regime (i.e., increased fire from historical levels) and the spread of non-native annual plants. This has resulted in drastic changes to plant community structure, species diversity, and plant productivity (Brooks et al., 2004; D’Antonio and Vitousek, Peter M, 2004; Maxwell and Germino, 2022).

Other disturbances, such as mechanical, or physical disturbance from human activities (e.g., cross country travel by off-road vehicles) can also impact dryland vegetation. Disturbance from off-road vehicles has been shown to alter the physical properties of soil, shift species composition and reduce above ground biomass of woody vegetation (Ploughe and Fraser, 2022). Responses to these types of disturbances in the western U.S. is of high concern to the United States Department of Defense (DoD) which administers 27 million acres of land across the continental U.S., the majority of which (approximately 70%) is in dryland ecoregions (Jordan et al. 2024). DoD managed lands provide training for military activities such as munitions testing, and training exercises that involve extensive offroad travel by military vehicles (Anderson et al., 2005; Wang et al., 2014). However, these vast instillations also play a pivotal role in protecting natural resources and provide critical habitat for large numbers (> 500 nationwide) of threatened, endangered, and at-risk species (DOD 2022).

Collectively, climate change and disturbance are expected to alter dryland ecosystem structure and function. Yet our understanding of how climate change will affect dryland ecoregions with different species assemblages composed of arrays of plant populations adapted to different historical climate regimes remains limited. In order to better understand the response of dryland vegetation to the individual and combined stressors of a shifting climate and human caused disturbance, I utilized experimental rainfall and disturbance manipulations in three climatically distinct dryland ecosystems spanning a large latitudinal and aridity gradient across western North America. Specifically, I asked how annual growth in desert shrubs is impacted by a sustained multi-year drought, physical disturbance via mechanical crushing, and the interactions of drought and disturbance. I paired measurements of annual growth with instantaneous ecophysiological measurements of net photosynthesis (A_{net}) to determine whether direct measures of ecophysiology correspond with more seasonally integrated measures of plant growth. Across all three ecoregions I expected droughted shrubs to grow less than reference (ambient rainfall) control shrubs. Similarly, I expected disturbed shrubs to have less growth than undisturbed shrubs, and the interaction drought and disturbance to have overall negative synergistic effects on shrub growth. However, I expected these responses to vary across ecoregions with the overall driest location to experience the most detrimental impacts and the more temperate location to have the smallest effects of the experiment.

Methods

Study Sites

Experiments took place at three desert locations spanning a large latitudinal gradient: a Great Basin site located within the Orchard Combat Training Center in southern Idaho (OTCT;

43.276854, -116.246181), a Mojave Desert (hereafter Mojave) site located within the Nevada National Security Site (NNSS; 36.826738, -116.016001) in southern Nevada, and a northern Chihuahuan Desert (hereafter Chihuahuan) site located at the Jornada Experimental Range (JER; 32.549718, -106.771039) in southern New Mexico (Figure 1).

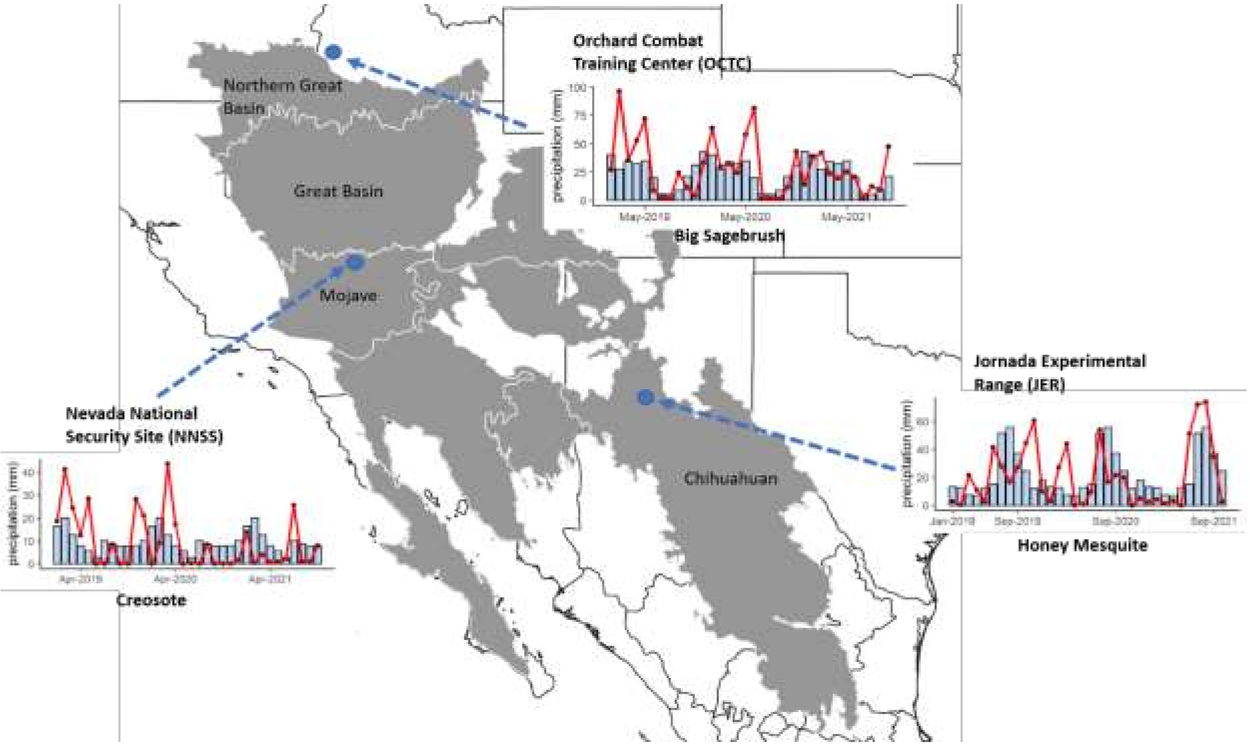

Figure 1. Study sites spanning a large geographic gradient across desert ecosystems in western North America. Each study site has a unique precipitation regime. Inset panels shows precipitation (mm) during sampling periods from 2019-2021 (red lines) and long (1991-2021) term monthly means in precipitation (barplots) for each site.

Each of these dryland ecosystems is distinct in terms of its precipitation and temperature regime, and vegetation community. The northern most site, located in the northern Great Basin, is a cold desert shrubland with an average summer daytime high temperature in July of 32.9 °C, and winter January highs of 3.9 °C. Of our three study locations, this one has the highest mean annual precipitation (MAP; 301 mm) receiving the majority (>80%) during the winter and spring months (November-May). In contrast, the southernmost site, located in the warm Chihuahuan desert is located in what was historically a black grama (*Bouteloua eripoda*) grassland that has been converted to a Honey Mesquite (*Prosopis glandulosa*) shrubland. This site receives most (70%) of its rain fall (257 mm MAP) as seasonal thunderstorms (June-October) as a result of monsoonal moisture from the Gulf of Mexico (Havstad et al. 2006). The Mojave, located at intermediate latitudes between the Great Basin and Chihuahuan, is often considered a transitional desert between the warm desert systems to the south (Sonoran, Chihuahuan) and the cooler Great Basin to the north. The Mojave site receives most (72%) of its annual precipitation (119 mm, MAP) from winter and spring (November-April) storms coming off of the Pacific Ocean. However, rainshadow effects from the Sierra Nevada, Transverse, and Peninsular Mountain ranges, combined with warmer temperatures make the Mojave site the most arid on average of our three study locations (Figure 2, PRISM Climate Group, 2022).

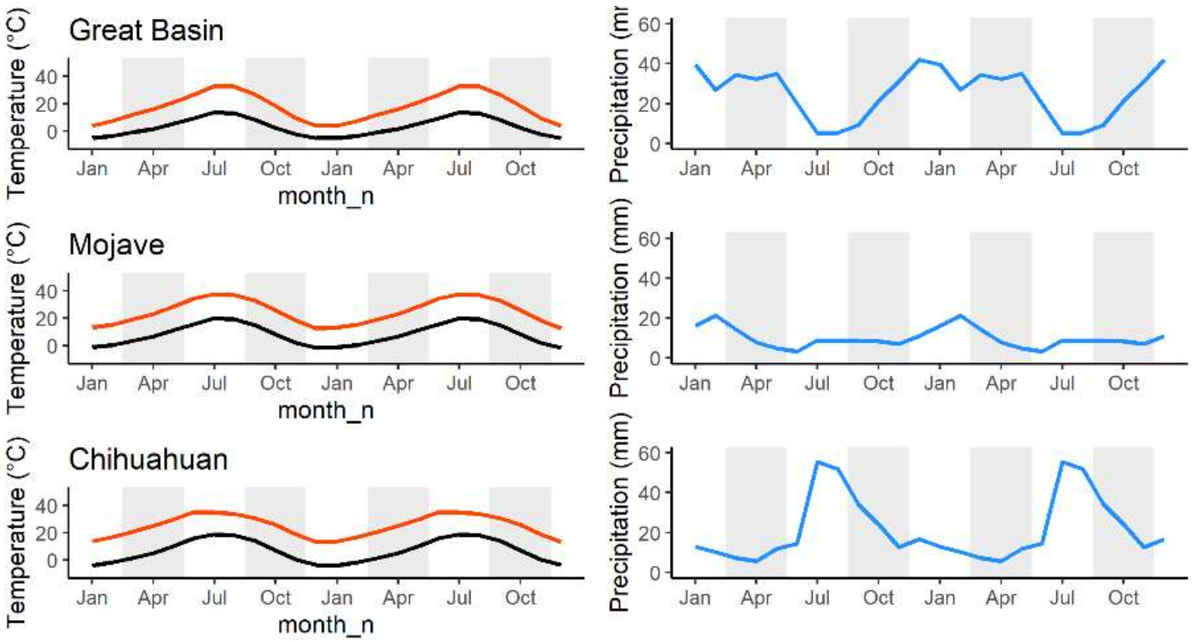

Figure 2. Long term (1991-2020) mean temperature, and precipitation profiles for three different desert study locations (PRISM Climate Group, 2022).

Experimental Design

At each location I used 40 focal shrubs, each a geographically widespread, dominant representative of emblematic vegetation community types for the three ecoregions. From North to South, these were sagebrush (*Artemisia tridentata*) in the Great Basin (OCTC), Creosote bush (*Larrea tridentata*) in the Mojave (NNSS), and Honey Mesquite (*Prosopis glandulosa*) in the Chihuahuan (JER). Shrubs were selected in terms of size, spacing (e.g., neighborhood density of woody plants), and local associated plant communities, to be representative of the site vegetation. Each shrub was randomly assigned to one of four experimental treatments, each replicated 10 times at each site: drought, disturbed, droughted x disturbed, and a control. Each focal shrub was used as the center of a 2.5 x 5 m experimental unit, hereafter referred to as "plots."

For droughted plots (i.e., drought & drought x disturbance), I used a passive rainfall-interception technique commonly referred to as “rainout shelters” to reduce ambient precipitation into local surface soils (Fig. S2.1). The total amount of rainfall intercepted by the rainout shelters differed across sites to correspond to simulated first-percentile precipitation for a 100-year period based on long-term climate data for each site (Lemoine et al. 2016). The percent difference between the simulated first-percentile amount of precipitation and the long-term mean annual precipitation (MAP) for each site provided the amount of rainfall reduction for the rainout shelters at each site: 40% reduction for the Great Basin, 60% reduction for the Mojave, and 70% reduction for the Chihuahuan plots. Rainout shelters were constructed using “v” shaped clear acrylic slats to intercept incoming rainfall while having minimal impact on photosynthetically active radiation. The percent of aerial coverage of slats for each plot corresponded with the intended reduction percentages of ambient rainfall. At least 30 cm of space between all rainout shelter components and the shrub canopies was ensured at the start of the experiment and to minimalize additional disturbance to soils, plot boundaries were not trenched. Rainout shelters were installed prior to peak biomass at each site in 2019 and maintained through the peak season of productivity of 2022.

Disturbed plots (i.e., disturbance & drought x disturbance) were treated with a JRCO model MSAT 48” (122 cm) spike drum aerator pulled by a 4-wheel drive all-terrain vehicle (ATV; Figure S2.2). The drum contained 102 (7cm) spikes and weighed 165 kg when filled with water. Each plot received 4 overlapping (8 total) passes with the ATV and drum aerator in alternating directions. A 1-meter buffer around each plot received an additional 4 overlapping passes. These treatments were done in a single event immediately following 2019 baseline sampling (see below) and immediately prior to the installation of the rainout shelters.

Field Sampling

In 2019 target variables were measured before any treatments were applied in order to capture local site variation and quantify immediate single year disturbance effects. I then sampled all plots annually for the 2020-2022 seasons. The timing of sampling periods varied across sites, in order to correspond with seasonal plant phenology and biomass production for each location. I sampled Mojave plots in mid-April, Great Basin plots in May-early June, and Chihuahuan plots in September after the annual monsoonal peak in precipitation.

Data collected for each plot included vegetation cover along three, parallel 5-meter cover lines separated by 50 cm, centered along the short axis of each plot and running the length of the plot (see Jordan 2024). Along each cover line, plant cover at a 1-cm resolution was recorded using the line intercept method (Heady 1959). Measurements 20 cm or less from the plot boundary were excluded to avoid potential influences of "edge effects" on the data. Focal shrub volumes were recorded by measuring the diameter of the widest section of each shrub, and paired with a second diameter recorded perpendicular to the first diameter and a shrub height. Shrub volumes were calculated as a length x width x height. Shrub volume is among commonly used metrics (e.g., height, canopy diameter, total basal area, volume) in the development of allometric equations to estimate above ground biomass. All three focal species have been previously studied. For instance, Cleary et al. (Cleary et al., 2008) found that crown (canopy) volume alone was the strongest predictor ($R^2 > 0.92$) for total above ground biomass in *Artemisia tridentata* across multiple locations and multiple stages of recovery after disturbance from fire. Similar allometric models have been developed for *Larrea tridentata* (Allen et al., 2008), and *Prosopis glandulosa* (El Fadl et al., 1989; Martínez and López-Portillo, 2003), each highlighting the ability to estimate above ground biomass from simple canopy measurements in dryland shrubs. This general relationship was also validated at our own study sites. In 2022 (3-years post disturbance; Devine et al., *In Review*), using highly detailed structure for motion 3-d imagery, found that coarse estimates of canopy volumes using convex hulls were better at estimating above ground biomass for both disturbed and undisturbed shrubs universally across our study sites than more highly detailed voxel (1 mm^3) measurements that attempted to remove inter-canopy voids in volume estimates.

Leaf photosynthetic rates under saturating light conditions were measured for each focal shrub once during each growing season (2019-2022) using a portable gas exchange system (model 6400xt; LiCor, Lincoln, NE). However, due to constraints from the Covid19 pandemic, I was unable to sample NNSS, and only able to sample 50% of the plots at OCTC during the 2020 season. A sample of representative leaves for each shrub were placed in a conifer chamber where they were exposed to standardized levels of photosynthetically active radiation (PAR) of 2,000 mmol photons $m^{-2}s^{-1}$; relative humidity of 50-80%; and sample CO_2 of 400 ppm. Ambient leaf temperatures ranged between 26-34 °C. Photosynthetic rates were recorded for 10-minute intervals with a recording taken every 10 seconds. It usually took approximately 5 minutes for photosynthesis rates to stabilize. The maximum recorded stabilized photosynthesis rate (A_{net}) was then extracted to be used in further analysis. Leaf area for each sample was estimated using ImageJ v.1.51S (National Institutes of Health, Bethesda, MD, USA) and was used to scale gas exchange measurements to a one-sided leaf area.

Data Analysis

All analyses were performed using R v. 4.3.2 (R Core Development Team 2020). I conducted a one-way analysis of variance (ANOVA), with “treatment” as a fixed-effect, on all pretreatment focal shrub volumes to ensure that shrub samples were balanced across treatment groups. I then assessed how each focal shrub responded in terms of shrub volume and relative change in volume from one year to the next (Δ Vol) (Figure 4), and A_{net} to the individual and interactive effects of drought and disturbance across time by constructing a series of independent generalized linear mixed-effects models (GLMM) with the plot identity and sampling year as random effects to account for the repeated sampling study-design in all models.

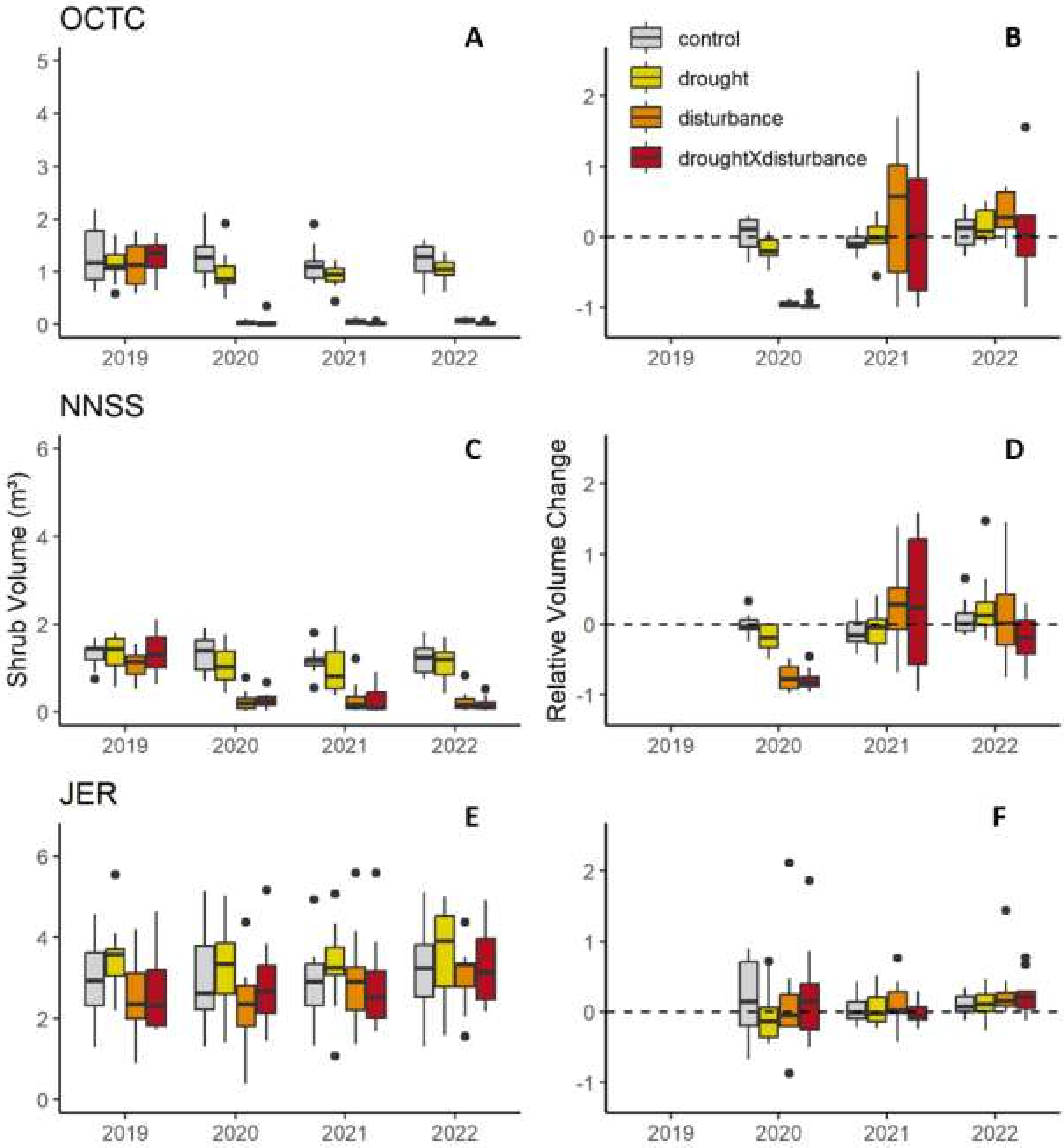

Figure 3. Boxplots of annual shrub volume (A, C, E) and relative annual change in shrub volume (B,D,F) from three deserts study locations: Orchard Combat Training Center (OCTC;A,B), Nevada National Security Site (NNSS; C,D) and Jornada Experimental Range (JER; EF). Boxplot colors indicate experimental treatment groups (grey=control; yellow=drought; orange= disturbance; red= drought x disturbance).

I created separate models for all three desert sites. In addition to treatment (control, drought, disturbance, drought x disturbance) I incorporated several covariates that had potential to influence shrub growth in desert systems. These included annual precipitation measured across the preceding 365 days before sampling (R365), and annual neighborhood estimates of living vegetation cover. While neighborhood influences can be interpreted multiple ways, for example positive effects (and correlations) of shrub volume with neighboring plant cover may be indicative of facilitative biological processes (e.g., shrub island effect), it may also be due to generally favorable local conditions that promote plant growth across space or time, while negative effects might be due to competition between plants for limited resources. Because shrub size can have different physiological responses to soil water availability (e.g., transpiration demand) I used shrub volume as a covariate for both ΔVol (as preceding years volume) and A_{net} (as current years volume) models. For the Chihuahuan desert site (JER), we also included the previous 90 days (RQ4) leading up to sampling along with R365 as a predictor to capture annual variability in Monsoonal moisture.

For each model, I estimated 95% confidence intervals of standardized parameter estimates (β coefficients) for the fixed effects using the MuMIn package (Barton 2015). I also used this package to quantify the marginal fit (R^2) of the fixed effects and the conditional fit (R^2_C) of entire models (i.e., both fixed and random factors; Nakagawa and Schielzeth, 2013). I considered variables significant if their 95% CIs did not overlap zero. I then constructed GLMM models to look at relative change in focal shrub volume from one year to the next. Because of obvious structural disturbance impacts to shrub volume between 2019-2020 I split the dataset into groups of disturbed plots and non-disturbed plots and assessed shrub volume change post treatment (2020-2021 & 2021-2022) (Figure 5). All models were constructed using a Gaussian distribution and identity link function. Model fits and normality of residuals were examined using diagnostic plots. I assessed possible collinearity issues between fixed effects by estimating the variance inflation factors (VIF) for each model. VIF values were <5, indicating little collinearity among predictors (Akinwande et al., 2015).

Results

Preliminary ANOVA showed no significant difference in shrub volumes for each site at the onset of the experiment (pretreatment; OCTC $p = 0.80$; NNSS $p = 0.79$; JER $p = 0.20$). I found shrub growth as measured by shrub volume, Δ volume, and A_{net} to vary broadly across species, years, and treatments. Shrub volume responses to disturbance were asymmetric, with large reductions in above ground volume for both *A. tridentata*, and *L. tridentata* in disturbance and drought x disturbance plots, but no discernable difference from control for *P. glandulosa* (Figure 3). We found marginal effects from drought on shrub volume on *A. tridentata* ($p = 0.06$; Figure 5), but not for *L. tridentata* (Fig. 6) or *P. glandulosa* (Fig. 7) (Table 1). Annual precipitation had a positive relationship with shrub volume for *A. tridentata*, but not for *L. tridentata* or P. glandulosa. We found a positive relationship with neighborhood cover for all three species. For Δ volume we found significant negative relationships between the preceding year's volume and the change so that smaller shrubs tended grow more relative to their size than larger shrubs, while larger shrubs were observed to grow less or in some cases have reductions relative to their previous years volume. We also found that in the cases of *A. tridentata*, Δ volume had a negative relationship with neighborhood cover.

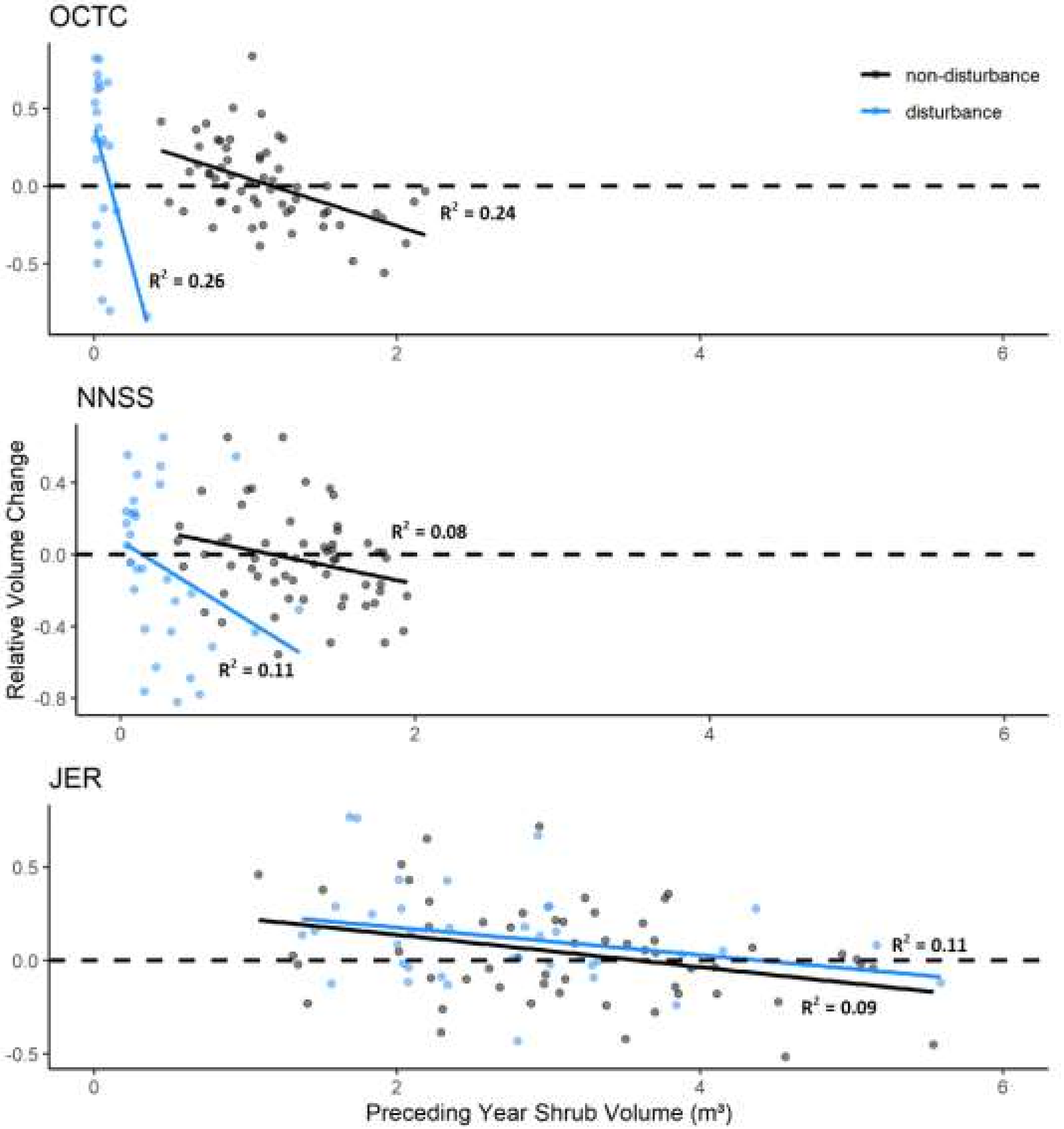

Figure 4. The relationship between preceding years shrub volume and the relative change in shrub volume (Δ volume) for 2020-2022 in non-disturbed shrubs (black), and 2021-2022 in disturbed shrubs (blue).

Measures of A_{net} varied idiosyncratically compared to shrub volume. For *A. tridentata*, we found significant negative relationships between A_{net} and droughted shrubs (Fig. 6). We also detected a significant negative relationship with leaf temperature within the sampling chamber. For *L. tridentata* we found no significant relationship between A_{net} and treatment for any of the years sampled. However, we did find a relatively strong positive relationship with neighborhood cover (R^2=0.66). For *P. glandulosa*, we found a positive relationship between A_{net} and disturbed shrubs (disturbance & drought X disturbance). Post-hoc Kruskal Wallace tests on treatments in individual years showed that this relationship was driven by the year-1 post treatment measurements (Fig. 11).

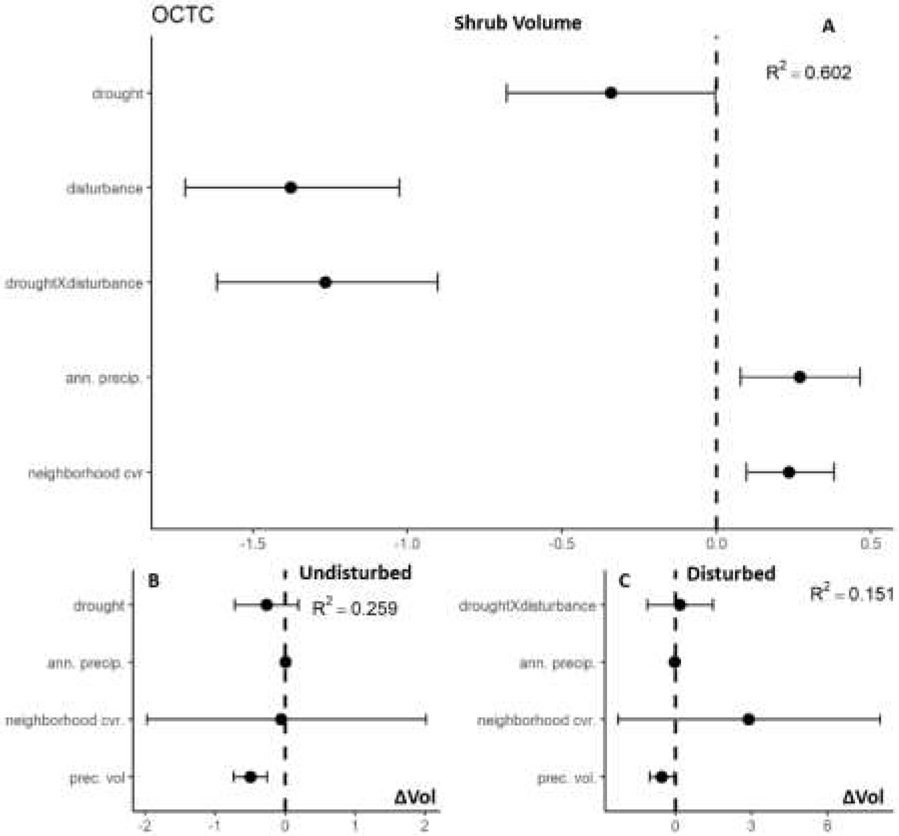

Figure 5. Forest plots showing standardized beta coefficients for fixed effects (see Table 1) from generalized linear mixed effect models (GLMMs) for shrub volume (A), and change in shrub volume for undisturbed (B), and disturbed (C) for *Artemisia tridentata* focal shrubs from the Orchard Combat Training Center (OCTC) in southern Idaho. Error bars indicate 95% confidence intervals.

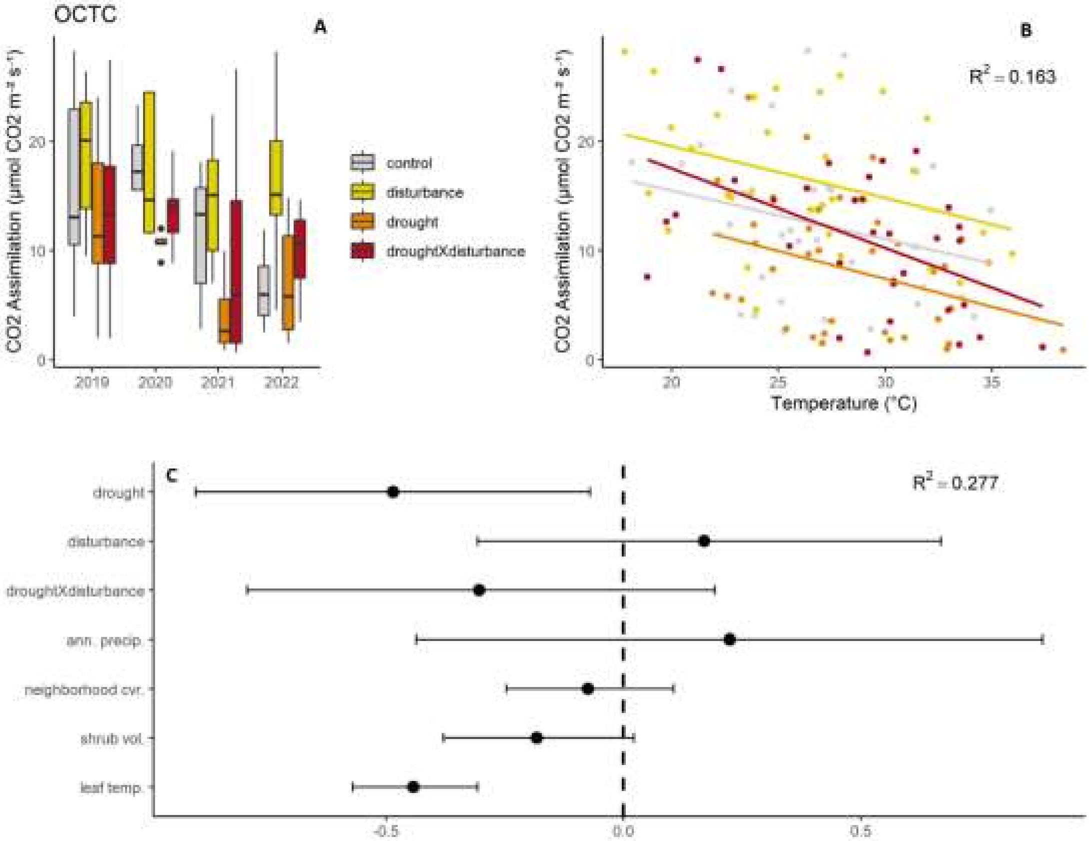

Figure 6. Photosynthetic rates (A_{net}) to drought, disturbance, and drought x disturbance for *Artemisia tridentata* from the northern Great Basin (A). Panel B shows the relationship between A_{net} and leaf temperature (°C) at time of sampling. Panel C shows forest plot of standardized beta coefficients of fixed effects from a generalized linear mixed-effects model for A_{net}.

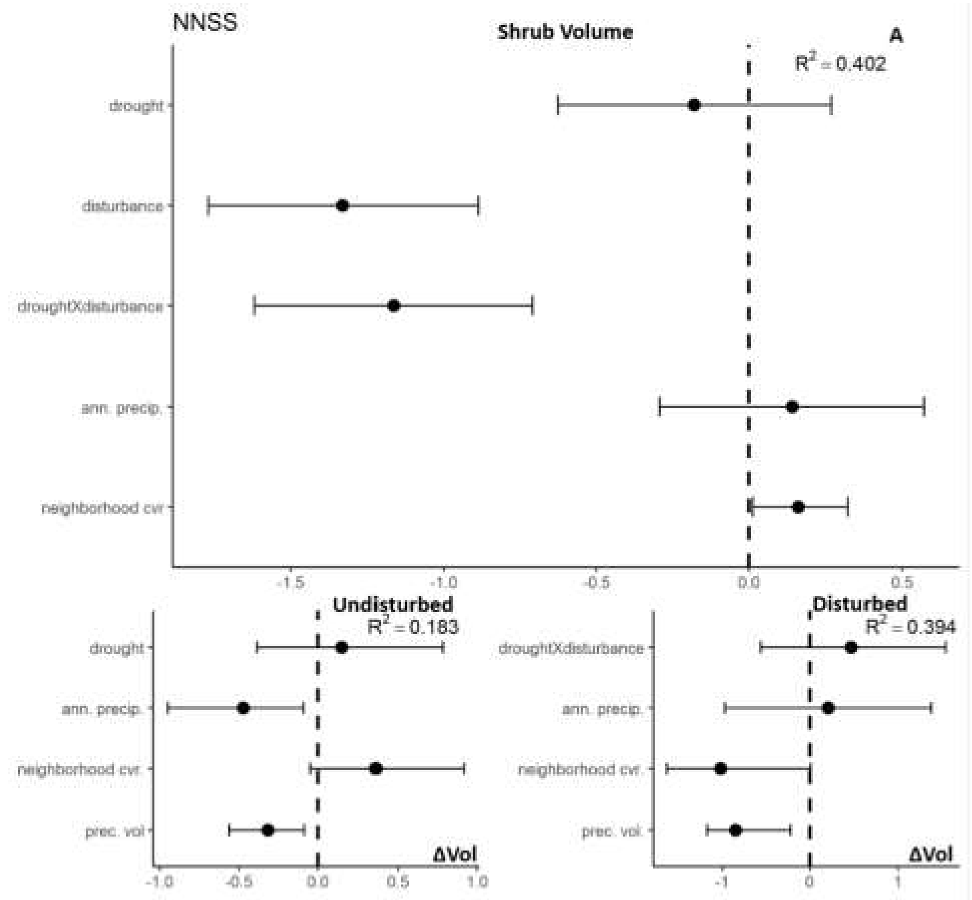

Figure 7. Forest plots showing standardized beta coefficients for fixed effects (see Table 1) from generalized linear mixed effect models (GLMMs) for shrub volume (A), and change in shrub volume for undisturbed (B), and disturbed (C) for *Larrea tridentata* focal shrubs from the Nevada National Security Site (NNSS) in the Mojave Desert in southern Nevada. Error bars represent 95% Confidence Intervals.

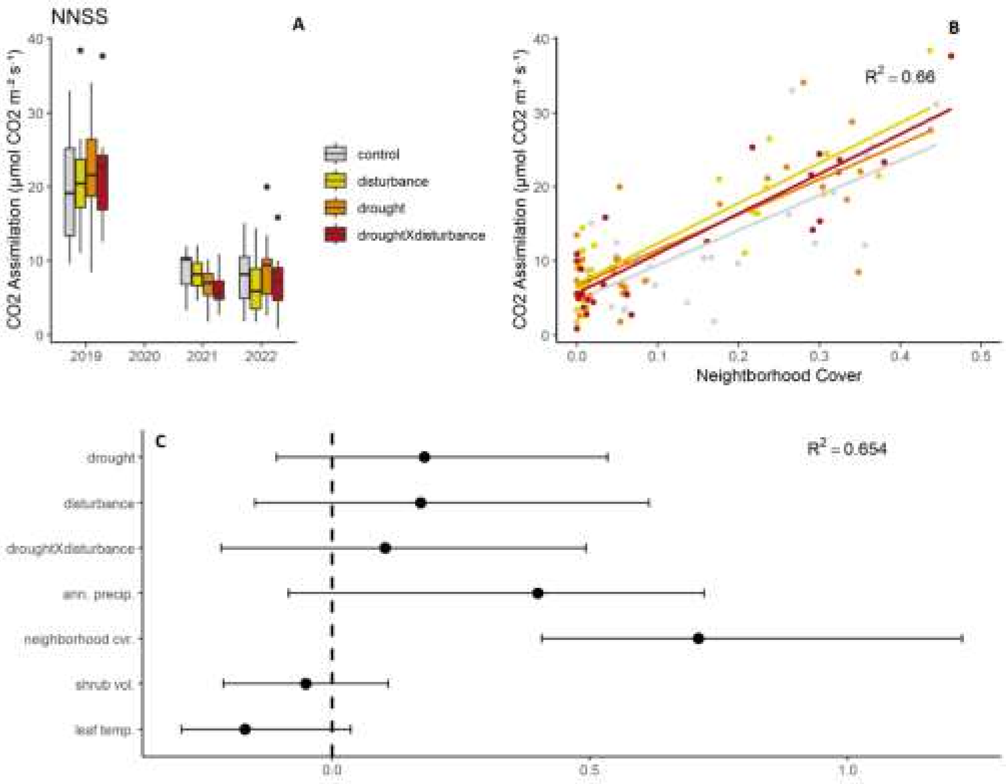

Figure 8. Photosynthetic rates (A_{net}) to drought, disturbance, and drought x disturbance for *Larrea tridentata* from the northern Mojave Desert (A). Panel B shows the relationship between A_{net} and leaf temperature and cover of neighborhood plants at time of sampling. Panel C shows forest plot of standardized beta coefficients of fixed effects from a generalized linear mixed-effects model for A_{net}.

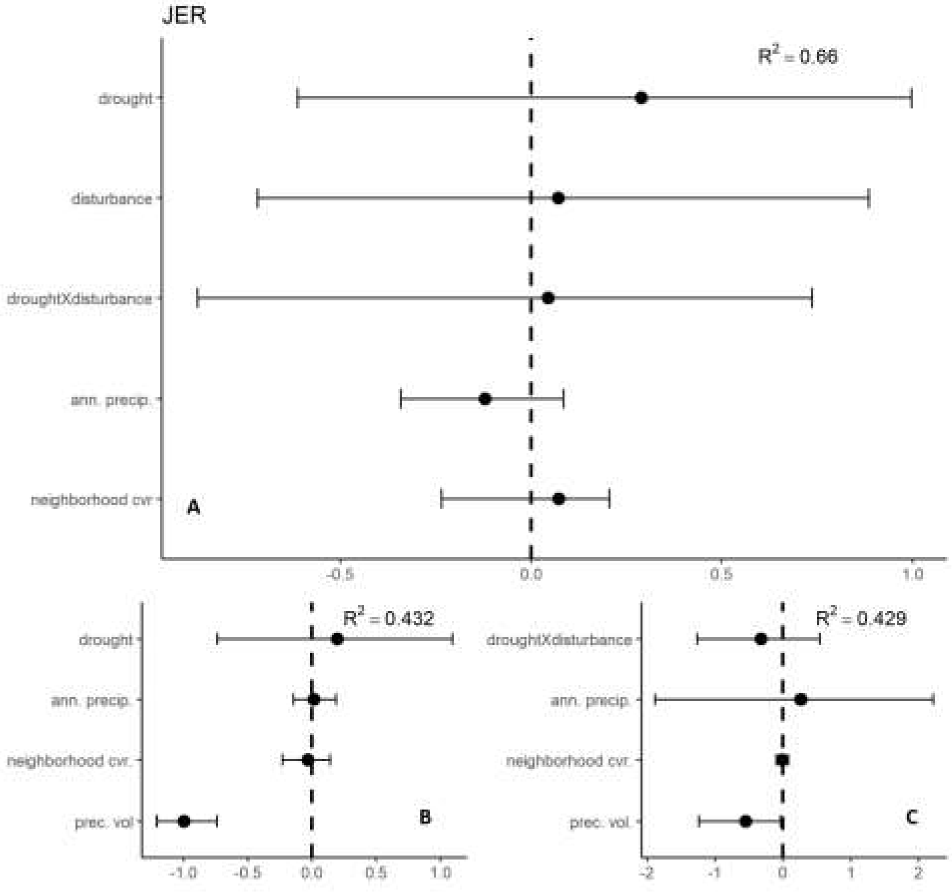

Figure 9. Forest plots showing standardized beta coefficients for fixed effects (see Table 1) from generalized linear mixed effect models (GLMMs) for shrub volume (A), and change in shrub volume for undisturbed (B), and disturbed (C) for *Prosopis glandulosa* focal shrubs from the Jornada Experimental Range (JER) in the northern Chihuahuan Desert. Error bars represent 95% Confidence Intervals.

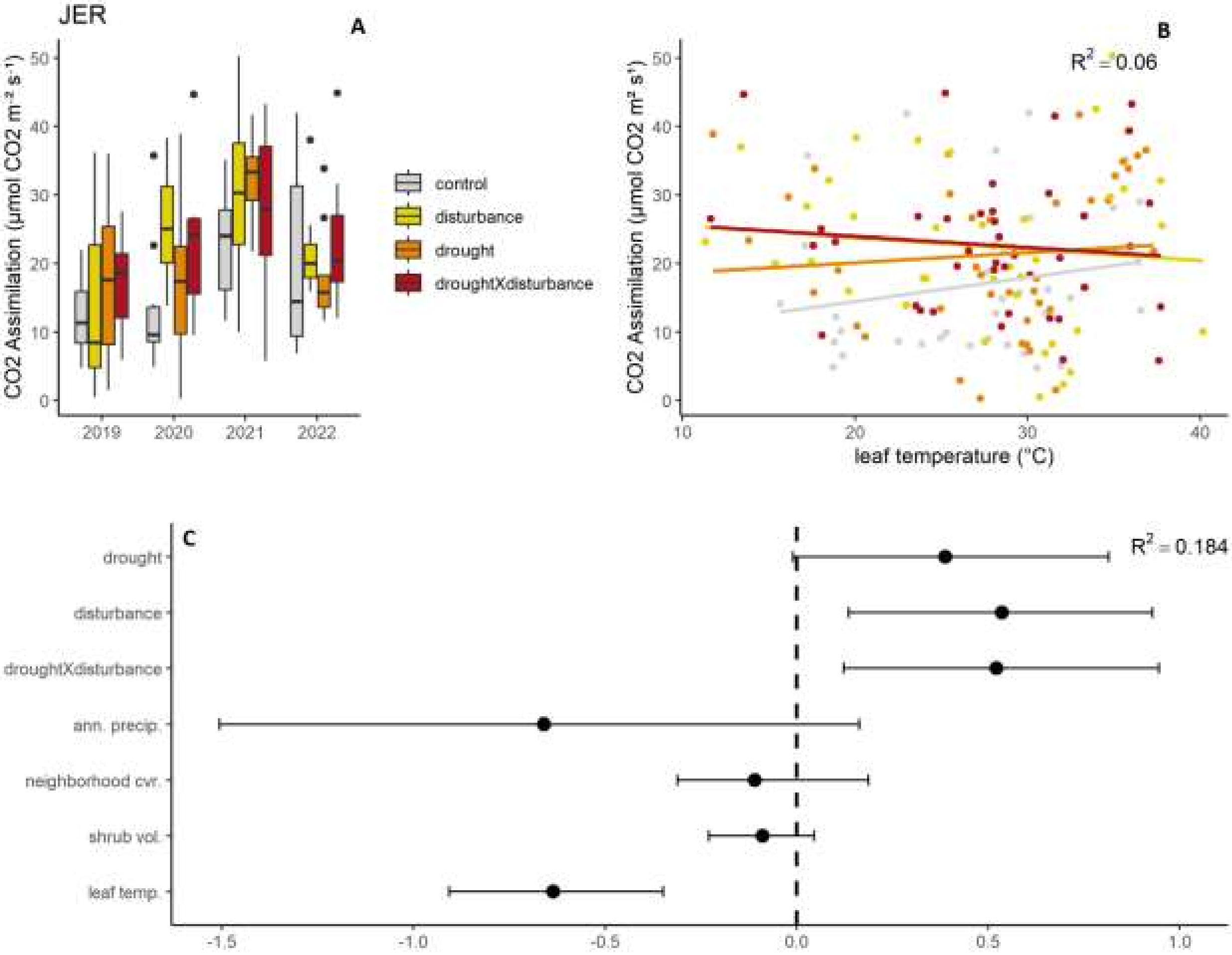

Figure 10. Photosynthetic rates (A_{net}) to drought, disturbance, and drought x disturbance for *Prosopis glandulosa* from the northern Chihuahuan Desert (A). Panel B shows the relationship between A_{net} and leaf temperature and cover of neighborhood plants at time of sampling. Panel C shows forest plot of standardized beta coefficients of fixed effects from a generalized linear mixed-effects model for A_{net}.

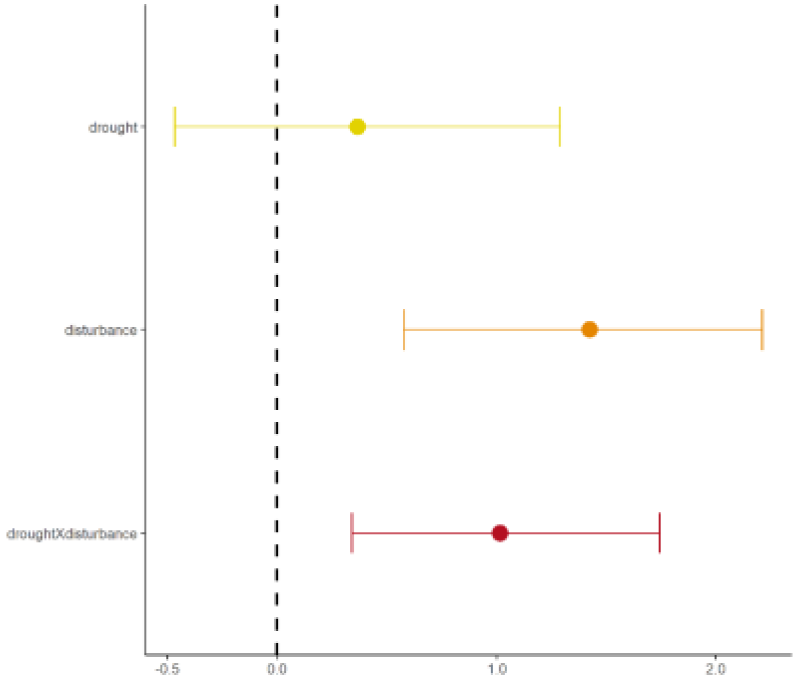

Figure 11. Treatment effect sizes (Cohen's D) relative to control for net rates of photosynthetic CO2 assimilation (A_{net}) in Honey Mesquite (*Prosopis glandulosa*) one year post treatment (2020).

Table 1. Results in the form of marginal and conditional R^2 values for each of the individual generalized linear mixed-effect models assessing shrub growth and ecophysicological function.

Site	Response	R^2 (marg.)	R^2 (cond.)
Great Basin (OCTC)	shrub volume	0.60	0.64
	Δ shrub volume (undisturbed)	0.25	0.30
	Δ shrub volume (disturbed)	0.15	0.18
	A_{net}	0.28	0.44
Mojave (NNSS)	shrub volume	0.42	0.59
	Δ shrub volume (undisturbed)	0.18	0.41
	Δ shrub volume (disturbed)	0.39	0.62
	A_{net}	0.65	0.72
Chihuahuan (JER)	shrub volume	0.66	0.69
	Δ shrub volume (undisturbed)	0.43	0.87
	Δ shrub volume (disturbed)	0.24	0.57
	A_{net}	0.18	0.67

Discussion

Global mean annual temperature is predicted to increase by 2 to 6 ℃ by 2100, leading to more variable precipitation and a greater frequency of droughts (Melillo et al., 2014). Changing precipitation and temperature regimes in western North America are predicted to be highly variable across dryland ecosystems (Bradford et al., 2020), and vegetation responses are likely to be similarly heterogeneous and idiosyncratic across space and time (Palmquist et al., 2021). Thus, understanding the context of ecoregions and individual species' responses to variable climate conditions is crucial for predicting how specific ecosystems will be affected by climate change. Different ecoregions have unique climatic patterns, soil types, and historical disturbance regimes, all of which influence how plant species respond to environmental stressors. By studying these responses, we can better anticipate shifts in species composition, productivity, and ecosystem function.

We evaluated the response of three dominant shrubs, each a major representative of cover in the ecoregions we sampled. These included a cool desert system in the north (northern Great Basin) that receives the majority of its rainfall in the winter and spring, and a hot desert in the south (northern Chihuahuan) that has an almost inverse pattern of annual precipitation, receiving the majority of its rainfall during the summer monsoon months. The Mojave Desert, while still a hot desert, typically receives most of its precipitation in the winter months, leading to a long, hot dry summer season. The shrubs in each of these ecoregions—Basin Sagebrush in the Great Basin, Creosote Bush in the Mojave, and Honey Mesquite in the Chihuahuan—have unique adaptations.

Occupying approximately 76 million ha, sagebrush-dominated plant communities are widespread across temperate and cold desert dryland systems of North America (Rigge et al., 2020). However, sagebrush populations are generally in decline, largely due to the impacts of disturbance and the spread of exotic plants (Knick et al., 2003). Sagebrush is slow to recover after disturbance, including from physical disturbances like our experimental treatments (Lavin et al., 2013; Riginos et al., 2019). The alteration of vegetation and disruption to soil nutrient cycling that accompanies disturbance has, in many cases, pushed sagebrush communities past critical thresholds (McIver and Starr, 2001). Data from our experiment directly supports this. Once our disturbance treatments were initiated, we observed very little recovery in terms of above-ground change in shrub volume, and in the case of three sagebrush individuals, disturbance actually led to mortality. However, we did see positive effects of precipitation and neighborhood cover on shrub growth. The most abundant species besides sagebrush in our plots was the native cool-season bunchgrass *Poa secunda*. This species is sensitive to fluctuations in temperature and rainfall (Link et al., 2003) and may be a good indicator of beneficial growing conditions for the site. In general, changes in shrub volume were related to the previous year's shrub size. We found A_{net} in sagebrush to be sensitive to the effects of our drought treatment. This may be related to the seasonality of water use by sagebrush roots, which have been shown to have moisture use zones that shift outwards and downwards from shallow soils near the base of the plant as the summer season progresses (Sturges 1983).

Similar to sagebrush, disturbance treatments caused significant and sustained reductions in above-ground volume in creosote at our Mojave site. We also documented a similar positive relationship with neighborhood cover, which may be indicative of better local growing conditions. Unlike sagebrush, creosote bush more readily resprouts after damage from disturbance (Gibson et al., 2004); however, timelines for recovery can be long, sometimes taking decades to return to pre-disturbance levels (Abella, 2010). Observationally, we saw resprouting on most of the disturbed focal creosote shrubs over the course of the study, and none of them suffered mortality like sagebrush. But similar to sagebrush, there was a negative relationship between shrub growth (Δ Volume) and preceding year's shrub size. Comparable patterns have been documented with creosote at other desert sites. For instance, Franco et al. (1993), working at the NMSU College Ranch, noted that smaller creosote shrubs tended to grow at rates much higher than larger shrubs during the monsoon season. Similarly, Molinari et al. (2019), working in the eastern Mojave Desert, recorded rates of growth in younger burned-area creosote, higher than in older nearby reference plants. This may be a difference in resource allocation based on plant size or age, where larger plants spend more resources on root growth or reproduction. For photosynthesis, we found a strong positive relationship with neighborhood plant cover. This may be due to increased rates of photosynthesis being associated with favorable conditions. However, more dynamic relationships with herbaceous understory plants could lead to similar patterns. Creosote is an evergreen shrub that is the dominant vegetation component for many plant communities across the Mojave, Sonoran, and Chihuahuan Deserts (Barbour and Billings, 2000). Adaptations to extremely harsh environmental conditions have allowed this plant to live in some of the hottest and driest places on the planet. Part of its success is its ability to maintain physiological function while other species are forced to go dormant. For instance, Creosote has the ability to photosynthesize at extremely low xylem water potentials (Odening et al., 1974), which may increase its competitive effects during moderately drier periods.

Unlike sagebrush and creosote, we were unable to detect any of our treatment effects on shrub growth (shrub volume or Δ volume) in honey mesquite. However, we did document a relatively small but significant negative relationship between shrub growth (Δ volume) and shrub size, a pattern observed at the other two sites as well. The differences in growth for different shrub sizes across all three sites may be because smaller shrubs have less above-ground tissue and transpiration surface area, and therefore less demand for water than larger shrubs. Related patterns with mesquite and Anet have been observed at JER, where smaller shrubs can have greater photosynthetic rates when near-surface water is present (De Soyza et al., 1996). While we were unable to detect differences in Anet based on shrub volume, we did find a significant positive treatment effect from disturbance. Post-hoc analyses of the treatments within the year show this was largely driven by the 2020 Anet measurements. Mesquite readily resprouts from axial buds when stems are damaged from both mechanical disturbance (Ansley et al., 2010) and in some cases herbivory (Martínez et al., 2009). A large number of broken stems has the potential to stimulate compensatory regrowth in mesquite, which could be further boosted by a temporary size reduction from our treatments. Conversely, reductions in shrub volumes across our sites could be related to plant dieback as an important strategy in dealing with water stress in shrubs (Koepke et al., 2010). By reducing the amount of transpirational surface area, leaf and shoot dieback can change root-to-shoot ratios and improve water status within the plant (Davis et al., 2002).

Conclusion

Our results indicated that disturbance significantly reduced above-ground shrub volume for sagebrush (*Artemisia tridentata*) and creosote bush (*Larrea tridentata*), but not for honey mesquite (*Prosopis glandulosa*). Drought had a marginal negative effect on sagebrush growth, while annual precipitation positively influenced its growth. Interestingly, the relationship between neighborhood cover and shrub growth was positive for sagebrush and creosote bush, suggesting that local vegetation density might facilitate growth under certain conditions. Photosynthetic responses varied, with sagebrush showing a negative response to drought and mesquite exhibiting increased photosynthesis after disturbance, possibly due to compensatory regrowth mechanisms.

Overall, the study highlights the complex and site-specific nature of plant responses to altered precipitation and disturbance in dryland ecosystems. The findings underscore the importance of considering local ecological contexts when predicting vegetation dynamics under future climate scenarios. The differential responses among species and ecosystems suggest that management strategies should be tailored to specific conditions to effectively mitigate the impacts of climate change and anthropogenic disturbances on dryland vegetation.

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Supplementary Material

Figure S.2.1. Rainfall exclusion (rainout) shelters at the Mojave(let), Chihuahuan (center), and Great Basin (right) sites. Plots were centered over individual focal shrubs representing dominant cover species for each ecoregion (photo by Samuel Jordan).

Figure S.2.1.1 Four wheeled all-terrain vehicle (ATV) equipped with a pull behind spiked rum aerator used for physical disturbance treatments at each site (photo by Samuel Jordan).

CHAPTER 3

INTERACTION OF CERAMBYCID TWIG GIRDLING BEETLES ON ABOVE GROUND BIOMASS OF HONEY MESQUITE IN THE NORTHERN CHIHUAHUAN DESERT

Abstract

This study investigates the impact of the mesquite twig girdler (*Oncideres rhodosticta*), a cerambycid longhorn beetle, on the above-ground biomass (AGB) of honey mesquite (*Prosopis glandulosa*) in the northern Chihuahuan Desert. Over a four-year period (2019-2022), I examined the beetle's activity and its influence on mesquite biomass at the Jornada Experimental Range in southern New Mexico. Through the development of site-specific allometric models, we quantified the biomass of both intact shrubs and girdled branches. Our results revealed significant year-to-year variability in beetle activity, with the highest girdling rates observed in 2019 and 2022. Despite this variability, the beetles consistently caused measurable reductions in mesquite biomass each year. Notably, the mean annual biomass loss due to girdling was found to be as high as 12% in some years, highlighting the beetle's potential role in shaping system-level productivity. The study underscores the importance of incorporating cross-trophic interactions, such as herbivory, into assessments of ecosystem function and primary productivity in arid environments. The findings also suggest that climatic variations may influence beetle population dynamics and, consequently, their impact on mesquite shrubs. This research contributes to a more comprehensive understanding of the ecological processes shaping dryland ecosystems and the potential ramifications of climate change on plant-insect interactions.

Introduction

Above-ground net primary productivity of plants (ANPP) is a critical integrative variable for assessing ecosystem function (Knapp and Smith, 2001). ANPP is typically estimated as the amount of above-ground biomass (AGB) that plants accumulate over a period, standardized to a unit area. As a measure of biomass accumulation, ANPP represents a crucial aspect of how energy from sunlight enters biological systems via photosynthesis. Estimates of ANPP are often based on empirical models known as allometric equations, which relate the size of a plant to its biomass using measurable parameters such as stem diameter or height (Jordan, 2024).

In the northern Chihuahuan desert, honey mesquite (*Prosopis glandulosa*) has significantly increased in density over the last century, converting many historically intact black grama (*Bouteloua eriopo*da) grasslands into mesquite shrublands (Brown and Archer, 1989). This shift from grassland to shrubland has altered the ANPP dynamics of the ecosystem. Because ANPP effectively integrates ecosystem function, considerable efforts have been made in the northern Chihuahuan Desert to understand its relationships with climate, vegetation community dynamics, and edaphic factors (Gherardi and Sala, 2015; Huenneke and Schlesinger, 2006; Peters, 2021). However, cross-trophic variability is rarely included in measures of biomass change over time.

The mesquite twig girdler (*Oncideres rhodosticta*) is a cerambycid longhorn beetle that primarily targets honey mesquite during its reproductive process. Gravid female beetles girdle stems with their mandibles and lay eggs within the woody plant tissue on the distal side of the girdle. The girdling stops distal sap flow, effectively killing that portion of the plant, reducing its chemical defense, and ensuring nutrient capture within the dead tissue for developing beetle larvae. This girdling action has been hypothesized to exacerbate desertification in the

Chihuahuan desert (Duval and Whitford, 2008) through a multistep process: 1) female beetles girdle branches, 2) this reduces the ratio of the inhibitory/outgrowth hormones auxin and cytokinin, which initiates growth of new branches by breaking dormancy in the axillary buds (Shimizu-Sato and Mori, 2001), 3) the growth of new branches captures wind-transported sediment, altering the physical and chemical properties of the soil, and 4) the increase in branches attracts more *O. rhodosticta* to continue the process.

Understanding the impact of biotic factors, such as herbivory by *O. rhodosticta*, on ANPP and ecosystem dynamics is essential, especially in the context of climate change and land use changes. Climatic variability, particularly changes in temperature and precipitation, has profound effects on the population dynamics and activity of herbivorous insects, including cerambycid beetles. Generally, cerambycids, like many other insects, are sensitive to climatic conditions which directly impact their development, survival, and reproductive success (Bale et al., 2002). Drought conditions, in particular, have been shown to influence herbivory rates by cerambycids. During periods of water stress, plants such as honey mesquite exhibit reduced oleoresin pressure, which lowers their defense mechanisms against insect herbivory (Huberty and Denno, 2004). This reduced defense can make drought-stressed mesquite more susceptible to attacks by twig girdling beetles. For example, Ansley and Jacoby (1990) observed higher beetle activity on moisture-stressed mesquite, indicating a direct link between plant water status and herbivory intensity. Conversely, increased precipitation can enhance plant vigor, potentially reducing susceptibility to beetle attacks. However, heavy rainfall and humidity can also create favorable conditions for the proliferation of certain insect populations by providing necessary moisture for their reproductive cycles (Huberty and Denno, 2004).

During early September of 2019, I noticed widespread "flagging" of mesquite across southern New Mexico, southwest Texas, and southern Arizona. The following spring, I found previous years' girdling on honey mesquite in the Colorado desert of California and along the Virgin River in Nevada. Compared to observations from 2018, this appeared to be a widespread eruptive pruning event by *O. rhodosticta*. At the Jornada Experimental Range, where a group of collaborators and I were installing the drought and disturbance experiment that would become Chapter 2 of this dissertation, the beetles were active on site (Figure 1).

To better understand the influence of *O. rhodosticta* on mesquite at the study site, I evaluated annual estimates of biomass and biomass change over four years due to active girdling. In this effort, I developed site-specific allometric models for living biomass at full shrub size and biomass of girdled stems. These insights will help improve our collective understanding how biotic stressors, like herbivory, can influence our measures of ANPP beyond basic climatic relationships, and help predict future ecosystem responses and guide adaptive management strategies.

Figure 1. Observed girdling by female mesquite twig girdlers at the Jornada Experimental Range, in southern New Mexico.

Methods

Field Methods

The interaction between *O. rhodosticta* and *P. glandulosa* was studied concurrently with the drought and disturbance manipulation experiment detailed in Ch. 2 of this dissertation, and carried out in the northern Chihuahuan Desert, at the Jornada Experimental Range (JER; 32.549718, -106.771039) in southern New Mexico. In the drought and disturbance experiment (see Chapter 2), 40 individual mesquite shrubs had been randomly selected for experimental treatments and monitoring within a 15ha area. In September of 2019, I randomly selected 30 additional shrubs within the 15ha area, each spaced at least 25 meters apart from each other and any experimental treatment shrubs. Shrub volume for each individual (n=70) was estimated by measuring two perpendicular diameters and height. I also recorded stem density and basal diameter of all living stems that protruded from the soil surface.

I made weekly field observations to track *O. rhodostica* activity at the site from September through October 2019. After ensuring no new activity had occurred on site, I measured branch diameters at the location of each year of (<1 year) girdle, as well as branch length distal to the girdle for each mesquite. Ten of the 30 non-experimental monitoring shrubs were randomly selected and destructively harvested to be used in developing allometric models. These were then air dried in ovens at 60°C and weighed to determine dry biomass. Shrub volume, and girdle measurements were sampled annually from 2019-2022 for the remaining 60 shrubs (40 experimental + 20 non-experimental). In fall of 2022, 10 additional shrubs were destructively harvested from the experimental treatment plots. These were also dried and weighed in ovens increasing the total number of full shrub biomass samples to 20 individuals. In order to develop an allometric model for branch girdle weights, I harvest simulated girdled branches (stem branches from 5-15 mm diameter), and true girdled branches from 30 individual shrubs on site. These were shrubs not used for any other purpose.

Data analysis

All analyses were performed using R v. 4.3.2 (R Core Development Team 2020). Simple linear allometric models were developed for full shrub dry weight ($Y=\beta_0+\beta_1X+\epsilon$), where X = shrub cubic volume (length x width x height), and girdled branch dry weight ($Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_3(X_1\times X_2)+\epsilon$), where X_1 = branch diameter at the girdle, and X_2 = branch length distal to the girdle. For each intact shrub (40 experimental, 20 monitoring), I calculated the change in AGB from one year to the next. These values were then converted to ANPP units of $(g)m^{-2}$ and relative biomass loss to girdling for 2020-2022 was calculated. Because the data violated normality, I used a non-parametric Kruskal-Wallis test to assess the relationship between girdle counts and relative change in AGB from beetles across treatments and years. A post-hoc Mann-Whitney U Test with Bonferroni correction was done to test for differences between years.

Results

Allometric models were able to explain a substantial amount of the variation in biomass for both girdled branch sections (Figure 2; R^2= 0.89) and for entire shrub (Figure 3; R^2= 0.7). The mean diameter of girdle stems was 8.87 mm (s.d.=3.1, Figure 4). Mesquite twig girdling beetles were active across all four years of the study, however the amount of girdling varied by year (Figure 4). For all years, the mean number of girdlers per shrub was 4 (s.d.=2.4), and the mean amount of biomass killed was 56.9 g (Figure 3; s.d.= 42.2). Kruskal-Wallis tests indicated that there were no significant differences in girdle counts from 2020-2022; however, there was a significant effect of year. Post-hoc tests show that 2022 was significantly different from 2020 (H=19.4, $p < 0.001$) and 2021 (H=19.33, p = < 0.001), but those years showed no difference (H = 7.04, p = 0.14). The Kruskal-Wallis test did not reveal any statistically significant differences ABG loss among the treatments (H = 0.787, p = 0.375), but there was statistically significant difference across years (H = 19.33, $p < 0.001$), with ABG in 2022 being statistically higher than 2020 or 2021.

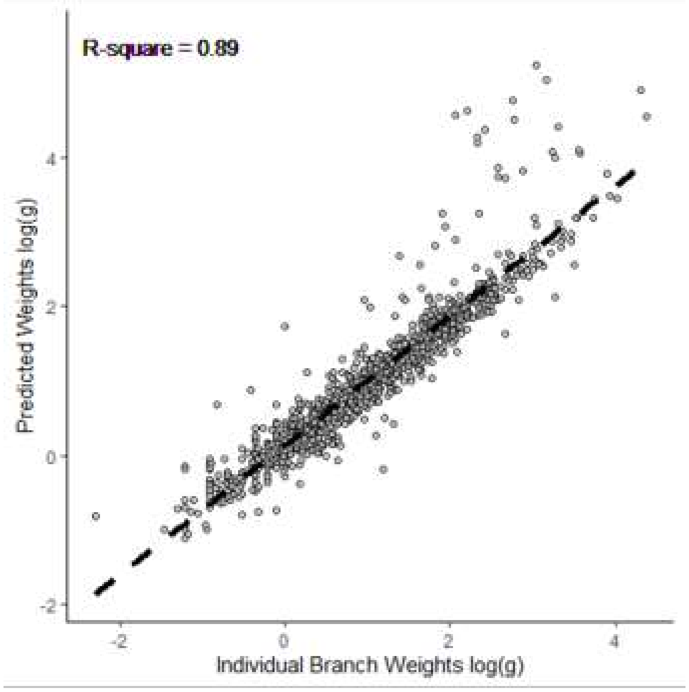

Figure 2. Predicted allometric model estimates for girdled branch sections plotted against the measured branch weights.

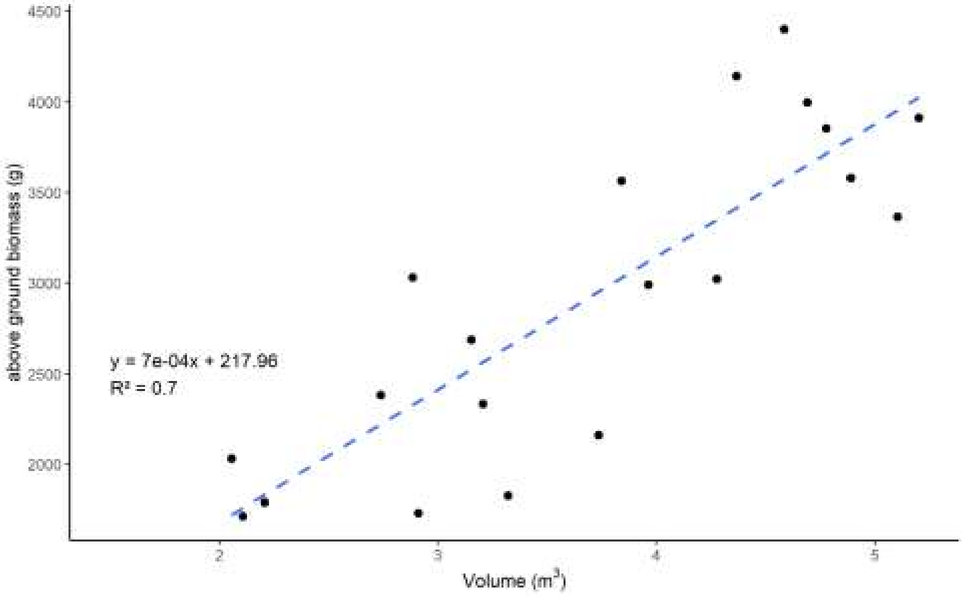

Figure 3. Full shrub biomass as a function of field measured cubic volume of shrubs. The linear fit model was used to estimate full shrub biomass across experimental control and reference shrubs.

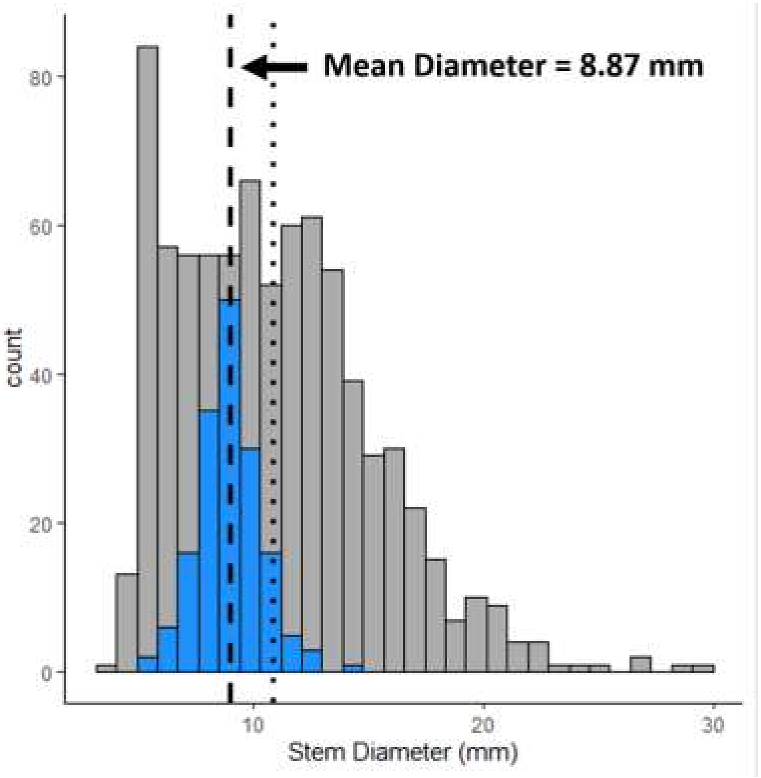

Figure 4. Observed girdle diameters (blue) of mesquite branches measured from 2019-2022. Grey bars represent basal diameters of mesquite main stems at the soil surface. Mean branch diameter at girdles was 8.87 mm.

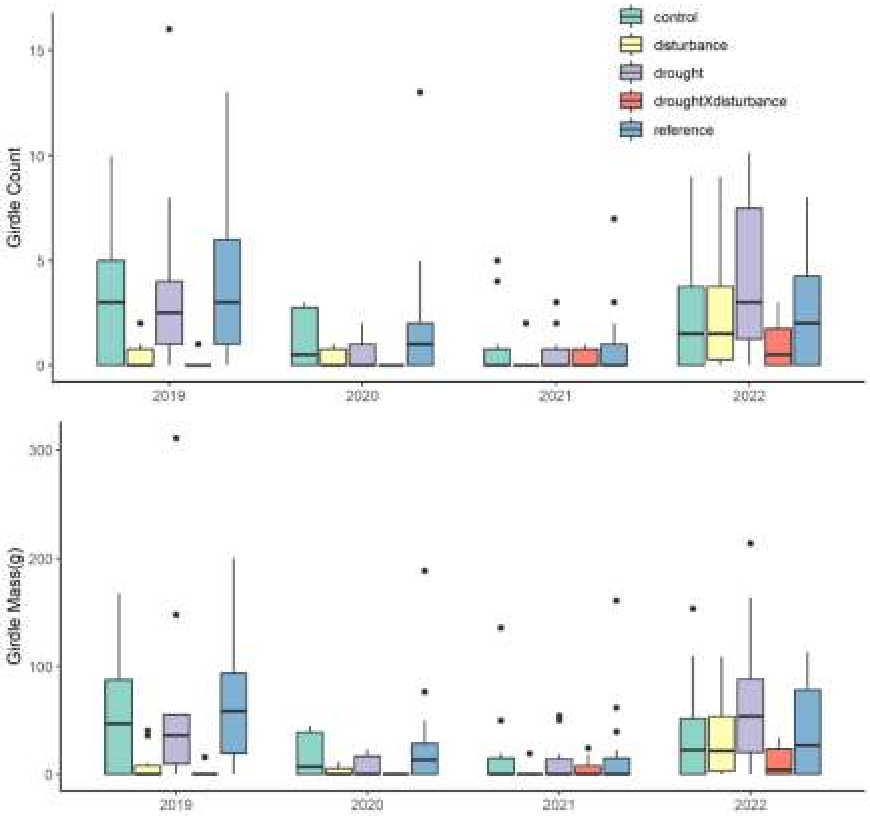

Figure 5. Girdle counts (top) and estimated tissue lost (Girdle Mass; bottom) in *P. glandulosa* by *O. rhodosticta* girdling across experimental treatment plots and non-experimental reference shrubs from 2019-2022.

Table 2. Mean girdle counts and Mass by treatment for all years (2019-2022).

Treatment	Count	Mass
Control	3.9 (2.43)	56.9 (42.2)
Drought	4.09 (4.04)	49.3(30.2)
Disturbance	2.36 (2.21)	25.2 (12.95)
Drought X Disturbance	1.56 (0.88)	20.4 (9.2)
Reference	3.58 (2.91)	51.3 (47.7)

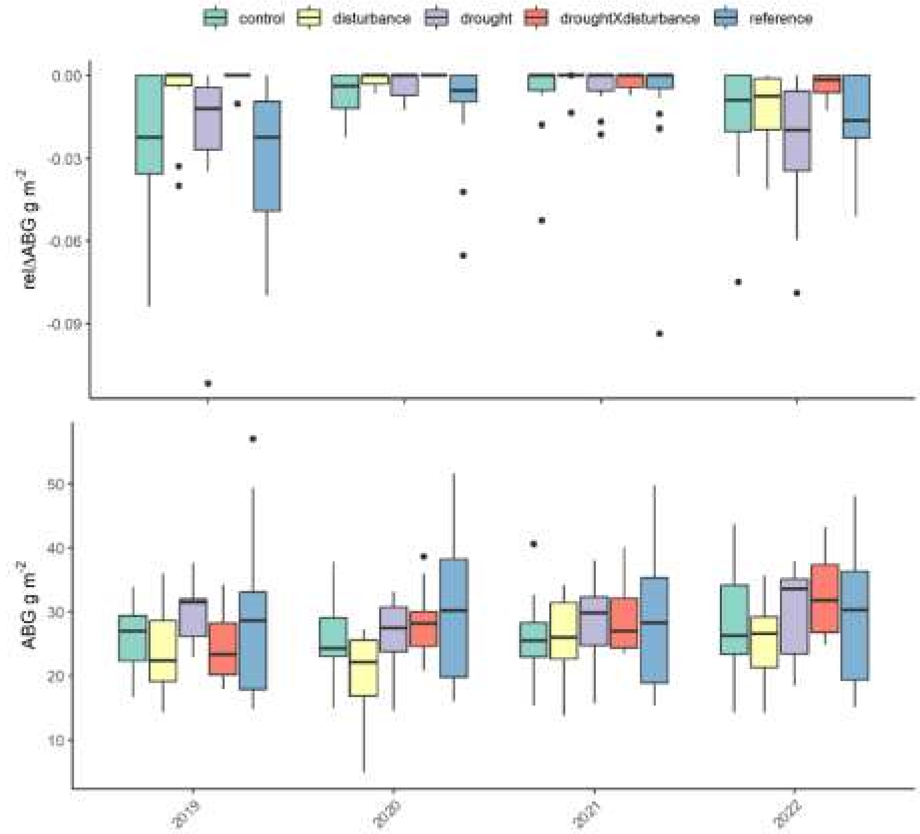

Figure 6. Estimated relative loss (top) in above ground biomass (ABG) and estimate full shrub above ground biomass scaled to above ground to net primary productivity units (g m^{-2}) for *Prosopis glandulosa* across experimental and reference shrubs from 2019-2022

Discussion

Invertebrates are among the most diverse and abundant components of terrestrial fauna on Earth. Globally, insect herbivory leads to an estimated annual loss of approximately 18% of plant biomass in terrestrial environments (Cyr and Pace, 1993). In dryland ecosystems, invertebrates play a crucial role in structuring plant communities through pollination (Minckley et al., 2000), seed predation, and dispersal (Ostoja et al., 2013). They also accelerate nutrient cycling by transporting litter into soils (Sagi and Hawlena, 2021). Our results show that beetles can further contribute to this process by girdling mesquite branches, converting living tissues into dead organic material. We observed beetles actively girdling shrubs at our study site every year. Besides adding bulk organic matter from mesquite branches, beetles contribute fine organic particles, such as frass, to the soil. These particles significantly impact microbial respiration rates, alter soil nitrogen availability, and can shift plant germination rates (Cobb et al., 2010).

Wood-boring insects like *O. rhodosticta* have complex population dynamics often influenced by climatic variations. They generally thrive when reduced oleoresin pressure accompanies drought stress, leading to decreased plant defenses (Huberty and Denno, 2004). This has been observed with *O. rhodosticta*, where mesquite suffering from water stress are more susceptible to beetle attacks (Ansley and Jacoby, 1990). However, our study found the most active girdling years (2019 and 2022) had significant differences in monsoonal rainfall, with 2019 being 18% below and 2022 about 22% above the 30-year average for July-September. The higher girdling rates in these contrasting rainfall years suggest that climatic legacy effects or other environmental factors could influence beetle activity in addition to or in relation to contemporary climate. Drought conditions in 2019 may have reduced plant defenses, making mesquite more vulnerable to beetle attacks, while increased rainfall in 2022 may have supported a larger beetle population through enhanced nutrient availability and reproductive success. Yet understanding when mesquite experiences drought stress or exhibit reduced defenses without further study is unclear, particularly given its ability to create and maintain exceptionally large and deep root systems.

While my study does not examine the potential influence of twig girdling on land degradation processes such as erosion and sedimentation, my result indicate that total aboveground biomass of mesquite shrubs is unlikely to be killed by O. rhodosticta after reaching a threshold basal stem diameter. Once basal stems exceed the target size of the beetle, girdling will be limited to branches and stems higher on the plant which could reinforce size or height limits on aboveground biomass. Understanding how girdling within the "canopy" of mesquite shrubs affects wind and water transport of sediments or the structure of vegetation layers, however, will require further study.

Understanding the complex interactions between climate, plant physiology, and insect herbivory is essential for predicting the impacts of climate change on dryland ecosystems. As climatic variability increases, the dynamics of plant-insect interactions are likely to shift, potentially exacerbating the effects of herbivory on mesquite biomass. Current efforts to monitor ANPP in mesquite primarily focus on the relationship between precipitation and plant growth (Gherardi and Sala, 2015). While precipitation is the dominant limiting factor in primary production in arid ecosystems, our study found that biomass reduction from girdling could be as high as 12% in some years, a value that can match or exceed the estimated change in AGB of some mesquite shrubs from climate alone. Twig girdling beetles introduce variability in ANPP estimates, complicating our ability to make valid inferences about ecosystem function. Across biomes, insect herbivory is a significant ecological process with important implications for carbon and nutrient cycling. As climate conditions change, the dynamics of insect populations and their interactions with plants are likely to shift, potentially increasing the overall impact of herbivory on ecological systems. Improving our understanding of the extent and impact of biomass loss due to *O. rhodosticta* is important for monitoring mesquite in the northern Chihuahuan Desert.

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CHAPTER 4

HOMOGENIZATION OF SOIL SEED BANK COMMUNITIES BY FIRE AND INVASIVE SPECIES IN THE MOJAVE DESERT

Abstract

Soil seed banks help maintain species diversity through temporal storage effects and function as germination pools that can optimize fitness across varying environmental conditions. These characteristics promote the persistence of native plant communities, yet disturbances such as fire and associated invasions by non-native species can disrupt these reserves, fundamentally altering successional trajectories. This may be particularly true in deserts, where native plant communities are less adapted to fire. While studies of fire effects on desert plant communities are not uncommon, information regarding the short- and long-term effects of fire on seed banks is less available. To better understand the influence of fire and invasive species on desert seed banks, we investigated soil seed bank biodiversity from 30 wildfires that burned between 1972 and 2010 across the Mojave Desert ecoregion of North America. We assessed how characteristics of fire regimes (frequency, time since fire, and burn severity) interacted with climate and invasive plants on measures of α-, β-, and γ-diversities. Because β-diversity is a direct measure of community variability and reveals important information about biodiversity loss, we further examined the nestedness and turnover components of β-diversity. Mean α and γ diversities were generally higher for burned locations than in unburned reference sites, however individual fire variables had little influence on patterns of seed bank diversity. Burned area seed banks tended to be dominated by non-native invasive species, primarily two grasses, (*Bromus rubens*, *Bromus tectorum*), as well as an invasive forb (*Erodium cicutarium*). The most striking pattern we

observed was a collective sharp decline in α, β, and γ diversities with increased invasive species dominance, indicating the homogenization of seed bank communities with the colonization of invasive species after fire. Evidence of homogenization was further supported by reduced turnover and increased nestedness in burn areas compared to reference areas indicating potential biodiversity loss.

1 Introduction

Disturbance plays a pivotal role in influencing biodiversity across ecosystems (Huston 1979, Sousa 1984). Characterized by heterogeneity in time and space, disturbances create a patchwork of varying resources and habitats that directly contribute to the maintenance of diversity (Petraitis et al. 1989). Ultimately, disturbances moderate the balance among deterministic (environmental and biotic filtering) and stochastic (random dispersal and recruitment) assembly processes that shape local ecological community composition and structure, and determine levels of similarity and turnover in species pools across communities (Kraft et al. 2008, Chesson 2000, Ferrenberg et al. 2013). In light of global change pressures, including novel species introductions, and climate and land-use that can rapidly alter disturbance regimes, understanding the effects of disturbance on species diversity remains crucial (Pulsford et al. 2016).

In western North America, global change pressures are reshaping historical fire regimes, increasing the frequency, severity, and extent of fires (Abatzoglou and Williams 2016). A large proportion of this region is composed of arid desert ecosystems (Barbour & Billings 2000). Lacking frequent exposure to fire over evolutionary time, native desert vegetation is thought to be less adapted and more vulnerable to fire compared to plants of more mesic fire-prone environments (Brooks et al. 2018, Chambers and Wisdom 2009). As such, changes to the historical fire regime in deserts can result in a long-term transformation of native vegetation and a shift in the trajectory of recovering post-fire plant communities. This has been well documented in the Mojave and Great Basin deserts, where disturbance to native woody plant cover and surface soils from fire has led to post-fire communities dominated by herbaceous plants, often non-native annual grasses of genus *Bromus*. The spread of *Bromus* has combined with climate and land-use change to alter the fire regime and promote positive feedback resulting in a “grass/fire cycle” that lead can to further invasions (D’Antonio and Vitousek 1992, Brooks et al. 2004).

Introductions of non-native species like *Bromus* complicate the relationship between disturbance and plant diversity. Disturbance often reduces the abundance of competitively dominant species and increases the availability of limiting resources (Petraitis et al. 1989), which can promote colonization by less competitive species and lead to higher levels of diversity (Chesson and Huntly 1997, Cadote 2007). However, the rapid spread of invasive annual grasses after fire can suppress the recruitment of native species and reduce overall diversity (Brooks 2000, DeFalco 2007). While extensive research has explored the link between disturbance, invasive plants, and their combined effects on native plant communities (Hobbs et al. 1992, McIntyre and Lavorel 1994, Keeley et al. 2005), most studies focus on aboveground plant assemblages, often overlooking the crucial role of soil seed banks (Faist et al. 2013, Vanvick et al. 2016, Hosna et al. 2023). Seed banks, through dormancy strategies, enable plants to disperse across space and time, contributing to the maintenance of diversity via temporal "storage effects"

(Chesson 2000, Anderson et al. 2012). This is an important strategy in arid ecosystems where climatic conditions that promote successful recruitment may be sporadic across growing seasons and years (Gremer & Venable 2014). The impact of altered disturbance regimes, coupled with non-native species introductions, on seed banks remains unclear for most ecosystems including deserts.

In this study, we assess the interactive roles of fire frequency, time since fire, burn severity, climate, topography, and the abundance of invasives on plant diversity in seed banks in the Mojave Desert, USA (Figure 1). Vegetation cover across the Mojave Desert varies as a function of local climate regimes (Beatley 1975, Aronson and Shmida 1992), with high aridity producing sparse, heterogeneous vegetation cover which translates to high spatial variability in both plant community types, and the risk and severity of fire (Abella 2009). Patterns of diversity in aboveground vegetation and belowground seed banks are likely to reflect such variation (Engel and Abella 2011). However, given temporal storage effects, the rate at which seed banks come to reflect aboveground vegetation patterns remains unclear. Following fires, plant diversity in the Mojave Desert is expected to vary as a function of the initial community, the dispersal potential of species in local and regional pools, local environmental characteristics, and the severity and time since fire as successional processes take place (Keeley et al. 2005, Safford and Harrison 2004). Collectively, the combination of these factors determines diversity across different spatial scales while simultaneously shaping variability among vegetation communities (β-diversity). Consequently, observed aboveground plant diversity patterns in both burned and unburned landscapes can vary greatly based on annual and seasonal rainfall (Winkler and Brooks 2020). Therefore, evaluations of seed banks provide temporally integrated insights into local communities, offering a more representative measure of potential plant diversity than short-term aboveground observations. To better understand how seed bank diversity varies with disturbance we specifically ask:

1. What relationship does seed bank diversity have with climate and topography?
2. How is seed bank diversity affected by the frequency, severity, and time since fire?
3. How is seed bank diversity influenced by invasive species with and without fire disturbance?

2 Materials and Methods

2.1 Study Sites

This study occurred in the Mojave Desert ecoregion of North America (Mojave hereafter). The Mojave is the smallest North American desert (≈152,000 km^2) but encompasses large variations in landforms and climate. Elevation ranges from -85 m to 3635 m with most of the ecoregion being between 600 m and 1600 m. A majority of precipitation, ~ 70%, occurs during the cool season between October and March with annual totals ranging from 50–130 mm in lower elevations to 250 - 750 mm at higher elevations. Temperatures range from minimums of -20° C (high elevation) to -5° C (low elevation) during the winter and highs of 30° C (high elevation) to 50° C (low elevation) in the summer (Hereford et al. 2006; Tagestad et al. 2016). This large variation in climate and landform results in distinct vegetation communities across climatic and soil gradients: lower elevations (< 1200 m) feature low-stature shrubs with sparse herbaceous cover, mid-elevations (1200 to 1800 m) exhibit denser shrubs and increased herbaceous cover, and high elevations (> 1800 m) host a mix of large shrubs and small trees, with limited herbaceous vegetation and bare interspaces (Barbour & Billings 2000).

2.2 Experimental Design and Soil Sampling

Our seed bank study was conducted concurrently with assessments of above-ground vegetation response to fire and detailed descriptions of methods for site selection are given in Klinger and Brooks (2017) and Klinger et al. (2021). In brief, we acquired fire perimeters and burn severity (differenced normalized burn ratio; dNBR) from the Monitoring and Trends in Burn Severity program (MTBS; https://www.mtbs.gov) for fires ≥ 405 ha (the MTBS minimum fire size) that occurred throughout the Mojave from 1972-2010 (Eidenshink et al. 2007). We then used a Geographic Information System (GIS; ESRI http://www.esri.com/) to map fire frequency (number of times a site burned since 1972) by overlaying the perimeters and calculating their overlap through time. We then used GIS to randomly select sites within (burned) or adjacent (unburned) to the perimeters of 53 fires across the Mojave Desert. While fires in the Mojave spanned a large range of elevations, most occurred in middle to high-elevation zones (Brooks et al. 2018). We accounted for differences that may occur due to topography, soils, and land use history by randomly selecting 1 km^2 site polygons entirely within or outside the fire perimeters, then randomly selecting 3 to 7 plots within each site polygon. Each plot was 0.1 ha (32 m × 32 m) containing three randomly positioned, parallel 30 m transects. Five subplots of 1 m^2 were spaced at 5 m intervals along the three transects for a total of 15 subplots per plot (Figure 2). Visual assessments were conducted in the field to ensure that no unburned plots had evidence of burning to avoid inaccurate burn perimeters or smaller fires not reported in the MTBS database.

Soil samples for seed bank assays were collected once from 432 burned plots across 30 unique fires and 111 unburned plots (N=543; Figure 1); this was a subset of the plots sampled in Klinger et al. (2017). Within each plot, we collected four samples from each subplot—one at each corner—that were pooled together. Each soil sample was collected using a cylindrical tin measuring 6.0 cm diameter x 4.4 cm deep (volume = 124.4 cm^3). This approach focused on the top 4 cm of soil where the bulk of viable seeds are located in desert soils (Young and Evans 1975, Kemp 1989, Ferrandis et al. 2001). Soil samples were collected in the fall (October-November) of 2009, 2011, and 2012, when annual plants had senesced, and the majority of seed bank inputs for the year had occurred. Seed bank samples were then stored in a cool (temperatures ranging from -10 to 20 degrees C), dry, dark location for two to three months, to maintain viability and aid germination (Baskin and Baskin 1998).

We used an emergence method, where germinated seedlings are used as a surrogate for counting seeds, to determine seed bank composition and abundance. Individual soil samples were homogenized by crushing soil aggregates, removing rocks and litter >1 cm diameter, and thoroughly mixing. Soil on rocks and litter was brushed back into the samples to capture any seeds before discarding them. Litter with crevices or potentially seed-bearing surfaces was placed back into the soil sample. One-half cup of soil (~118 cm^3) from each sample was thoroughly mixed with ½ cup vermiculite to help with moisture regulation of the soils. Soil-vermiculite samples were then placed in plastic bulb pots (15.72 cm outside diameter × 9.21 cm height) and spread to approximately 2 cm deep on top of weed block fabric. Pots were arranged randomly on greenhouse benches and watered overhead using a gentle rain nozzle. Greenhouse temperature was maintained between 5-30 °C.

Two consecutive germination trials, each lasting ~ 50 days, were completed with pots monitored every 1 to 3 days for seedlings and soil moisture. Pots were watered as needed (every 1 to 5 days) to maintain adequate moisture for seeds and seedling growth and prevent wilting. Each trial was stopped once two weeks had passed with no new germination. Soils were then allowed to dry for three weeks between the first and second trials—an approach that simulates natural wetting from rainfall and is needed to break dormancy of some seeds (see Faist and Collinge 2015, Haight et al. 2019). Seedlings were identified to species, counted, and plucked to quantify species abundance by subplot without allowing crowding or competition to reduce germination rates. Species not readily identifiable after germination were allowed to grow until features supported their identification. In cases where features remained non-descript, individuals were identified to *Genus* or higher taxonomic groups (this was the case for a very small number of seedlings). Because cheatgrass (*Bromus tectorum*) and red brome (*Bromus rubens)* are difficult to differentiate at the seedling stage, they were collectively identified as *Bromus sp.* Nomenclature for emerging species followed the U.S. Department of Agriculture, Natural Resource Conservation Service PLANTS database (plants.usda.gov; 2013).

2.3 Data Analysis

2.3.1 Diversity Indices

Using count data of species emergence from our subplot samples, we partitioned diversity into plot-scale α, β, and γ components and constructed diversity profiles for each based-on Hill numbers (Hill 1973) of diversity using the 'entropart' package (Marcon & Herault 2015) for R (R Core Team 2023). Hill numbers are a parametric family of diversity indices that incorporate species richness and relative abun dance information to quantify diversity (Jost 2007). These are broken into three primary orders (q): q0, species richness; q1, the exponential of Shannon entropy; and q2, the inverse of Gini-Simpson index. An advantage of assessing diversity via Hill numbers is that each diversity metric is expressed in units of effective numbers of species (i.e., the number of equally abundant species that would be needed to give an equivalent measure of diversity; Chao et al. 2014). We focused our assessment of diversity across the Mojave landscape at the order of q1, which is considered "true diversity" or the effective number of species in a community (Jost 2013). We did this because these metrics are generalizable across samples and have intuitive interpretations of our dataset: α-diversity for q1 is the mean effective number of species across 1-m^2 subplots within a plot; γ-diversity is the effective number of species for the entire 0.1 ha plot, and β-diversity represents the effective number of distinct localized communities within a plot, a direct measure of community variability (Jost 2007, Silva Pedro et al. 2016).

Beta diversity was calculated following Whittaker's (1972) multiplicative law ($\alpha \times \beta = \gamma$), which, when combined with Hill numbers, produces a β independent of the plot α values (Jost 2007). Additionally, utilizing the subplots as individual samples, we decomposed β-diversity via Sørensen dissimilarity into plot-level nestedness (i.e., the degree to which species losses are a function of being a subset of a larger community) and turnover (i.e., species replacement across local assemblages) components using the 'nestedbetasor' function in the 'vegan' package (Oksansen et al. 2020). Separating β-diversity into various components may help determine whether local community variability is the result of environmental and dispersal processes thought to reflect species turnover versus patterns of local colonization and extinction that can influence levels of species nestedness (Soininen et al. 2018). We derived β at the 0.1 ha (plot) scale to characterize variability within the seed bank at a spatial scale relevant to potential biological processes and interactions (e.g., species competition, nurse plant effect). Furthermore, by having a measure of variability at the plot scale, we could then model β as a response to environmental, fire, and biotic factors.

2.3.2 Explanatory variables

We identified 10 explanatory variables across four categories influencing diversity in the Mojave landscape: climate, topography, biotic, and fire (see Table 1). Climate variables included 30-year normals (1984–2014) for mean annual precipitation (MAP) and maximum July temperature (tmax7) using PRISM data. (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 19 August 2019). Topographic variables included elevation, hillshade (an index of solar radiation that utilizes aspect and slope) and a terrain ruggedness index (TRI; Wilson et al. 2007). Due to the strong correlation between elevation and temperature ($r > 0.8$; Appendix 1), we withheld temperature in favor of elevation in our analyses for its significant role in determining both climate and landscape position. Interactions among plant species can strongly influence pattern diversity in vegetation communities (McIntire & Fajardo 2014, Lucero et al. 2020). To address this, we incorporated the relative cover of above-ground woody vegetation (shrub and tree cover) and the relative abundance of non-native plants from soil seed bank greenhouse trials as biotic factors. Woody cover plays a crucial role in shaping plant composition patterns in desert ecosystems (Schade et al. 2003; Haas-Desmarais & Lortie 2023), and non-native species can impact biodiversity (Underwood et al. 2019). We classified each species as either native or non-native (alien), and calculated the relative abundance of non-native plants for each plot. Fire variables included burn severity (dNBR), years' post-fire (YPF), and fire frequency (0,1 vs 2-3 times since 1972). YPF was transformed as 1 divided by the time since the last burn, establishing a gradient supporting theoretical successional states along a directional time axis. Unburned plots were assigned a YPF value of 0, facilitating the inclusion of burned and unburned plots in the same model along a time since disturbance gradient. Data on burn severity and fire history can be found in Klinger et al. (2022).

2.3.3 Diversity modelling

We used generalized linear mixed models (GLMMs) to examine the relationship between plot-level diversities and various climate, topography, biotic, and fire-related variables (Table 1). We constructed individual GLMMs incorporating a gamma distribution and log link function for the q1 order α, β, and γ diversities, designating "site" as a random effect. Additionally, we developed individual GLMMs for the decomposed nestedness and turnover components of Sørensen dissimilarity, using a Gaussian distribution and identity link function, with site specified as a random effect. For each model, we employed model averaging using the MuMin package (Bartoń 2020) to estimate 95% confidence intervals of standardized parameter estimates (β coefficients) for each explanatory variable. We considered variables ecologically significant if their 95% CIs did not overlap zero. The use of multi-model inference allowed us to assess the relative importance of each variable. To address non-linear relationships identified in preliminary analyses between diversity responses and the relative abundance of non-native species, as well as mean annual precipitation (MAP), we incorporated quadratic terms for these variables into each model. We used the lme4 package (Bates et al. 2015) to construct all GLMMs and model fits were checked (Appendices 2–4) using the DHARMa (Hartig 2022) and performance packages (Lüdecke et al. 2020**).** We assessed possible collinearity issues between fixed effects by estimating the variance inflation factors (VIF) for each model (Appendix 5). VIF values were <5, indicating little collinearity among predictors (Akinwande et al., 2015). All analyses were run with R 4.3.1 (R Core Team 2023).

3. Results

We recorded the emergence of 173 unique plant species from the soil seed bank, the majority of which were native annual plants. We documented 14 non-native species, the most abundant being the invasive annual grasses *B. tectrorum* and *B. rubens* and the annual forb *Erodium cicutarium* (Appendix Table 1). In general, plot level species richness (γ at q0) was higher in burned areas, 9.61 (95% CI = 8.50 – 10.57), than in unburned areas, 6.75 (95% CI = 6.00 – 7.37; Figure 3). In terms of true diversities (q1), a subset of explanatory variables tended to have significant influences on seed bank diversity at subplot (α) and plot (γ) scales, as well as plot-scale community variability (β), nestedness, and turnover. Additionally, all measures of diversity had a non-linear relationship with the relative abundance of non-native plants found within the seed bank, particularly in burned sites, where measures of diversity initially increased with non-native abundance before peaking and rapidly declining as non-native plants became dominant (Figure 4).

3.1 Alpha diversity (α)

At the local 1 m^2 subplot scale, the effective number of species (α diversity at q1) tended to be greater in areas that burned, 1.92 (95% CI = 1.79 – 2.05), than in unburned areas, 1.56 (95% CI = 1.45 – 1.68). Our GLMM was able to explain roughly half of the variation in α-diversity ($R^2 = 0.51$). Alpha diversity had a significant positive relationship with topographic complexity (TRI) and burn frequency, and a negative relationship with relative cover of woody plants and elevation (Figure 3). However, the largest influence on local α-diversity was the relative abundance of non-native plants within the seed bank, which had a strong non-linear relationship with α-diversity across both burned and unburned locations (Figure 4, 5).

3.2 Beta diversity (β)

Plot-scale variability in community composition among (β-diversity at q1) was generally lower in burned sites, 1.87 (95% CI = 1.72 – 2.05), than in unburned sites, 2.47(95% CI = 2.31 – 2.65; Figure 3). Our GLMM explained a relatively high amount of variation in β-diversity ($R^2 = 0.62$). Beta diversity had a significant positive relationship with relative cover of woody vegetation and a negative relationship with burn frequency. Similar to α-diversity, β-diversity had a non-linear relationship with the relative abundance of non-native plants within the seed bank, where in burn plots β-diversity increased with low levels of non-native abundance, but declined drastically after a threshold of higher non-native abundance was crossed (Figure 4).

Plot-scale Sørensen dissimilarity was similar across burned ($\mu = 0.74$, 95% CI = 0.65 – 0.83) and unburned ($\mu = 0.78$, 95% CI = 0.65 – 0.90) sites, with the majority of dissimilarity contributed to by species turnover (losses and gains that appear as “replacements” in species composition) as opposed to nestedness (changes in abundance where local communities are subsets of the larger, regional or site-level pool). Species turnover was higher across unburned (87% of dissimilarity) than burned locations (72 % of dissimilarity). Accordingly, species nestedness was twice as high in burned (28%) compared to unburned plots (13 %), indicating that a greater proportion of observed differences in composition within burn plots was composed by variable subsets of local species pools with a shrinking role of replacement via turnover (Figure 6). The GLMMs explained slightly less of the total variation in plot-scale dissimilarity for both nestedness ($R^2 = 0.42$) and turnover ($R^2 = 0.44$) than standard measures of diversity. However, both turnover and nestedness had similar, non-linear relationships with the relative abundance of non-native plants (Figure 6). Turnover exhibited a negative relationship with burn frequency and a positive relationship with the relative cover of woody vegetation. Nestedness had a significant positive relationship with the relative cover of woody vegetation, and a negative relationship with burn frequency.

3.2 Gamma diversity (γ)

The effective number of species at the 0.1 ha plot scale (γ at q1) was similar for burned and unburned sites. Mean γ-diversity was 3.63 (95% CI = 3.26 – 4.04) for burned and 3.82 (95% CI = 3.41 – 4.24) for unburned plots. Similar to α- and β-diversity models, the model explained a little over half of the variation in γ-diversity ($R^2 = 0.55$; Figure 5). Gamma diversity was significantly and positively related with tmax7 and negatively related with Hillshade. Also similar to the other diversity measures, γ-diversity had a strong non-linear relationship with the relative abundance of non-native species.

4 Discussion

Fire, while historically rare and infrequent across North American deserts (Wright and Bailey 1982), has become an increasingly significant disturbance on the landscape. An examination of Mojave fires over the last four decades indicates a highly heterogeneous regime with varying frequency, severity, and size (Klinger et al. 2021). Shifts in fire frequency and severity can promote transitions toward communities dominated by herbaceous and non-native plants (Brooks et al. 2004, Klinger and Brooks 2017). Notably, certain *Bromus* grass species, once introduced, exhibit explosive invasiveness in post-fire areas in the Mojave and other regions (Reid et al. 2006). The rapid alteration of local plant community dynamics by invasives raises concerns about the emergence of persistent alternative ecological states. Our findings in the Mojave indicate that fire can increase seed bank species richness (γ at q0) and the effective number of species (α & γ at q1) at relatively small subplot (1 m) and plot (0.1 ha) spatial scales. This likely underscores the crucial role of disturbance in promoting variability in resources that sustain plant diversity within this ecoregion. However, seed bank diversity was minimally influenced by measures of fire severity, frequency, and YPF. Instead, diversity was strongly shaped by the invasion severity of non-native plants and the cover of woody perennial plants—factors reflecting the long-term effects of climate and disturbance history on plant communities. Effectively, invasion of the Mojave ecoregion by non-native annual plants homogenizes the soil seed bank by rapidly driving a decline in native plant diversity beyond a critical threshold in non-native plant relative abundance, and a concomitant decrease in the compositional variability of the seed bank across the landscape (i.e., a decrease in β-diversity). While unburned locations also host non-native plants at lower abundance than burned, fire disturbances allow for a rapid increase in the relative abundance of non-native plants, driving more rapid losses of native diversity and resulting in greater homogenization across space. Further efforts to quantify this threshold will be pivotal for developing management strategies and designating urgent restoration zones to support native plant biodiversity in the Mojave system.

4.1 Disturbance and changes in native plant species diversity

Measures of q1 diversity (i.e., effective number of species) at the subplot (α; 1-m^2) and plot (γ; 0.1 ha) scale were higher in burned than unburned areas. The effective number of species in burned areas, however, was not significantly influenced by the severity, frequency, or years since fire such that areas that burned once differed little from sites that burned multiple times over the data timeline.

The seemingly weak influence of fire variables on the effective number of species at local subplot and plot scales may also be because the strongest influence we observed in determining diversity at both scales was the abundance of non-native species within the seed bank. This relationship was variable across unburned and burned sites but was non-linear and often parabolic. The relationship was consistent in that the effective diversity initially increased as the relative abundance of non-native species in the seed bank increased before reaching a threshold peak that was followed by a rapid loss of diversity at higher non-native seed abundance. This relationship was strongest in burned sites—an outcome that was expected given the positive influence of disturbance on the abundance of non-native plants in the Mojave and other ecoregions. While the common non-native plants of the Mojave benefit from disturbances, these species can still invade unburned sites where they persist at lower abundances than in more heavily disturbed locations. For example, the earlier emergence of *B. tectoroum* from the seed bank relative to native plants allows it to capture greater amounts of soil nitrogen, increasing its abundance while elevating resource competition that causes a decline in native plant diversity (Prevéy et al. 2014). Similar plant community responses and outcomes of soil nutrient pulses have been documented in other prolific plant invaders (Besaw et al. 2011). *Bromus tectorum*, and some other non-native annual plants, have also been shown to capitalize on resources provided by soil-surface biocrust communities (Ferrenberg et al. 2018, Havrilla et al. 2019) which are more common and widespread in less frequently disturbed locations of drylands (Weber et al. 2022). Fire effects on vegetation and soils typically cause short-duration pulses in soil inorganic nitrogen, which have been shown to amplify non-native plant invasion in the Mojave Desert (Esque et al. 2010).

We also found a negative relationship between the effective number of species and woody plant cover at the local subplot (1-m^2) scale. This result seems contrary to expectations of shrubs and trees acting as "nurse plants" that promote species diversity in arid ecosystems (Madrigal-Gonzalez et al. 2020). However, an overwhelming majority of nurse plant studies report patterns derived from aboveground plant assemblages and are not measures based on the larger plant community found in soil seed banks which can harbor additional species diversity (Hosna et al. 2023). Woody plant cover is also correlated to local climate and disturbance histories; areas with more woody plants are likely to have experienced fewer or less severe disturbances over time (Sühs et al. 2020). In the context of our study, the presence of woody vegetation in burned areas likely reflects the natural heterogeneity in fire effects across study sites and transects, impacting local vegetation community structure and the average age/size of shrubs. This aligns with findings in the Chihuahuan Desert, where nurse plant effects depend on shrub size and species, emphasizing the role of both floristic composition and disturbance regimes in shaping the plant diversity of arid systems (Ferrenberg et al. 2023).

4.2 Fire as a homogenizing influence on soil seed banks

Disturbance is expected to alter β-diversity in several ways. In the short term, fire may increase β-diversity by altering environmental heterogeneity, reducing local α-diversity, and pushing fire intolerant species to be more clumped or in "patches" (Myers et al. 2015). Under classical post-disturbance recovery models, β-diversity would have a trajectory towards pre-disturbance levels as time passed. However, invasion can disrupt this process (e.g., Kuebbing et al. 2014). We observed that the abundance of native species represented in the seed bank declined linearly with non-native relative abundance at burned sites, but not at unburned sites. β-diversity similarly declined, although non-linearly, with the increase in relative abundance of invasives. This nonlinear relationship might reflect changes in biotic interactions (e.g., competitive or facilitative effects), environmental filtering, or responses by plants to localized resource pools. This relationship might also reflect stochastic influences on seed bank community assembly, particularly dispersal processes and the effects of fire disturbance on the probability of seed movements among heterogenous resource and vegetation patches (Applestein et al. 2022).

The decline in both α- and β-diversity indicates that the seed bank communities of this system are being homogenized by non-native plant invasion. Fire disturbance plays an important role in the progress of seed bank homogenization: we observed a relative reduction in species turnover and a greater than 200 % increase in species nestedness in burned compared to unburned sites. Thus, across burned sites, seed banks experience less species turnover (replacements) while dwindling toward a subset of plants found in the more diverse γ-level communities. This increased similarity in community composition is produced by the loss of species from a community and the non-random replacement of those species by more widespread occurring species (Clavel et al. 2011). This phenomenon has been documented widely across biota and ecosystems in response to the proliferation of invasive non-native species (Olden and Poff 2003). This occurs in the Mojave, where the suppression of recruitment of native species by invasive annual grass and forb species has been observed (Brooks 2000, DeFalco et al. 2007). Meanwhile, the greatest difference in turnover was driven by fire frequency with two or more fires increasing turnover suggesting that ongoing increases in fire frequency are likely to produce alternate community states within soil seed banks.

Beta diversity is a crucial concept in ecology, representing variation in species composition between different ecological communities. Beta diversity is important as it provides insights into the mechanisms of community assembly and biodiversity patterns across different habitats or environmental gradients. For, instance, studies have shown that beta diversity can vary with elevation (Kraft et al. 2011) and shift in response to fire disturbance and time since fire (Ferrenberg et al. 2013). This variation in beta diversity across elevations or disturbed habitats can indicate the influence of various ecological processes, such as environmental filtering, species interactions, or spatial constraints on community composition. Understanding these patterns is vital, as it helps in identifying drivers of biodiversity and understanding the impact of environmental changes on plant communities.

Conclusions

Variability and maintenance of native species in local plant assemblages has important implications for the conservation and ecological integrity of Mojave Desert ecosystems. We measured the effects of fire severity, frequency, and history on seed bank species diversity. We found that invasive plants are driving a homogenization process of desert plant communities, which is amplified by the positive effects of fire disturbance on the abundance of key invaders, particularly annual *Bromus* grasses. Such homogenization could have profound impacts on the maintenance of regional biodiversity pools, including across trophic levels where numerous species, such as the threatened desert tortoise (*Gopherus agassizii*), are already taxed by habitat alteration. Understanding the mechanistic pathways through which plant invasion and disturbance combine to alter seed bank composition and abundance patterns, and what role direct and indirect effects of disturbance on soil systems play in seed bank homogenization, is crucial for identifying targets for restoration as well as conservation goals.

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4.1 Tables

Table 1. Variables used to assess patterns of soil seed bank diversity across the Mojave Desert ecoregion, USA

Category	Variable	Source
Climate	30-year mean annual precipitation (MAP)	PRISM Climate Group, Oregon State University, Corvalis, Oregon (http://www.prismclimate.org
	30-year mean July maximum temperature (tmax7)	PRISM Climate Group, Oregon State University, Corvalis, Oregon http://www.prismclimate.org
Topography	Elevation (Elev)	30-meter Digital Elevation Model (National Elevation Dataset, https://www.usgs.gov/programs/national-geospatial-program/national-map).
	Hillshade (Hllshd)	Derived from DEM
	Terrain Ruggedness Index (TRI)	Derived from DEM; Wilson et al. 2007
Biotic	Relative cover of above ground woody plants (prWoody)	Klinger, R.C., 2017, Cover of woody and herbaceous functional groups in burned and unburned plots, Mojave Desert, 2009-2013: U.S. Geological Survey data release, https://doi.org/10.5066/F79022PZ.
	Relative abundance of non-native plants from seed bank (prAlien)	reported here
Fire	Number of times burned 1984-2010 (Freq)	Klinger, R.C., Underwood, E.C., McKinley, R., and Brooks, M.L., 2022, Fire regimes in the Mojave Desert (1972-2010): U.S. Geological Survey data release, https://doi.org/10.5066/P99YGHSJ.
	Burn Severity (dNBR)	Klinger, R.C., Underwood, E.C., McKinley, R., and Brooks, M.L., 2022, Fire regimes in the Mojave Desert (1972-2010): U.S. Geological Survey data release, https://doi.org/10.5066/P99YGHSJ.

	Years post fire (YPF)	Klinger, R.C., Underwood, E.C., McKinley, R., and Brooks, M.L., 2022, Fire regimes in the Mojave Desert (1972-2010): U.S. Geological Survey data release, https://doi.org/10.5066/P99YGHSJ.

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Figures

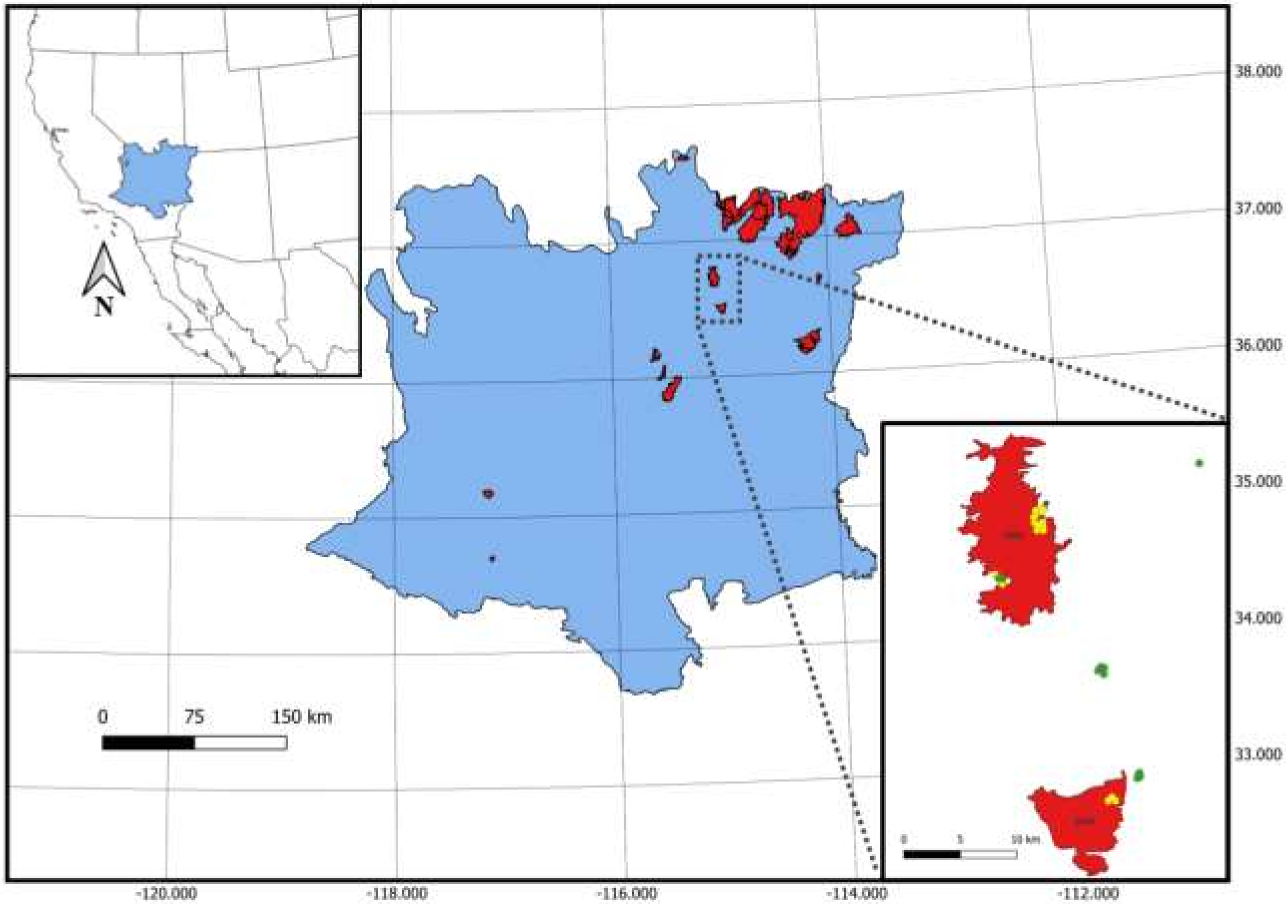


Figure 1. Burn perimeters (red) from 30 unique wildfires representing a chronosequence of fires that burned between 1972 and 2010 in the Mojave Desert of North America. Lower right inset panel shows an example of point locations for burned (yellow; total n = 432) and unburned (green; total n = 111) 0.1 ha plots where seed bank samples were collected. Mojave Desert Ecoregion and burn perimeter data provided by Klinger et al. 2022.

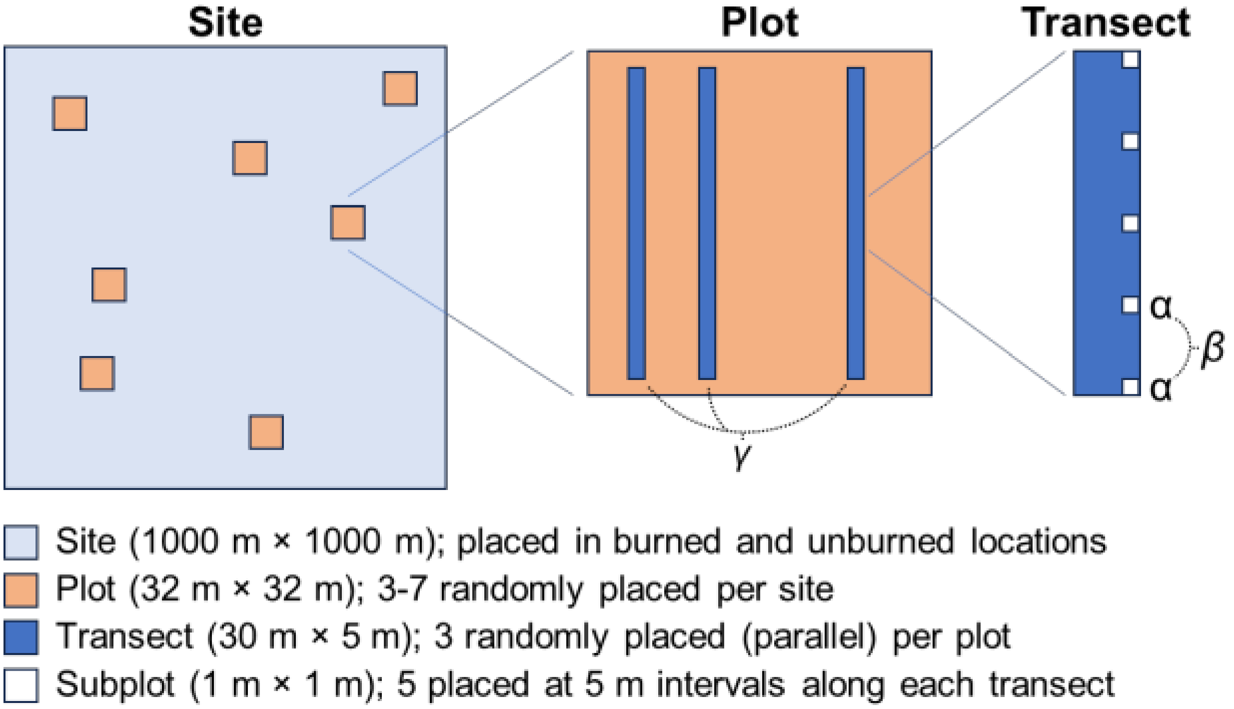


Figure 2. Conceptual diagram illustrating the scale and relationships between sampling sites, plots, transects, and subplots. Greek letters indicate the level at which each diversity metric was calculated, with alpha measuring species diversity of each subplot, beta diversity being calculated as the pairwise dissimilarities among the subplots, and gamma encompassing species diversity for plots.

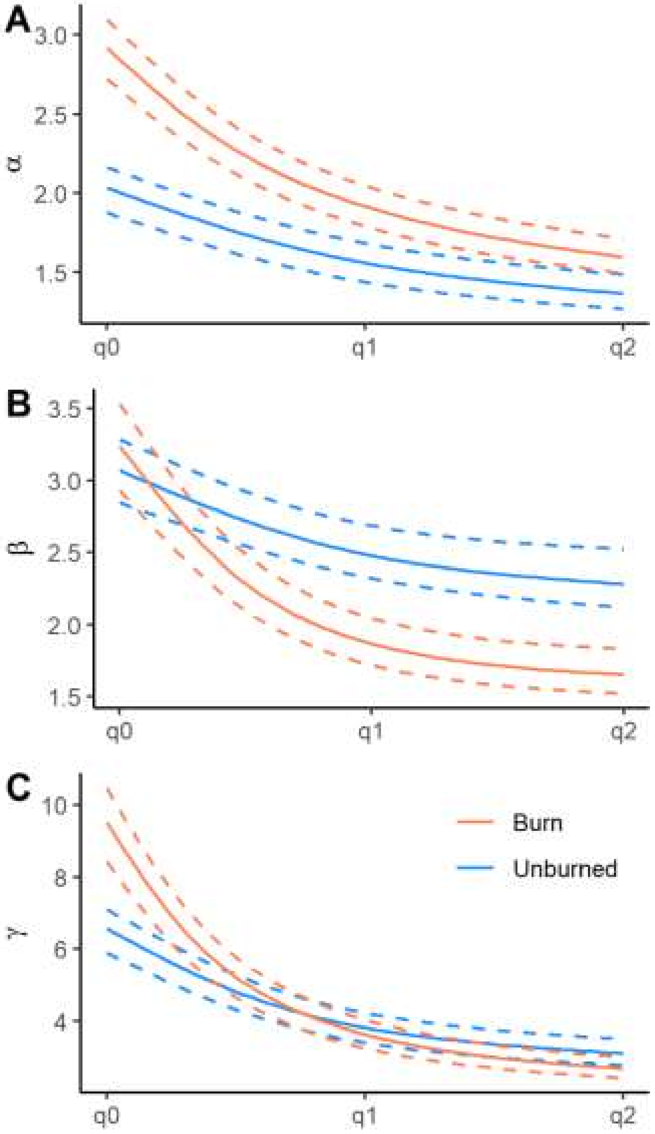


Figure 3. Diversity profiles for alpha (α, panel A), beta (β, panel B), and gamma (γ, panel C) diversities of burned (red) and unburned (blue) plots from the Mojave Ecoregion. Diversity orders range across species richness (q0), exponent of Shannon's entropy (q1) and the Gini-Simpson index (q2). Dashed lines indicate 95% confidence intervals.

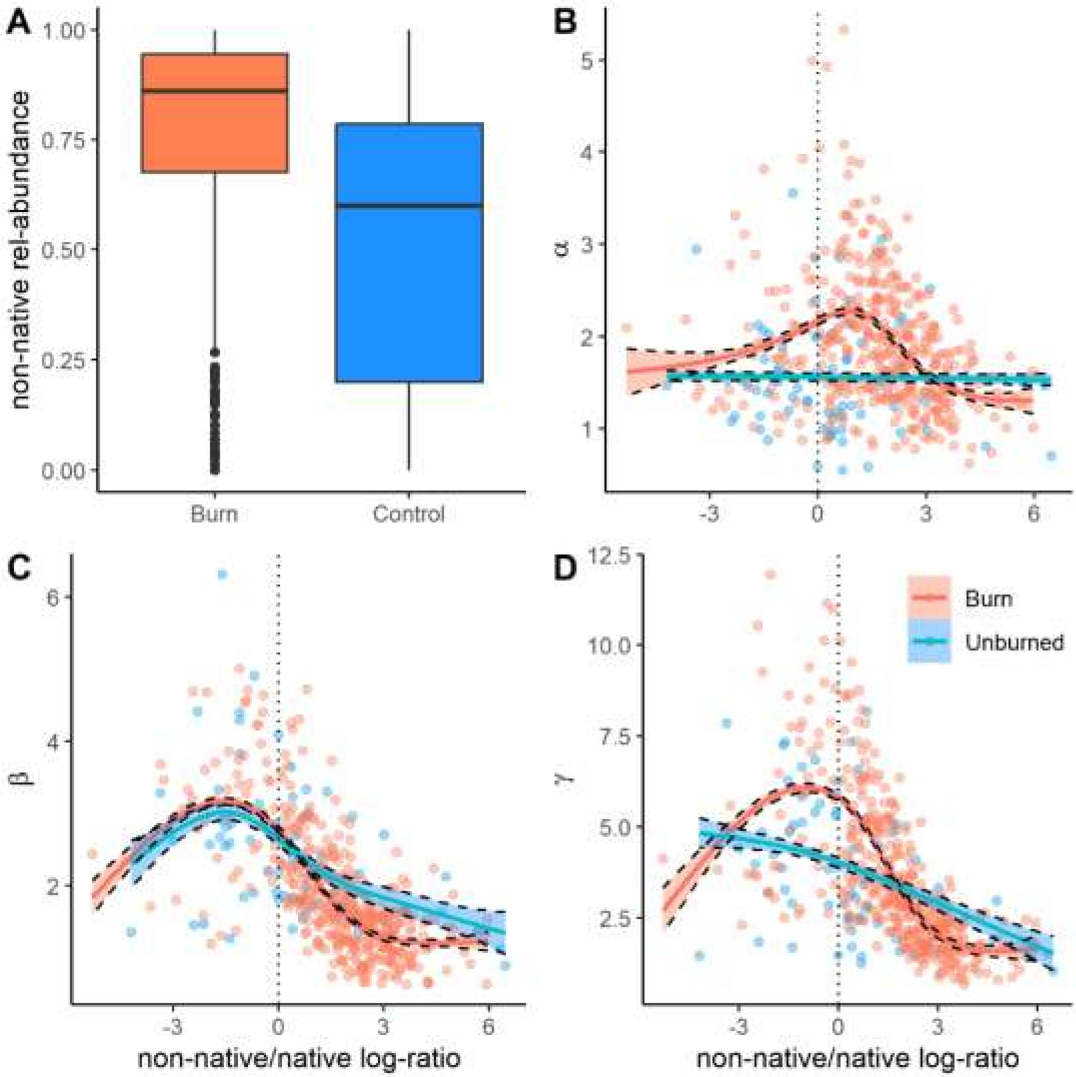


Figure 4. Box and whisker plots (A) of the relative abundance of non-native germinates from seed bank samples from burned (red) and unburned (blue) sites from across the Mojave Desert. Bold lines represent the median, boxes the upper and lower quartiles (interquartile range), whiskers 1.5x the interquartile range, and points outliers. Panels B-D show the relationship of α (B), β (C), and γ (D) diversity with the ratio (log) of non-native to native seed bank abundance.

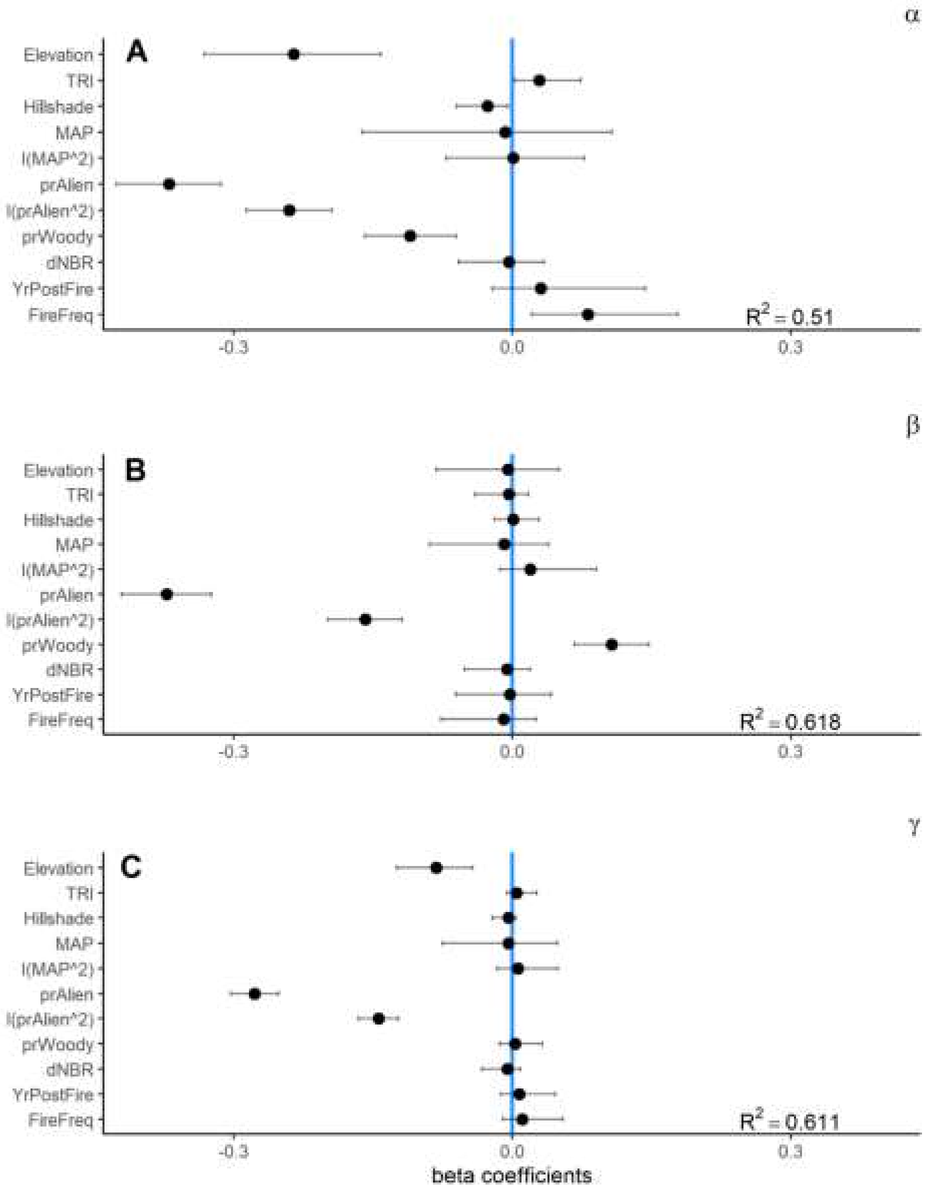


Figure 5. Standardized beta coefficients for fixed effects (see Table 1) from generalized linear mixed effect models (GLMMs) for seed bank alpha (A), beta (B), and gamma (C) diversity from a 35-year chronosequence of burned locations from across the Mojave Desert. Error bars indicate 95% confidence intervals.

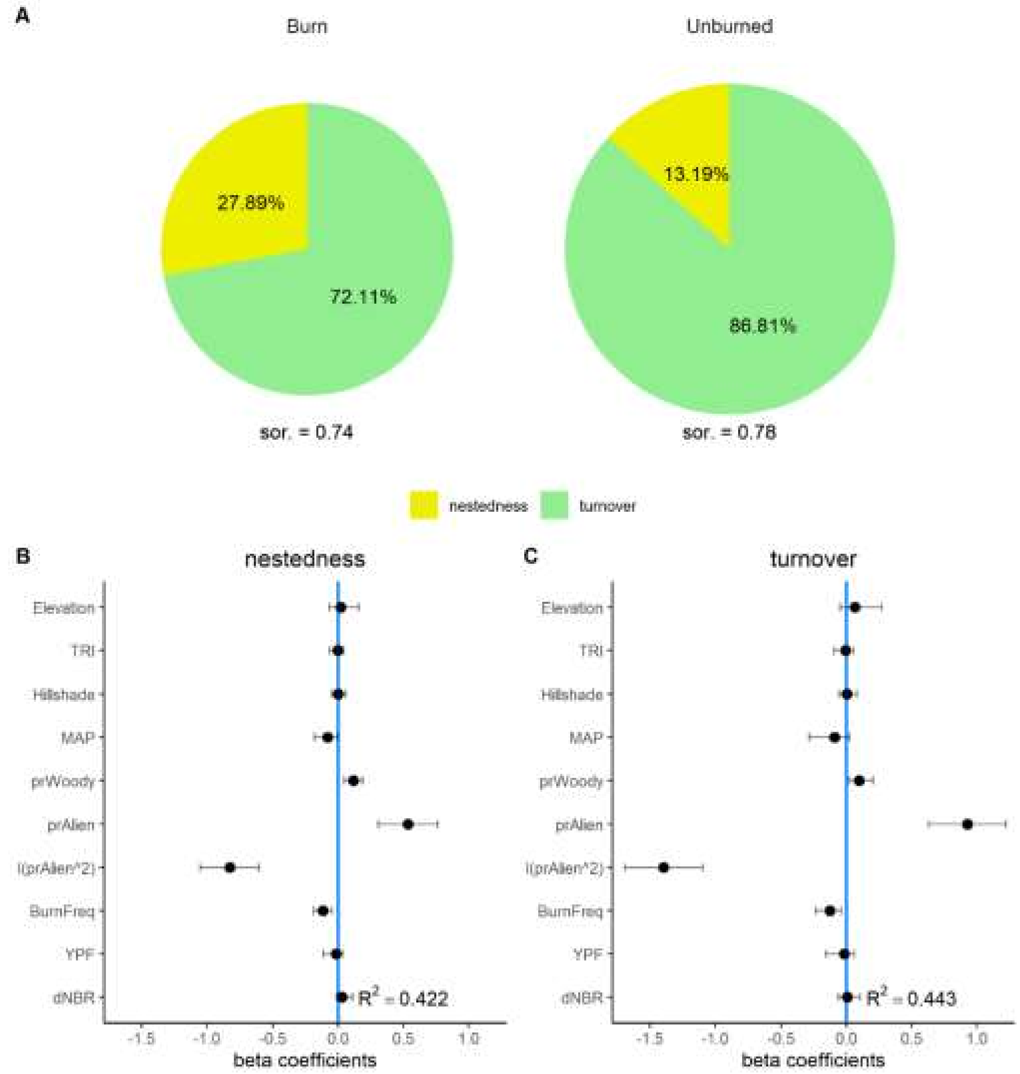
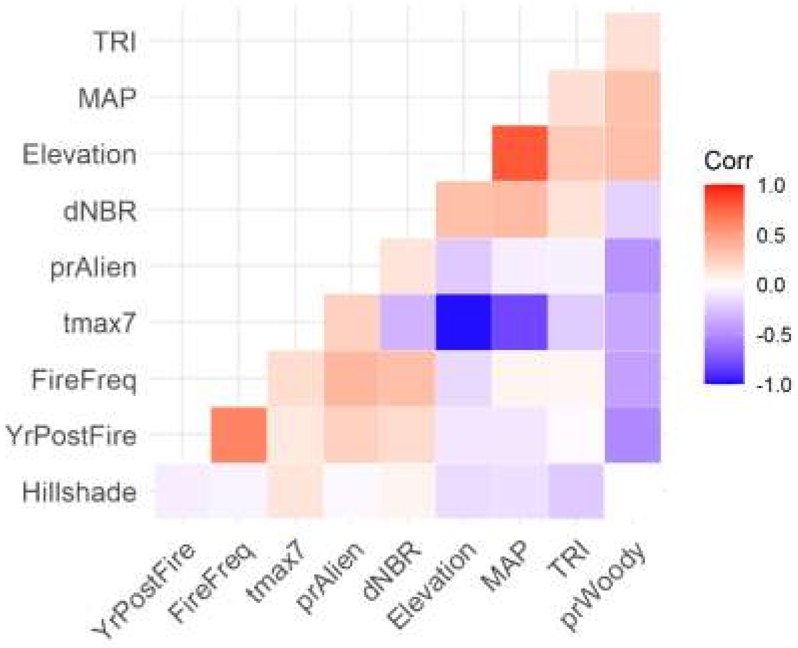


Figure 6. Nestedness and turnover components of beta diversity for burned and unburned sites across the Mojave Desert (A). Percent values within each pie chart represent the proportion of mean plot-level Sørensen dissimilarity (sor.) portioned into either nestedness (yellow) or turnover (green). Panels B and C are the standardized beta coefficients for fixed effects (see Table 1) from generalized linear mixed effect models (GLMMs) for seed bank nestedness (B), and turnover (C) from a 35-year chronosequence of burned locations from across the Mojave Desert. Error bars indicate 95% confidence intervals.

Supplementary materials



Appendix 1. Pearson's correlation coefficients for covariates used in the construction of generalized linear mixed effect models of seed bank assays from across the Mojave Desert, USA.

Appendix Table 1. Relative abundance for species recorded in burned and unburned plots from across the Mojave Desert. Species are ranked in descending order of abundance. Non-native species are highlighted in red.

Burned		**Unburned**	
Species	Lifeform	Species	Lifeform
Bromus sp. 0.54	annual grass	*Schismus barbatus* 0.433	annual grass
Erodium cicutarium 0.272	annual forb	*Bromus sp.* 0.168	annual grass
Schismus barbatus 0.049	annual grass	*Vulpia octoflora* 0.13	annual grass
Draba cuneifolia 0.016	annual forb	*Erodium cicutarium* 0.05	annual forb
Astragalus nuttallianus 0.016	annual forb	*Vulpia bromoides* 0.047	annual grass
Lesquerella hitchcockii 0.012	annual forb	*Astragalus nuttallianus* 0.019	perennial forb
Vulpia bromoides 0.008	annual forb	*Cryptantha circumscissa* 0.014	annual forb
Gilia inconspicua 0.006	annual grass	*Draba cuneifolia* 0.013	annual forb
Descurainia pinnata 0.005	annual grass	*Phacelia fremontii* 0.01	annual forb
Gilia transmontana 0.004	annual grass	*Pectocarya pencillata* 0.009	annual forb
Lappula occidentalis 0.004	perennial grass	*Gilia clockeyi* 0.007	annual forb
Amsinckia sp. 0.003	perennial grass	*Amsinckia tessellata* 0.006	annual forb
Amsinckia tessellata 0.003	perennial grass	*Gilia sinuata* 0.006	annual forb
Eriogonum palmerianum 0.003	annual forb	*Gilia transmontana* 0.006	annual forb
Gilia clockeyi 0.003	annual forb	*Plantago ovata* 0.006	annual forb
Lepidium lasiocarpum 0.003	annual forb	*Cryptantha sp.* 0.005	annual forb
Phacelia fremontii 0.003	annual forb	*Pectocarya recurvata* 0.005	annual forb
Thymophylla pentachaeta 0.003	annual forb	*Descurainia pinnata* 0.005	perennial forb
Elymus elymoides 0.003	annual forb	*Aristida purpurea* 0.005	perennial grass
Elymus repens 0.002	annual forb	*Gilia inconspicua* 0.004	annual forb
Collinsia parviflora 0.002	annual forb	*Gilia sp.* 0.004	annual forb
Cryptantha sp. 0.002	annual forb	*Elymus repens* 0.003	perennial grass
Cryptantha pterocarya 0.002	annual forb	*Cryptantha pterocarya* 0.003	annual forb

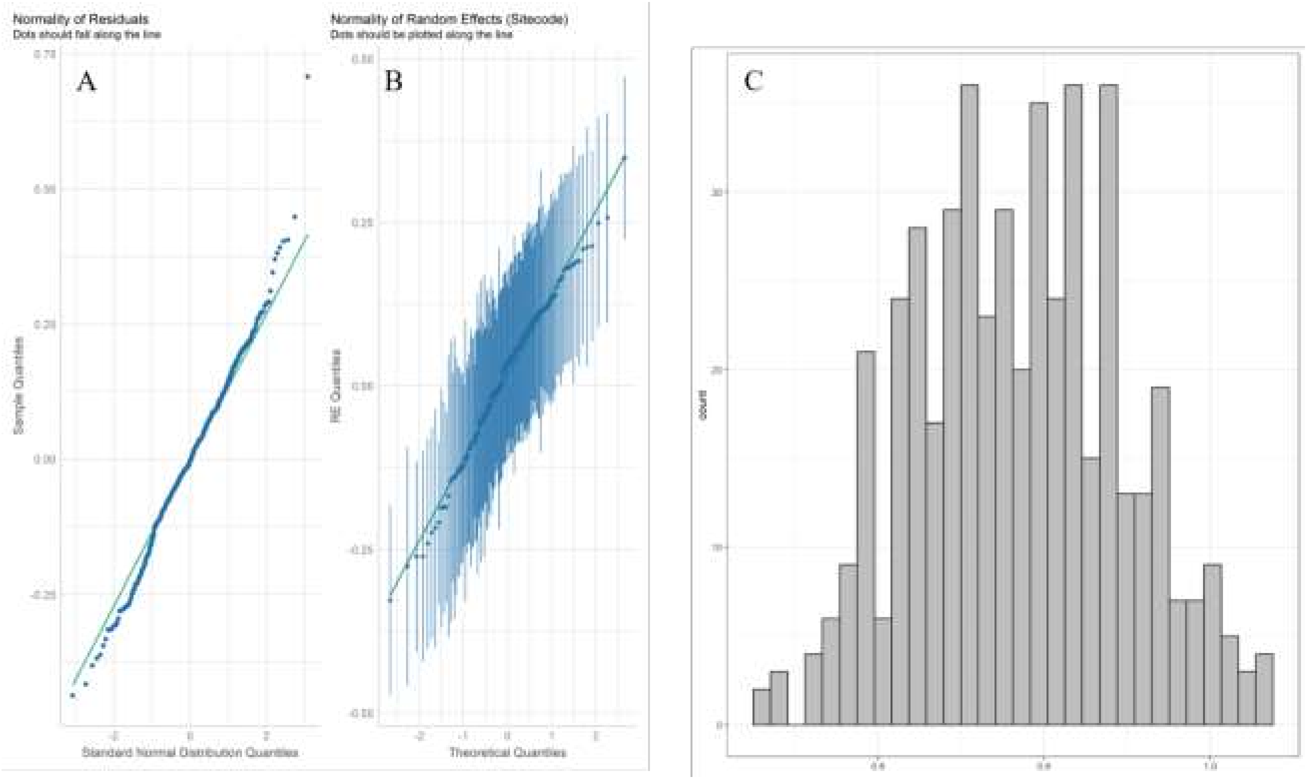
Gilia sinuata 0.002	annual forb	*Eriogonum palmerianum* 0.003	annual forb
Pectocarya pencillata 0.002	annual forb	*Guillenia lasiophylla* 0.003	annual forb
Pectocarya recurvata 0.002	annual forb	*Eriogonum sp.* 0.002	annual forb
Plagiobothrys arizonicus 0.002	annual forb	*Gilia brecciarum* 0.002	annual forb
Plantago ovata 0.002	annual forb	*Logfia californica* 0.002	annual forb
Brassica tournefortii 0.001	annual forb	*Thymophylla pentachaeta* 0.002	perennial forb
Sisymbrium altissimum 0.001	annual forb	*Poa secunda* 0.002	perennial grass
Chaenactis fremontii 0.001	annual forb	*Amsinckia sp.* 0.001	annual forb
Chamaesyce serpyllifolia 0.001	annual forb	*Chaenactis fremontii* 0.001	annual forb
Cryptantha circumscissa 0.001	annual forb	*Chorizanthe rigida* 0.001	annual forb
Eriogonum sp. 0.001	annual forb	*Eriastrum sparsiflorum* 0.001	annual forb
Eriastrum sparsiflorum 0.001	annual forb	*Lappula occidentalis* 0.001	annual forb
Gilia sp. 0.001	annual forb	*Lepidium lasiocarpum* 0.001	annual forb
Linanthus dichotomus 0.001	annual forb	*Linanthus dichotomus* 0.001	annual forb
Mentzelia albicaulis 0.001	annual forb	*Microsteris gracilis* 0.001	annual forb
Microsteris gracilis 0.001	annual forb	*Pectocarya sp.* 0.001	annual forb
Mimulus rubellus 0.001	annual forb	*Phacelia crenulata* 0.001	annual forb
Penstemon sp. 0.001	annual forb	*Plantago patagonica* 0.001	annual forb
Plantago patagonica 0.001	annual forb	*Bouteloua barbata* 0.001	annual grass
Silene antirrhina 0.001	annual forb	*Lesquerella hitchcockii* 0.001	perennial forb
Aristida purpurea 0.001	annual forb	*Packera multilobata* 0.001	perennial forb
Poa secunda 0.001	annual forb	*Elymus elymoides* 0.001	perennial grass
Sporobolus cryptandrus 0.001	annual forb	*Eragrostis cilianensis* 0.001	perennial grass
Encelia virginensis 0.001	annual forb	*Sporobolus contractus* 0.001	perennial grass
Gutierrezia microcephala 0.001	annual forb	*Sporobolus cryptandrus* 0.001	perennial grass
Sphaeralcea ambigua 0.001	annual forb	*Artemisia tridentata* 0.001	shrub
Lactuca serriola 0	annual forb	*Eriophyllum lanatum* 0.001	shrub
Portulaca oleracea 0	annual forb	*Opuntia phaeacantha* 0.001	shrub
Salsola tragus 0	annual forb	*Purshia mexicana* 0.001	shrub
Verbascum thapsus 0	annual forb	*Sisymbrium altissimum* 0	annual forb

Brassica elongata 0	annual forb	*Poa bulbosa* 0	perennial grass
Agropyron cristatum 0	annual forb	*Amsinckia menziesii* 0	annual forb
Amaranthus californicus 0	annual forb	*Camissonia brevipes* 0	annual forb
Amaranthus fimbriatus 0	annual forb	*Chaenactis carphoclinia* 0	annual forb
Amsinckia menziesii 0	annual forb	*Chaenactis steveoides* 0	annual forb
Antirrihnum filipes 0	annual forb	*Chenopodium leptophyllum* 0	annual forb
Calyptridium monandrum 0	annual forb	*Chenopoduim sp.* 0	annual forb
Camissonia brevipes 0	annual forb	*Eucrypta micrantha* 0	annual forb
Camissonia refracta 0	annual forb	*Gilia modocensis* 0	annual forb
Chaenactis steveoides 0	annual forb	*Ipomopsis polycladon* 0	annual forb
Chenopodium desiccatum 0	annual forb	*Langloisia setosissima ssp setosissimia* 0	annual forb
Chenopodium leptophyllum 0	annual forb	*Lotus humistratus* 0	annual forb
Chorizanthe rigida 0	annual forb	*Machaeranthera canescens* 0	annual forb
Collinsia callosa 0	annual forb	*Malacothrix coulteri* 0	annual forb
Conyza canadensis 0	annual forb	*Mimulus rubellus* 0	annual forb
Eriogonum deflexum var deflexum 0	annual forb	*Nicotiana attenuata* 0	annual forb
Erigeron divergens 0	annual forb	*Oxytheca perfoliata* 0	annual forb
Eriophyllum wallacei 0	annual forb	*Pectocarya setosa* 0	annual forb
Eschscholzia californica 0	annual forb	*Penstemon sp.* 0	annual forb
Eschscholzia minutiflora 0	annual forb	*Poa bigelovii* 0	annual grass
Eucrypta micrantha 0	annual forb	*Arabis sp.* 0	perennial forb
Gayophytum ramosissimum 0	annual forb	*Crepis acuminata* 0	perennial forb
Gilia brecciarum 0	annual forb	*Eriogonum inflatum* 0	perennial forb
Gilia modocensis 0	annual forb	*Lupinus andersonii* 0	perennial forb
Gilia ophthalmoides 0	annual forb	*Potentilla glandulosa* 0	perennial forb
Guillenia lasiophylla 0	annual forb	*Stephanomeria exigua* 0	perennial forb
Ipomopsis polycladon 0	annual forb	*Verbena goodingii* 0	perennial forb
Layia glandulosa 0	annual forb	*Tridens muticus* 0	perennial grass
Lepidium densiflorum 0	annual forb	*Ambrosia dumosa* 0	shrub
Linanthus sp. 0	annual forb	*Artemisia spinescens* 0	shrub

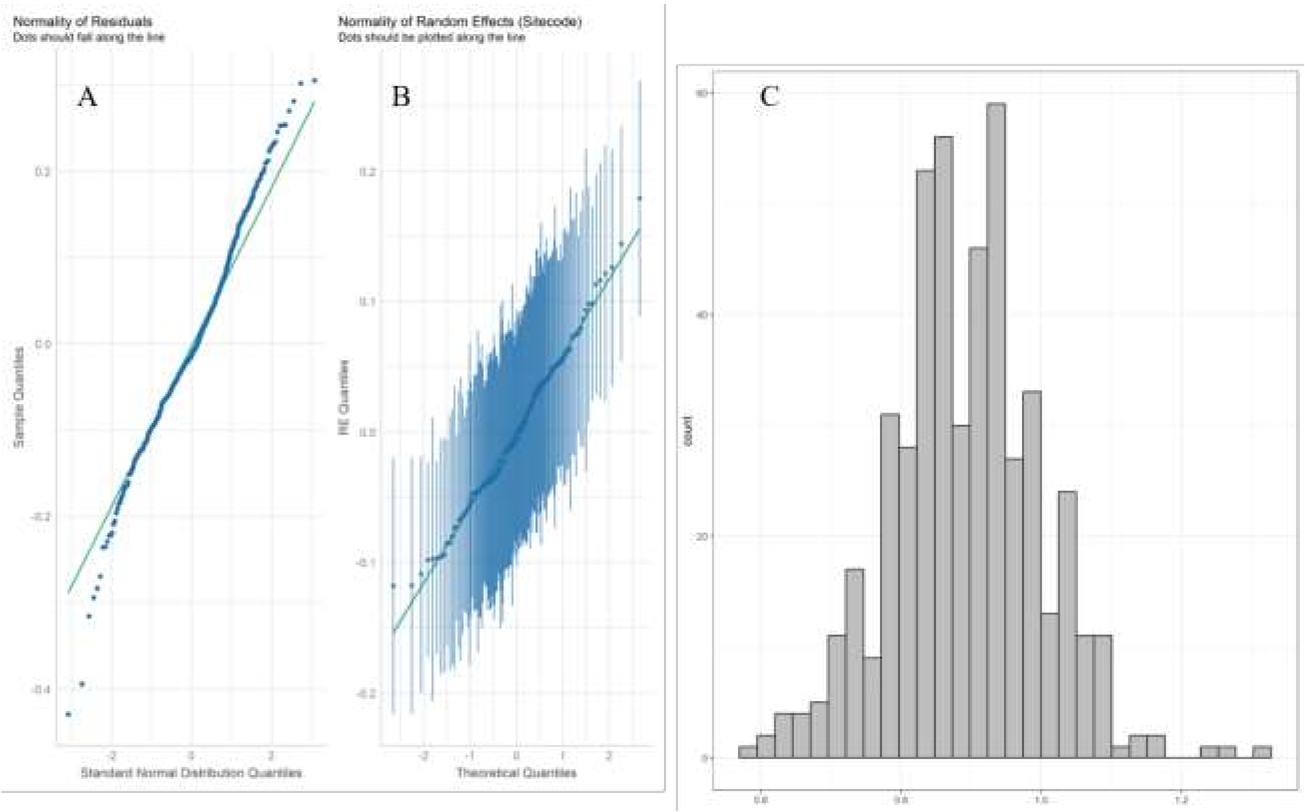
Linanthus demissus 0	annual forb	*Cylindropuntia acanthocarpa* 0	shrub
Logfia californica 0	annual forb	*Encelia virginensis* 0	shrub
Lotus humistratus 0	annual forb	*Grayia spinosa* 0	shrub
Lotus strigosus 0	annual forb	*Gutierrezia microcephala* 0	shrub
Lotus sp. 0	annual forb	*Phlox stansburyi* 0	shrub
Lupinus concinnus 0	annual forb	*Salvia dorrii* 0	shrub
Machaeranthera canescens 0	annual forb	*Sphaeralcea ambigua* 0	shrub
Mimulus bigelovii 0	annual forb	*Stanleya pinnata* 0	shrub
Nemacladus glanduliferus 0	annual forb		
Nicotiana attenuata 0	annual grass		
Pectocarya setosa 0	perennial forb		
Phacelia crenulata 0	perennial forb		
Phacelia sp. 0	perennial forb		
Phacelia distans 0	perennial forb		
Salvia columbariae 0	perennial forb		
Thysanocarpus curvipes 0	perennial forb		
Thysanocarpus laciniatus 0	perennial forb		
Uropappus lindleyi 0	perennial forb		
Bouteloua barbata 0	perennial forb		
Monroa squarrosa 0	perennial forb		
Poa bigelovii 0	perennial forb		
Arabis sp. 0	perennial forb		
Arabis perennans 0	perennial forb		
Artemisia ludoviciana 0	perennial forb		
Astragalus sp. 0	perennial forb		
Baileya multiradiata 0	perennial forb		
Castilleja sp. 0	perennial forb		
Chamaesyce albomarginata 0	perennial forb		
Circium sp. 0	perennial forb		
Delphinium parishii 0	perennial forb		

Dichelostemma capitatum 0	perennial forb		
Erigeron concinnus 0	perennial forb		
Eriogonum inflatum 0	perennial forb		
Galium sp. 0	perennial forb		
Heliomeris multiflora 0	perennial forb		
Linum lewisii 0	perennial forb		
Lupinus andersonii 0	perennial forb		
Nicotiana obtusifolia 0	perennial forb		
Oenothera sp. 0	perennial grass		
Oenothera suffrutescens 0	perennial grass		
Packera multilobata 0	perennial grass		
Phacelia ramosissima 0	perennial grass		
Potentilla glandulosa 0	perennial grass		
Stephanomeria exigua 0	perennial grass		
Verbena goodingii 0	perennial grass		
Achnatherum sp. 0	perennial grass		
Bouteloua gracilis 0	perennial grass		
Dasyochloa pulchellum 0	perennial grass		
Eragrostis cilianensis 0	perennial grass		
Hesperostipa comata 0	perennial grass		
Pleuraphis rigida 0	perennial grass		
Poa fendleriana 0	shrub		
Sporobolus contractus 0	shrub		
Tridens muticus 0	shrub		
Ambrosia dumosa 0	shrub		
Artemisia sp. 0	shrub		
Artemisia spinescens 0	shrub		
Artemisia tridentata ssp. tridentata 0	shrub		
Ceanothus greggii 0	shrub		
Cylindropuntia echinocarpa 0	shrub		

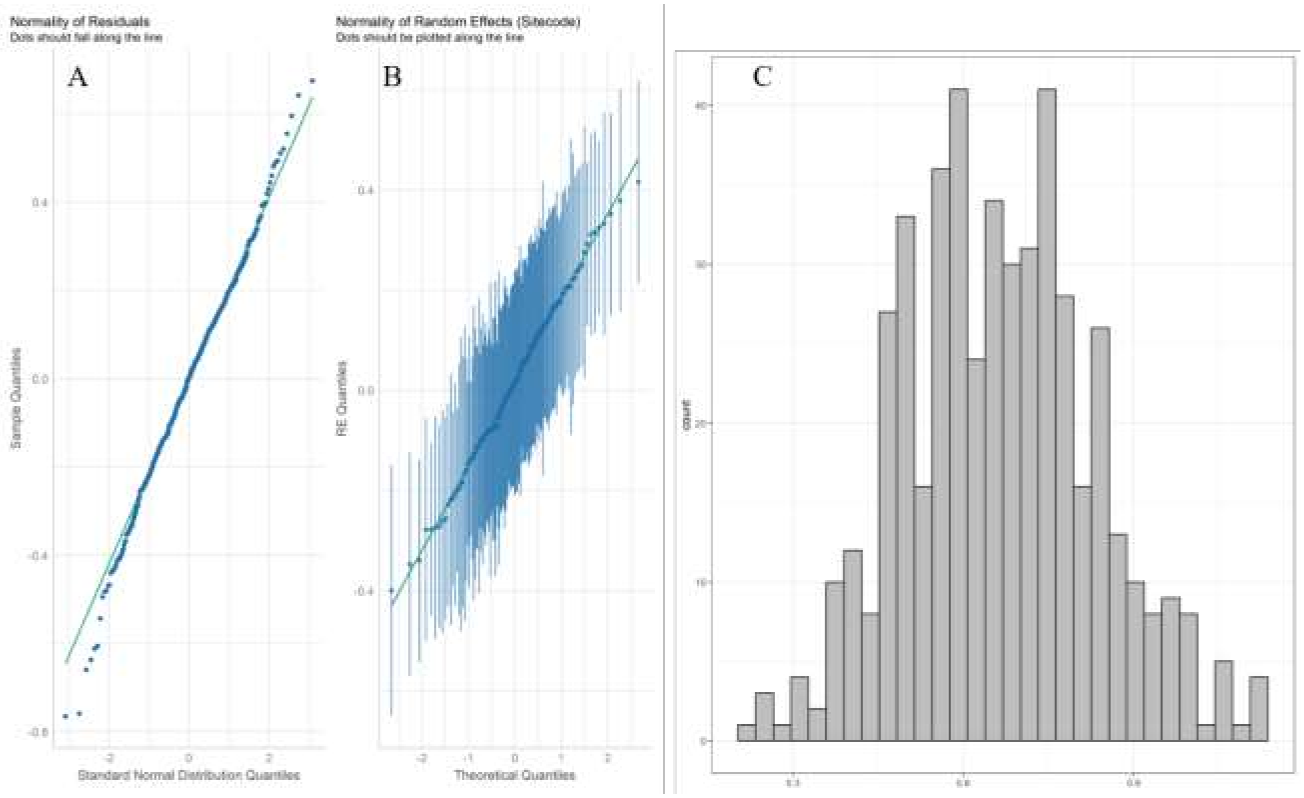
Cylindropuntia sp. 0	shrub		
Encelia actonii 0	shrub		
Eriophyllum lanatum 0	shrub		
Ericameria nauseosa 0	shrub		
Lycium cooperi 0	shrub		
Mirabilis laevis 0	shrub		
Phlox stansburyi 0	shrub		
Prunus andersonii 0	shrub		
Purshia mexicana 0	shrub		
Salvia dorrii 0	shrub		
Stanleya pinnata 0	shrub		
Stephanomeria pauciflora 0	shrub		



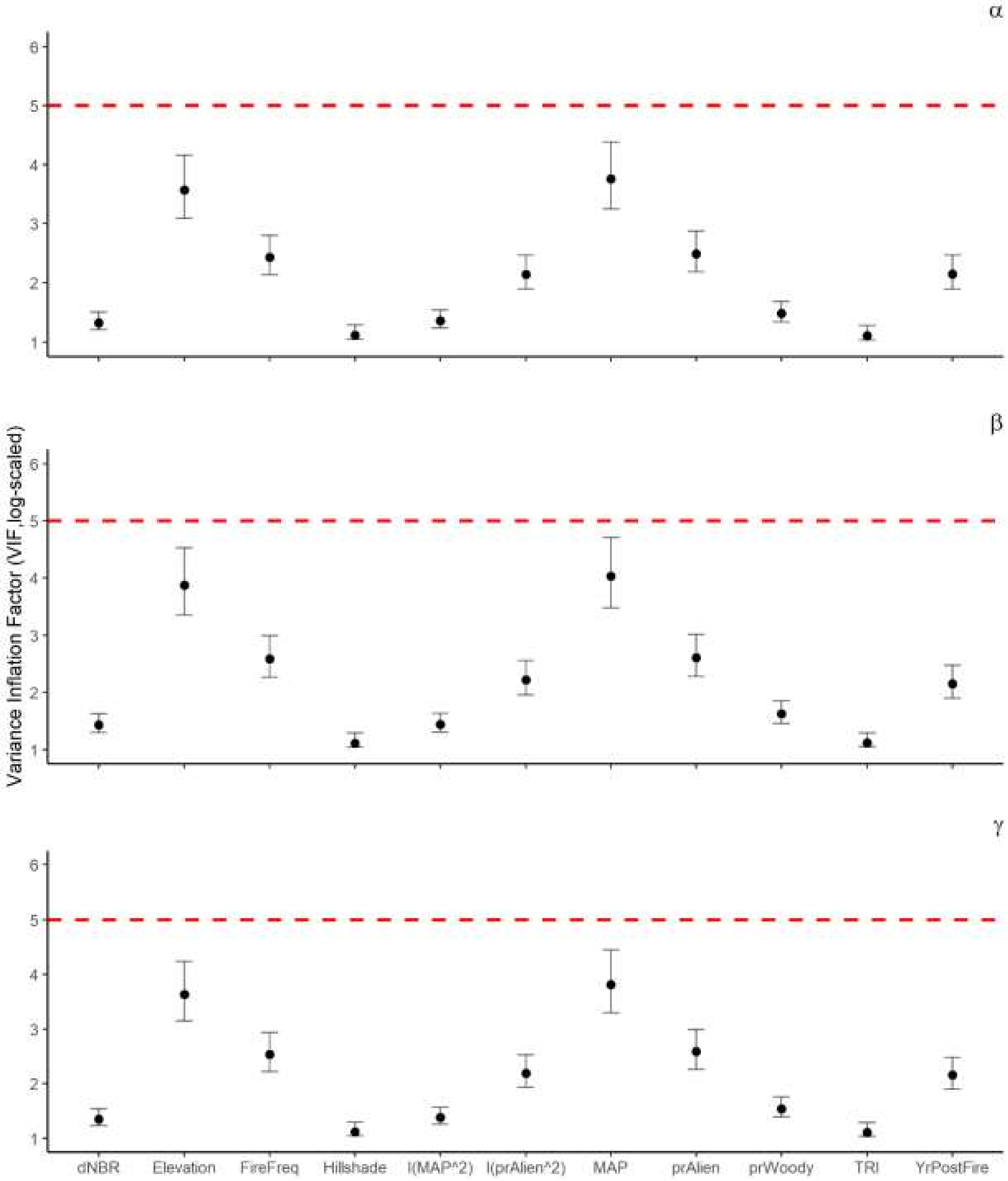
Appendix 2. Model assessments showing Q-Q normal plots (A, B) and distribution of the residuals for GLMM of alpha diversity.



Appendix 3. Model assessments showing Q-Q normal plots (A, B) and distribution of the residuals for GLMM of beta diversity



Appendix 4. Model assessments showing Q-Q normal plots (A, B) and distribution of the residuals for GLMM of gamma diversity



Appendix 5. Variance inflation factor (log-scaled) for variables used in generalized linear mixed effect models (GLMMs) of seed bank assays from across the Mojave Desert, USA

CHAPTER 5

CONCLUSIONS

Dryland ecosystems are particularly vulnerable to global change pressures such as rising temperatures, altered precipitation regimes, and the spread of invasive species. The Earth's climate is changing rapidly, exacerbating these pressures and threatening the productivity, biodiversity, and function of dryland ecosystems. The interactions between these shifting pressures and disturbances, both natural and anthropogenic, add layers of complexity that challenge our understanding of these ecosystems. The primary theme of this dissertation was to investigate the impacts of such disturbances on vegetation within dryland ecosystems, focusing particularly on the interactions between climate and biological factors known to influence the structure and function of plants. This was divided between three objectives, each considering a different aspect of how biological components can shape the structure and function of dryland vegetation across western North America.

Research objective 1 of my dissertation was to better understand how altered precipitation patterns interact with disturbance to influence plant growth across dryland ecosystem, which I address in Chapter 2. Through a combination of experimental rainfall manipulation and physical disturbance treatments, this study investigated how dominant shrubs in the Great Basin, Mojave, and Chihuahuan deserts responded over four years. The findings revealed significant reductions in shrub volume for *Artemisia tridentata* (sagebrush) and *Larrea tridentata* (creosote bush) under disturbance treatments, while *Prosopis glandulosa* (honey mesquite) exhibited notable resistance. Drought marginally reduced sagebrush growth, while annual precipitation positively influenced it. Positive correlations were observed between neighborhood vegetation cover and the growth of sagebrush and creosote bush. Photosynthetic rates varied by species and treatment, with sagebrush showing a negative response to drought and mesquite displaying increased photosynthesis in year one post-disturbance. One of the most notable findings was the negative relationship between shrub size and the amount of growth each individual shrub exhibited. This was a pattern observed across all three of the study sites, and suggests that individual traits such as plants age or size, may directly influence on how sensitive that individual is to changes in climate. Collectively, these results highlight the complex and site-specific nature of shrub responses to environmental stressors, suggesting that effective management strategies must consider local ecological contexts.

The second research objective was to investigate the impact of the mesquite twig girdler (*Oncideres rhodosticta*) on the above-ground biomass of honey mesquite in the northern Chihuahuan Desert, as discussed in Chapter 3. This study found significant year-to-year variability in beetle activity, with the highest girdling rates observed in 2019 and 2022. The beetles consistently caused measurable reductions in mesquite biomass each year, with mean annual biomass loss due to girdling as high as 12%. These findings underscore the importance of incorporating cross-trophic interactions, such as herbivory, into assessments of ecosystem function and primary productivity in arid environments.

Research objective 3 was to examine the effects of fire and invasive species on soil seed bank biodiversity in the Mojave Desert, which was addressed in Chapter 4. The study found that burned areas had higher mean α and γ diversities compared to unburned reference sites. However, fire variables had little influence on seed bank diversity patterns, but burned areas were dominated by invasive species like *Bromus rubens*, *Bromus tectorum*, and *Erodium cicutarium*. Increased invasive species dominance led to a sharp decline in α, β, and γ diversities, indicating the homogenization of seed bank communities and potential biodiversity loss. These results emphasize the significant impact of invasive species on biodiversity and the need for management practices that mitigate their spread.

This dissertation presents a multi-faceted approach to understanding the impacts of various disturbances on dryland ecosystems. The findings demonstrate that vegetation in the western U.S. exhibit different responses to drought and disturbances. Natural population cycles of native phytophagous insects can reduce aboveground shrub biomass to levels comparable to severe drought conditions. Additionally, abiotic and biotic factors, particularly exotic plant invasion, are reshaping native plant communities in response to changing fire regimes. These insights highlight the importance of considering multiple interacting factors in assessing the impacts of disturbances on ecosystem structure and function across dryland ecosystems. Effective conservation and management strategies can benefit by considering local ecological contexts to mitigate the adverse effects of climate change and disturbances on these fragile ecosystems. The differential responses among species and ecosystems suggest that management strategies should be specific to the conditions of each unique environment to effectively preserve the productivity and biodiversity of dryland systems in the face of rapidly changing global pressures. As we navigate these complexities, it becomes clear that our models, while informative, cannot capture all potential changes. Unexpected outcomes, novel species interactions, and the formation of new plant communities will continue to challenge and enrich our understanding of dryland ecosystem dynamics in an era of rapid climate change.

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APPENDIX A

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